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Phenotypic plasticity in response to climate change: the importance of cue variation

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Phenotypic plasticity is a major mechanism of response to global change. However, current plastic responses will only remain adaptive under future conditions if informative environmental cues are still available. We briefly summarize current knowledge of the evolutionary origin and mechanistic underpinnings of environmental cues for phenotypic plasticity, before highlighting the potentially complex effects of global change on cue availability and reliability. We then illustrate some of these aspects with a case study, comparing plasticity of blue tit breeding phenology in two contrasted habitats: evergreen and deciduous forests. Using long-term datasets, we investigate the climatic factors linked to the breeding phenology of the birds and their main food source. Blue tits occupying different habitats differ extensively in the cues affecting laying date plasticity, as well as in the reliability of these cues as predictors of the putative driver of selective pressure, the date of caterpillar peak. The temporal trend for earlier laying date, detected only in the evergreen populations, is explained by increased temperature during their cue windows. Our results highlight the importance of integrating ecological mechanisms shaping variation in plasticity if we are to understand how global change will affect plasticity and its consequences for population biology.

This article is part of the theme issue 'The role of plasticity in phenotypic adaptation to rapid environmental change'.

1. Introduction

Global change encompasses modifications of the environment both at a global scale (e.g. climate) and at a local scale but in such large proportion that the whole planet is affected (e.g. urbanization, invasive species). It thus represents complex modifications of the environments in which populations face radically new conditions (e.g. pesticides, roads), but also new modalities of historically known environments (e.g. extreme climatic events, invasive predator). Studying whether and how wild organisms adapt to these rapid environmental changes is both an opportunity for in-depth evolutionary ecology scrutiny, and a societal challenge.

Phenotypic plasticity is a major mechanism of response to environmental variability, which may allow organisms to cope with rapid environmental changes, including global change. It has indeed been identified as the main mechanism of phenotypic change in response to climate change [1–3] and other human-induced rapid changes such as urbanization [4]. Phenotypic plasticity is also suspected to have an important role in colonization of new environments, geographical range shifts and the success of invasive species [5,6].

However, whether or not plasticity will aid adaptation and population persistence in a new environment depends on whether it is adaptive there. When it is adaptive, phenotypic plasticity can increase the probability of population persistence [7], as exemplified in two great tit (*Parus major*) populations where phenotypic plasticity is predicted to increase the likelihood of population persistence under various scenarios of climate change [8,9]. However, these predictions are based on models that generally consider a 'static' estimate of plasticity, without taking into account potential changes in reaction norms owing to plasticity evolution, or the possibility that the adaptive nature of plasticity may be altered under new environmental conditions [10], as is the case under global change.

A core prerequisite for adaptive predictive plasticity is the existence of reliable cues, i.e. accurate environmental information about future selection on the expressed plastic phenotype [11–14]. While the definition of cues is fairly straightforward in theory, their empirical characterization may be a very arduous task (electronic supplementary material, Box S1). Yet it is a crucial step in order to understand how global change can affect adaptive plasticity and its consequences for population biology. For instance, theory predicts that if cue reliability decreases, plasticity may be selected to decrease [15], or else may drive populations to extinction by increasing the expected load caused by phenotypic mismatch with the optimum in a fluctuating environment [16–18]. This is just one possible scenario, but it illustrates the point that one of the most central tasks for understanding and predicting the ecological and evolutionary roles of phenotypic plasticity under global change is to decipher which environmental cues are used by organisms, why (i.e. which selective pressures), and the extent to which global change is likely to affect cue reliability.

To address these questions, we will start with a brief overview of the nature and evolution of cues in wild populations. We will then outline the potentially complex effects of global change on plasticity, through its effect on the availability and reliability of cues. Finally, we will illustrate some of these aspects with a case study comparing plasticity of phenology in four blue tit populations from contrasted habitats.

2. Nature and evolution of cues for phenotypic plasticity

For plasticity to be adaptive, the environment influencing the development and/or expression of a particular phenotypic trait (or set thereof) needs to be a reliable cue for the selective pressure on this trait. In a variable environment, this reliability implies that the cue(s) should predict the selective environment, i.e. the environmental conditions driving natural selection on the expressed plastic trait (figure 1 and [11,12,14]), so that the plastic response leads to increased fitness [10]. Reliable cues do not require that the same environmental variable affects both the expression of a trait and selection on this trait: any environmental variable that is correlated with the environment of selection through space or time can act as a reliable cue for phenotypic plasticity (e.g. red/infrared ratio signalling competitor presence [19]). In fact, environmental variables that are most informative about the selective environment at the time of phenotypic determination may differ from the selective environment itself at this time [20]. For instance, rain may be a better predictor of the peak of food abundance at time $t + \tau$ (where τ is the lag between phenotypic determination and selection on the trait) than is food abundance itself at time t. More generally, organisms are expected to respond to the linear combination of environmental variables that best predicts variation in the phenotypic optimum [15,20]. Very few case studies have investigated how an optimum phenotype is predicted by one environmental variable [21], and probably even fewer address the joint effect of several environmental variables. By contrast, many empirical studies have focused on the multidimensional aspect of plasticity, and highlighted that organisms respond to different environmental factors in an integrated way [22–25]. Responding to multiple cues allows organisms to fine tune their phenotype in complex environments: for example, prey can be simultaneously confronted by different types of predators [26,27], or plants face the need to respond to herbivory as well as to competition for light and water availability [24].

The aspect of cue reliability that influences the evolution of plasticity (in models of linear reaction norms) is the regression slope of the environment of selection on the environment of development [15,28]. When the time lag between these two environments increases, cues are expected to become less informative [29,30], to an extent that depends on the time scale of environmental fluctuations: strong temporal autocorrelation of the environment may allow the evolution of plastic responses to early cues. Similarly, dispersal between cue perception and selection causes a spatial lag analogue to the time lag [11], with an effect on plasticity evolution that depends on the degree of spatial autocorrelation over the typical dispersal distance. However, even a cue that reliably predicts the environment of selection can lead to maladaptive plastic responses if there is a development lag (time between cue perception and phenotype expression [14]), such that the 'set value' corresponding to that cue is not reached when selection operates on the trait. When the environment fluctuates on time scales longer than the generation time and dispersal is low, information about parental environment can be a reliable cue for offspring, and transgenerational plasticity is expected to evolve (figure 1, [31–33]). Transgenerational effects may be especially important for traits that are expressed and fixed early in the ontogeny (including many morphological traits), because offspring may lack sensory abilities during development [34], and have less time to integrate information about the environment. For example, in the nematode *Caenorhabditis elegans*, maternal provisioning in glycogen increases offspring fitness under anoxia. Using experimental evolution, Dey *et al.* [35] showed that when normoxia (i.e. normal levels of oxygen) and anoxia (less than 1% oxygen) were predictably alternating, mothers experiencing normoxia increased glycogen provisioning to their embryos (and *vice versa* for anoxia), demonstrating the evolution of maternal effects under predictable variation of the environment. In marine sticklebacks (*Gasterosteus aculeatus*), where body size is a key component of fitness, maternal effects could help adaptation to increased temperature under climate change, as offspring from mothers acclimated to 21°C were larger in this warm environment than conspecifics from mothers acclimated to 17°C thanks to different mitochondrial performance [36].

Recently, there has been growing interest in understanding theoretically how cue variability and reliability at different time scales interact to shape plastic responses. Organisms are predicted to integrate various sources of information, including cues from the current environment (for labile traits that change continuously in life), earlier cues perceived during development (early-life or carry-over effects) and transgenerational cues from the environment to which

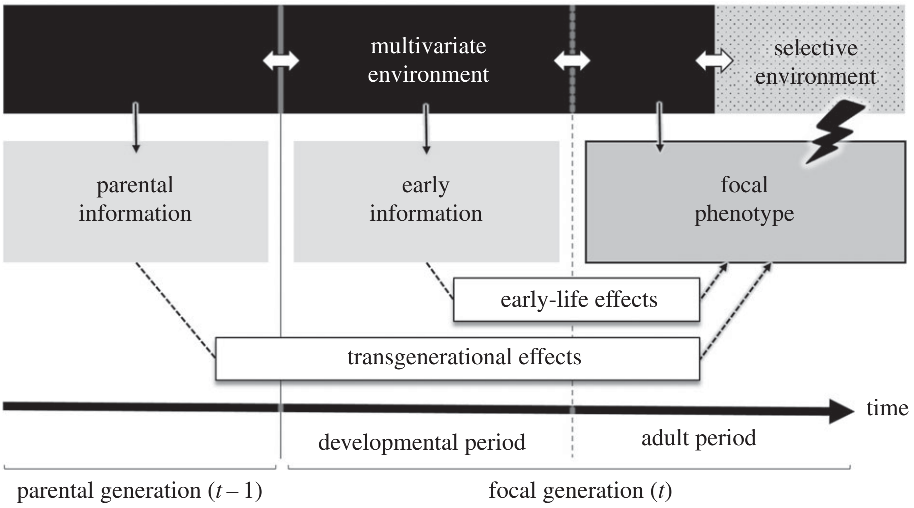

Figure 1. Summarized diagram of the relationships between the environment, cues and phenotypes in the framework of phenotypic plasticity. The multivariate environment can be used as a cue to initiate a plastic response in an individual (thin black arrows). The focal phenotype (on which selection is acting in our example, black thunderbolt) can be affected by current environmental conditions, earlier life events and the preceding parental generation. Information about past environments (either parental or from early-life) includes different sources, such as the phenotype itself (at the same or another trait), or epigenetics. For phenotypic plasticity to be adaptive, cues in the successive periods and generations have to be correlated with the future selective environment (white arrows).

previous generations were exposed (figure 1, [33]), including the parental phenotype itself [37]. The relative weight of these different types of cues is expected to vary depending on their predictive power over different time scales (related to the temporal autocorrelation of the environment) and the strength of selection [32,33,37].

Cue variation through space and/or time can lead to variation in plasticity, with an alternation of different ecotypes. A telling example of within-population variation in plasticity comes from the wild mosquitofish (*Gambusia holbrooki*). Fish born in the early spring (development at cool temperature) are expected to experience more variable environments than fish born in early summer (development at a warm temperature). Accordingly, metabolic rate is plastic in fish born in early spring, but not in early summer fish [38]. Following on from such encouraging case studies, more work is needed to assess, both theoretically and empirically, whether and how much variation in cue variability and predictability drives within-species variation in plasticity.

3. How may global change influence cues and plasticity?

Under global change, several aspects of the environment are expected to be modified, notably through the emergence of new environments (owing to local habitat change or dispersal in new habitats), alteration of covariances among environmental variables and increased climatic variability. These environmental changes can be gradual, but abrupt changes are also increasingly likely because of anthropogenic pressures [39], e.g. in the form of extreme climate events such as floods, droughts or storms. Altogether, environmental changes may affect the expression and evolution of plasticity through changes in cue reliability, cue perception and interpretation, and development of the phenotype.

(a) Changes in the availability and reliability of cues

The simplest way environmental change may affect cue use is by disrupting their detection, either by degrading the signal or by disturbing organisms' sensory abilities. For example, juvenile damselfish (*Pomacentrus wardi*) no longer respond to predator cues in degraded environments (dead coral reefs), and the likely mechanism is a degradation of the conspecific alarm cue [40]. Similarly, eutrophication can impair visual signals, leading to maladaptive plasticity in male sticklebacks, as their increased investment in courtship behaviour is not correlated with female interest [41]. Pervasive electrosmog, i.e. human-made electromagnetic noise, completely disrupts the magnetic compass orientation in the migratory European robin *Erithacus rubecula* [42].

When cues are still available, their reliability can be affected if the new environment is similar in some ways to a known environment. In the most extreme cases, a new environment is generating a signal similar to a previously known cue, but completely uncorrelated with both the original cue and the environment of selection. For example, asphalt and ponds polarize light in the same way, leading mayflies to lay their eggs on the road rather than ponds [43], and insecticides can trigger costly morphological defences in *Daphnia ambigua* in the absence of predators [44,45]. Such maladaptive responses based on cues that were previously reliable are termed evolutionary traps [46,47]. These traps will be all the more effective as the previous cue was highly reliable [46].

On the other end, the cue can be sampled from the same historical environmental variable, but the correlation between this variable and the selective environment may have decreased or entirely vanished. This is expected under climate change, for instance, because of increased climate stochasticity within years, or because the average temperature is not changing at the same rate for all seasons [48,49]. For example, the yellow-bellied marmot (*Marmota flaviventris*) has gradually emerged earlier from hibernation (study led between 1975 and 1999) because of warmer air temperature earlier in the spring. However, the date of snowmelt has not changed in the Rocky Mountains, leading to lower foraging opportunities at emergence. While warmer air was historically a good predictor of snow melt, climate change has led to a mismatch between air temperature and snow cover [50].

Because species are embedded in networks of ecological interactions, loss of cue reliability may arise from species responding differently to environmental changes, or interacting species responding to different cues. Changes in phenology are the most ubiquitous responses to climate change [51], and the best-documented cases of disruption of ecological networks are based on a loss of synchrony between ecological interactors, such as predators and their prey, or plants and their pollinators [52,53]. If interacting species are responding to the same cue, their phenological mismatch may increase because their reaction norms are different. This is generally the case in trophic interactions, where consumers tend to display shallower (flatter) reaction norms to climate than their resources [54]. This occurs because consumers generally have longer generation times than resources (owing to larger body size), and thus longer developmental lags for the expression of the plastic trait, which reduces their ability to predict the environment of selection, as temporal autocorrelation affecting cue reliability decreases on average with longer time lags [55]. Another possibility is that interacting species are actually using different cues that undergo different time trends. For example, four tree species of *Prunus* in Japan are flowering earlier owing to increased temperatures during the time window most related to their phenology, yet temperature remains unchanged during the time window related to the phenology of the butterfly *Pieris rapae* that uses them as host plants. This leads to strong plasticity of phenology in trees but not in butterflies [56], resulting in an increasing plant–insect phenology mismatch owing to warming (see also our case study in §4).

Some mechanisms may mitigate the loss of reliability in some cues. First, the potentially negative effects of loss of reliability of a particular environmental variable as a cue could be greatly alleviated if organisms are using multiple cues, because partial redundancy in information from different environmental sources may increase the robustness of the signal [57]. For example, in the above-mentioned case of the coral reef damselfish, the loss of olfactory cue in dead coral water can be compensated by the use of visual cues [40]. Similarly, we could expect that the mismatch in trophic webs could be alleviated if species are using each other's presence, abundance, or phenotype as cues (as investigated empirically by Phillimore *et al*. [58] with butterflies and their host plants), rather than using a unique climatic variable such as temperature alone. Second, the expression of maladaptive responses to an unreliable cue could be reduced through learning, for example, if females are able to recalibrate their cue use based on past experience [59].

(b) Consequences of the expression and evolution of plasticity

It is difficult to predict in general whether and how much plasticity will be adaptive in novel environments. It has been suggested that reaction norms should have random and erratic shapes in environments that were never or rarely encountered previously (as is expected to occur under global change), owing to the absence of past selection in these environments [10]. However, more quantitative arguments can be made by taking into account two realistic features of plasticity in new environments. First, environments are seldom entirely new; instead, major environmental shifts mostly mean that previously (perhaps very) rare environments have become common. How rare a new environment has been prior to the shift determines how relaxed selection has been in this environment, and the opportunity there has been for genetic drift to produce erratic reaction norms there [60]. Second, reaction norms do not evolve completely freely, even in environments where they have not been under selection, because their shapes are generally constrained to some extent by genetic correlations of trait values across environments. Considering these two points makes it likely that reaction norms remain at least partly adaptive over the new environmental range in the absence of major changes in the adaptive landscape, and simple quantitative statements can be made about this question based on the frequency of extremes and the correlations of trait values across environments [60].

Retaining partially adaptive plastic responses in novel environments also requires that cues remain reliable. In the specific case of extreme climatic events, whether such cues exist is still unknown. One recent study tackling this issue found no evidence that the Eurasian oystercatchers (*Haematopus ostralegus*) uses cues (lunar cycle, past and current water height) to avoid flooding of their nests during extreme precipitation events [61]. Furthermore, global change generally involves the variation of more than one environmental variable, and an alteration of the correlation structure of these variables within and between times. This may trigger conflicting ecological demands on organisms [24], such that new combinations of environmental variables become the best predictors of the optimum phenotype. The ability of organisms to track these altered patterns of change in the optimum phenotype is predicted to depend on their ability to evolve a new combination of environmental variables used as a cue [20]. This theoretical prediction has not been tested yet, but a couple of studies suggest that cue use can evolve relatively fast. A study in the pitcher plant mosquito (*Wyeomia smithii*) suggests that, over a period of 5 years, the critical photoperiod for diapause induction has shifted towards shorter day length (i.e. later in the season) owing to longer growing seasons [62]. Antipredator responses of the Iberian waterfrog (*Pelophylax perezi*) tadpoles to an invasive species (crayfish, *Procambarus clarkia*) is also a likely case of cue evolution. Tadpoles from this species have the ability to build morphological defences against native predators [63] but only tadpoles from populations that have co-existed with *P. clarkia* during 10–15 generations display anti-predator response to this new predator [64].

Changes in cue reliability are expected to have a major impact on the evolution of plasticity, including a transition between predictive plasticity and bet-hedging as adaptive strategies [13,65]. In the context of climate change and the associated increased variability of temperature, decreased predictability of the environment could, for example, impact the adaptiveness of transgenerational plasticity, and select for a strategy of bet-hedging, where parental effects increase variance in offspring phenotype rather than alter their mean phenotypes [66].

In terms of predictive plasticity, the reliability of the cue determines the steepness of the optimal reaction norm: the less reliable the cue, the shallower the reaction norm that evolves at equilibrium, as compared to 'perfect' plasticity, defined by how the optimum phenotype is affected by the environment [12,67]. In the case of an abrupt change in cue reliability, causing previously adaptive plasticity to become maladaptive (for instance because it overshoots the optimum, as in [16]), plasticity is expected to evolve towards a shallower reaction norm that matches the current level of cue reliability. Such plasticity shift may cause evolutionary rescue by reducing the load caused by stochastic fluctuations in the environment [17,18].

4. Case study: local variation of cues in Mediterranean blue tits and their prey

Investigating the mechanisms of plastic response to climate change and their limits in the wild is notoriously difficult (electronic supplementary material, Box S1). However, an exceptionally well-characterized research model of adaptive plasticity in wild populations is the earlier egg-laying date of temperate forest insectivorous passerines during warmer springs. This earlier breeding phenology allows birds to track the phenology of the caterpillars they use as the main food source for their offspring [21,68]. In the following section, we investigate in some detail how plastic phenological change relates to environmental cues and their reliability in four Mediterranean populations of blue tits (*Cyanistes caeruleus*).

The four wild populations of blue tits have been monitored for 20–42 years (electronic supplementary material, table S1). Two populations breed in forests dominated by the Deciduous downy oak *Quercus pubescens* (the D-Rouvière and the D-Muro populations, in the French mainland close to Montpellier and Corsica respectively, where 'D' stands for deciduous) and two in forests dominated by the evergreen holm oak *Quercus ilex* (the E-Muro and the E-Pirio populations, both in Corsica; 'E' stands for evergreen forest [69]). These ecological characteristics have induced local adaptation in birds [70], particularly in their life-history traits. Average phenology of two of these populations has been changing over time: mean laying date is increasingly early (more than three days per decade) for the populations breeding in evergreen, but not in deciduous forests (figure 2*a*; electronic supplementary material, table S2a), despite similar trends of climate warming in the four sites (electronic supplementary material, table S2c and figure S1; note that electronic supplementary material, table S1 reports trends in temperature over the spring—from April to end-June—while electronic supplementary material, figure S1 presents trends in temperature over the entire year). This pattern is all the more striking as the E-Muro and D-Muro populations are only 5.6 km apart [70], and connected by gene flow [71].

One plausible explanation behind the different time trends in laying date could be local variation of environmental cues for phenotypic plasticity. Females from different populations could be sensitive to different climate variables (e.g. amount of rain, mean temperature or presence of extreme climatic events), or to the same variables but at different time periods during the year (e.g. early versus late spring). In order to assess the population-specific cues for laying date plasticity in blue tits, we implemented sliding windows analyses using the package climwin [72,73]. For each population, we tested several weather variables: mean, maximum, minimum for both daily temperature and daily rain, and positive Extreme Climatic Events of temperature (ECE hereafter; see electronic supplementary material, Box S2 for details on the methods). Climate data were obtained from the national meteorological stations of Saint Martin de Londres for the mainland (about 24 km from D-Rouvière) and Calvi for Corsica (9–19 km from the three Corsican study sites). Temperatures from the meteorological stations are highly correlated with local temperature in study sites (electronic supplementary material, table S3).

In three of the populations (D-Rouvière, D-Muro and E-Pirio), the climatic factor that most influences variation in mean laying date is the mean temperature (electronic supplementary material, table S4), explaining between 54% and 75% of variability in laying date (table 1*a*). 'Evergreen' populations are also sensitive to the number of ECE. In E-Pirio, this effect is additive with the mean temperature effect, but not highly robust. In turn, the number of ECE within a window is the best predictor of average laying date in the E-Muro population (electronic supplementary material, table S4), but the simultaneous use of information from mean temperature cannot be excluded (mean temperature: -3.47 ± 0.88, $t = -3.94$, $p = 0.001$, ECE: -1.59 ± 0.42, $t = -3.79$, $p = 0.002$, $r^2 = 0.75$). We found no effect of other climate variables such as rainfall (electronic supplementary material, table S4). Hence, although some combination of other factors (e.g. bud development [74] or population density [75]) likely play a role, temperature is a key driver behind the plasticity of laying date. This is in line with other correlative studies in great tits, showing that the average spring temperature explains more than 50% of the variability of laying date [68,76], and with experiments showing that laying date responds to temperature treatments [77]. The underlying physiological mechanisms remain elusive, as no effect of temperature on the neuroendocrine system linked to reproduction has been detected yet [78,79]. Despite many studies on bird breeding phenology, knowledge about mechanisms driving phenological plasticity are still scarce, and the relative roles of direct and indirect effects of temperature (e.g. for the latter, a constraint on the timing of egg-laying mediated by food abundance or quality) are unknown [80].

The populations differ in the specific time window of mean temperature influencing laying date. Females from populations in deciduous habitats use a cue based on a long time period encompassing winter and early spring, while females from the E-Pirio population use a shorter and later time period corresponding to a month in spring (figure 3; electronic supplementary material, table S5). The pattern is qualitatively similar but not robust in E-Muro (figure 3; electronic supplementary material, table S4 and S5). Larger windows in deciduous populations could be related to the correlation between the best window and other possible windows remaining high across a larger range of time periods than in evergreen populations (electronic supplementary material, figure s2). A formal statistical comparison between the windows used in D-Rouvière and E-Pirio shows significant differences between the two populations in terms of ordinal calendar (electronic supplementary material, Box S2).

The use of different time windows in the four bird populations leads to contrasted rates of change of the cue over the study period. In the 'Evergreen' populations, where the window includes only spring temperature, the mean temperature inside the cue window increases over the 1991–2017 period (E-Muro: 0.4 ± 0.07°C/decade, $t = 6.18$, $p < 0.0001$; E-Pirio: 0.6 ± 0.08°C/decade, $t = 7.81$, $p < 0.0001$, figure 2*b*), but there is no such increase in the two other sites where the windows include information from spring

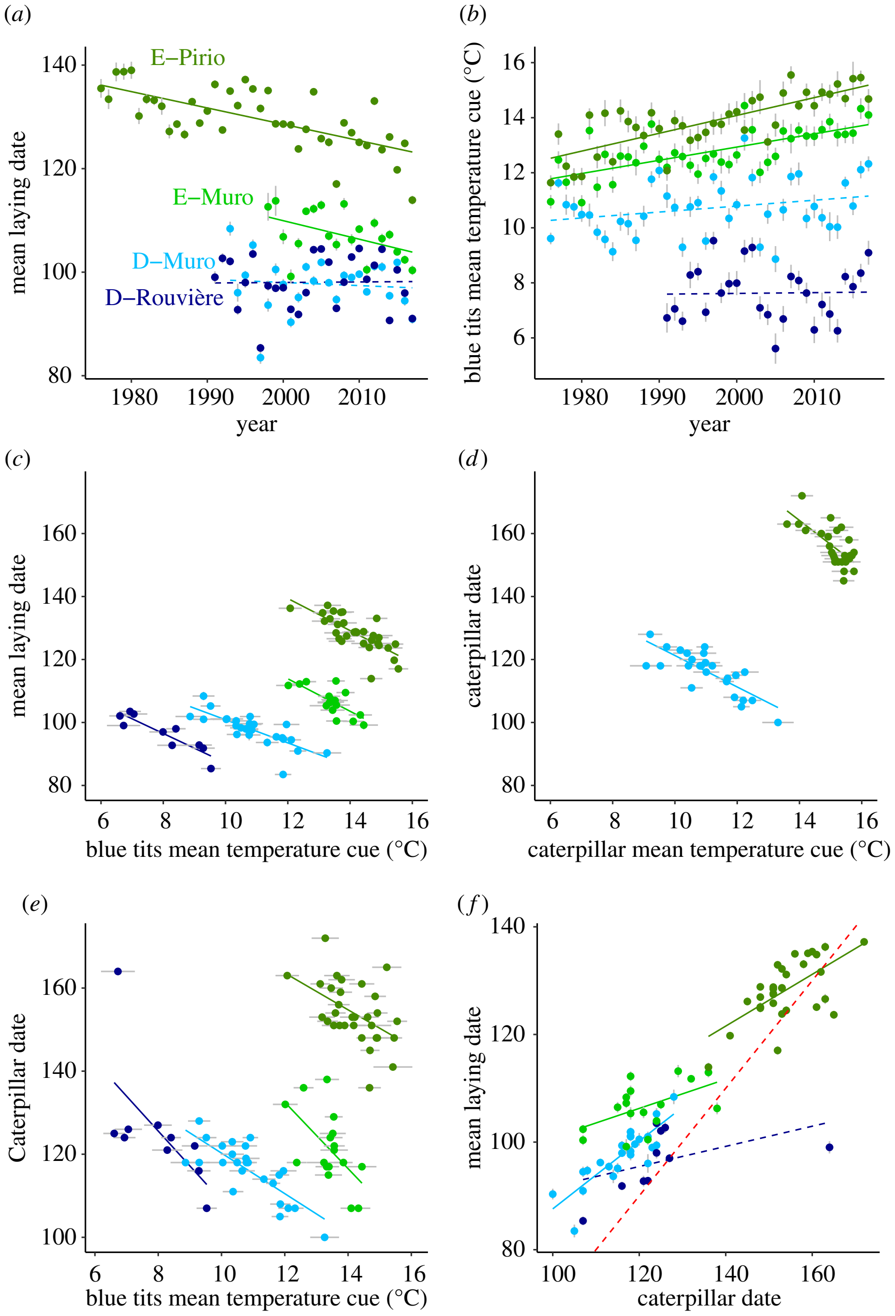

Figure 2. (*a*) Temporal trends in annual mean laying dates in the four blue tit populations (mean ± s.e.); (*b*) temporal trends in mean temperature (in °C ± s.e.) for the cue windows used by each population; (*c*) blue tit reaction norms: annual mean laying date (±s.e.) as a function of the estimated cue (in °C ± s.e.); (*d*) caterpillar reaction norm (only for E-Pirio and D-Muro): annual caterpillar peak date as a function of the estimated cue (°C ± s.e.); (*e*) Cue reliability for blue tits measured as the correlation between the caterpillar peak date and the cue (electronic supplementary material, table S7); (*f*) Synchrony between blue tits and caterpillars illustrated as the correlation between mean laying date of blue tits (±s.e.) and caterpillar peak date (see electronic supplementary material, table S8). In all panels, the 'Evergreen' sites are in green (dark green for E-Pirio, light green for E-Muro), and 'Deciduous' sites are in blue (dark blue for D-Rouvière, light blue for D-Muro). All dates are ordinal dates with 1 = 1^{st} January. In (*f*), the red dashed line represents the expected optimal relationship between laying date and caterpillar date. In some cases, error bars are not visible because they are very small compared to the figure scale.

and winter (D-Rouvière: 0.03 ± 0.3°C/decade, $t = 0.11$, $p = 0.91$; D-Muro 0.22 ± 0.12°C/decade, $t = 1.76$, $p = 0.09$). This is in line with the very slow or absent rate of climate change in winter as compared to spring in these Mediterranean areas (electronic supplementary material, figure S1). Climate change is also associated with increasing frequency of ECE, and their number increases in the window used by the E-Muro population (0.49 ± 0.16 positive ECE/decade, $t = 2.98$, $p = 0.005$; see electronic supplementary material table S6 for other populations). Hence overall, even though spring warming has been pervasive in all populations (electronic supplementary material, table S2c and figure S1), we only detect climate warming during the cue windows influencing bird phenology in E-Pirio and E-Muro. This difference of windows across habitats explains why laying dates are advancing in the evergreen avian populations but not in the deciduous populations.

It is also possible to investigate the reliability of cues in this system. The fitness consequences of phenological responses of blue tits depend on the phenology of caterpillars of *Tortrix*

Table 1. Average population reaction norms in response to the cues estimated with the sliding window analyses (figure 3; electronic supplementary material, table S5) for (*a*) laying date of blue tits, and (*b*) caterpillar date of peak abundance. Depending on the best predictors of phenology detected by sliding window analysis, the reaction norms were estimated using either the mean temperature (MeanT) or the number of ECE during the best window. Sample sizes are given in electronic supplementary material, table S1.

		intercept			slope			
	cue	estimates (± s.e.)	*t*-value	*p*-value	estimates (± s.e.)	*t*-value	*p*-value	r^2
(*a*)								
D-Rouvière	MeanT (17 Jan. to 1 April)	131.78 (± 3.82)	34.51	<0.0001	−4.42 (± 0.50)	−8.91	<0.0001	0.75
D-Muro	MeanT (4 Feb. to 7 April)	137.61 (± 6.78)	20.31	<0.0001	−3.67 (± 0.62)	−5.92	<0.0001	0.59
E-Muro	MeanT (15 March to 27 April)	175.33 (± 13.34)	1.14	<0.0001	−5.13 (± 1.00)	−5.11	<0.0001	0.57
	ECE (23 March to 15 April)	112.21 (± 1.21)	92.90	<0.0001	−2.41 (± 0.49)	−4.95	0.0001	0.55
E-Pirio	MeanT (31 March to 7 May)	200.53 (± 11.92)	16.82	<0.0001	−5.10 (± 0.84)	−6.07	<0.0001	0.54
(*b*)								
D-Muro	MeanT (11 Feb. to 7 April)	171.22 (± 9.01)	19.01	<0.0001	−5.00 (± 0.81)	−6.15	<0.0001	0.61
E-Pirio	MeanT (13 March to 7 June)	283.38 (± 20.04)	14.14	<0.0001	−8.47 (± 1.31)	−6.46	<0.0001	0.58

viridana, the main food resource for nestlings [81], thought to influence reproductive success through offspring survival. The synchronization of the nesting period (especially when nestlings reach the peak of their energetic needs, around 9 days after hatching [82]) with date of peak abundance in caterpillars depends on how reliably the environmental cue used by birds to modify their phenology predicts caterpillar peak date. We can thus measure the linear regression slope of the environment affecting selection on timing of breeding on the environment affecting timing of breeding itself, in order to quantify the reliability of the cue used by birds in a way that matches theoretical predictions (e.g. [15,28]). Caterpillar phenology is studied in the four sites thanks to coprometers (i.e. 50 × 50 cm cloth square collecting the frass of caterpillars under oak trees). The mass of frass collected during a given time period allows us to estimate the abundance of caterpillars throughout the season. The peak date of caterpillar abundance is the day with the highest collected quantity of caterpillar frass. To evaluate the cue used by caterpillars, we used the same sliding window analysis as for birds. Dataset sizes allow caterpillar sliding windows analyses only in E-Pirio and D-Muro (at least 20 years of data are required [73]). Temperature explained *ca* 60% of the variation in the date of caterpillar peak in both sites (table 1*b* and figure 3; electronic supplementary material, table S5). The reliability of the cue was high in both populations: 1.02 ± 0.04 ($t = 25.17$, $p < 0.0001$) in D-Muro and 0.70 ± 0.08 in E-Pirio ($t = 9.071$, $p < 0.0001$); with lower reliability in E-Pirio than D-Muro (negative blue tit cue × E-Pirio interaction: -0.32 ± 0.09, $t = -3.62$, $p = 0.0005$).

Another quantity of interest is how well the cue used by birds predicts the food peak itself. The slope of the regression of the caterpillar date on the cue used by blue tits is the reaction norm that is favoured by natural selection, if caterpillar date is taken as the optimum phenotype each year. This relationship is significantly negative in all sites (figure 2*e*; electronic supplementary material, table S7): early prey abundance is associated with high temperature in the cue window. However, the proportion of variation in the food peak that is captured by its relationship with the cue for plasticity is lower in E-Pirio ($r^2 = 0.21$) than in D-Muro ($r^2 = 0.59$, see §5), and also moderate in the two other populations (D-Rouvière: $r^2 = 0.33$, E-Muro $r^2 = 0.29$). The strength of this relationship in D-Muro is similar to that found for a Dutch great tit population in Hoge Veluwe [68]. If the food peak correctly predicts the optimum laying date, this suggests that plasticity in response to temperature in the time windows we identified only allows tracking a moderate proportion of temporal fluctuations in this optimum. However, note that caterpillar abundance data in the D-Rouvière site should be used with caution: data collection stopped in 2002 because of frequent rainfall, and 10 years of data may not be sufficient for analyses to be reliable.

A plasticity-mediated phenological mismatch between predators and their food source can arise from the use of different cues, or from different responses to the same cues. Regardless of the mechanism, theory predicts that the slope of the consumer should be shallower than the slope of the resource, because cue reliability is expected to be lower in consumers [55]. Accordingly, a wide scale analysis over 812 taxa revealed that secondary consumers have lower climate sensitivity than other groups (e.g. primary producers or consumers [54]). In line with expectations, in E-Pirio birds are less sensitive to temperature than caterpillars (figure 2*c*,*d* and table 1, species × temperature interaction: −4.06 (±1.28),

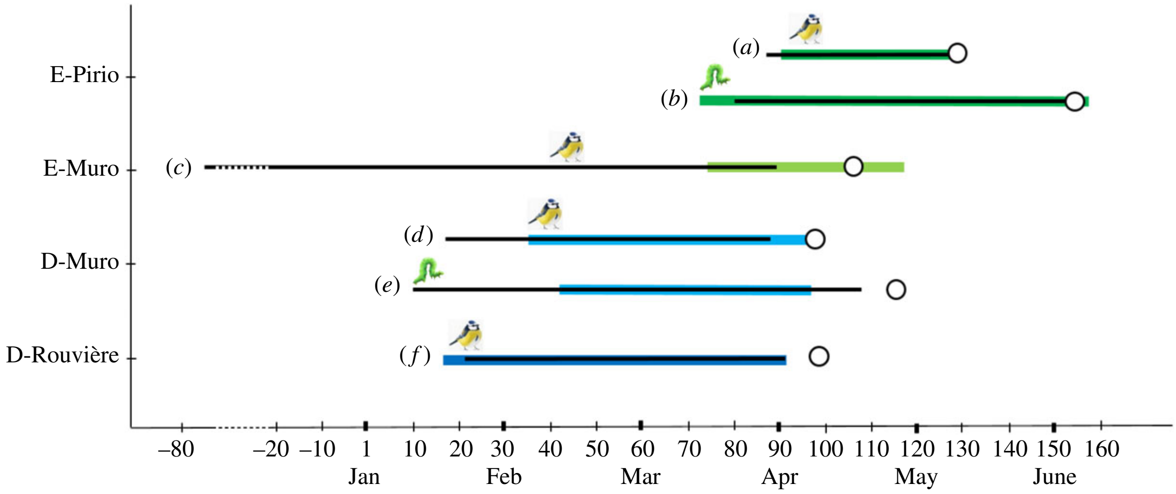

Figure 3. Estimated mean temperature cue windows for blue tits (*a,c,d,f*) and caterpillars (*b,e*) in each population. The open circles represent the mean phenology (mean laying date or mean caterpillar peak date). The first and last days of the window are given in ordinal day, with 1 = 1st January. Coloured lines represent the best windows (from the best model, green for evergreen and blue for deciduous); black lines represent the median windows from the 95% confidence set (see electronic supplementary material, Box S2 and [72,73]). A good agreement between best and median window is an indicator that the window is precisely estimated.

$t = -3.17$, $p = 0.002$). However, in the D-Muro site, the slopes of the reaction norms are similar in birds and caterpillars (figure 2*c*,*d* and table 1, species × temperature interaction: -1.32 (± 1.02), $t = -1.29$, $p = 0.20$). The abundance of caterpillars in D-Muro is (much) higher than in the three other populations (electronic supplementary material, table S1). This makes its likely that in other sites such as E-Pirio, birds are exploiting other resources, especially when caterpillars are rare [81,83]. When food sources are diversified, flatter reaction norms in birds than in caterpillars may not imply that the reaction norms are not adaptive, but that birds are responding to a more multidimensional environment [20]. An important next step would thus be to estimate how the cue for avian phenology and the date of caterpillars jointly predict the annual optimum laying date [21]. However, this may not be sufficient to get a full understanding of the role of plasticity in adaptation in this system. For example, even in D-Muro where average laying date tracks the caterpillar date accurately, birds are always late compared to the food peak (figure 2*f*; electronic supplementary material, table S8), and there is strong directional selection for earlier laying date [84]. An integrative estimate of optimal laying date, using multiple components of fitness such as survival or recruitment success (as in e.g. [85,86]), could help understand this lag, and whether or not it is adaptive.

5. Discussion and perspectives

Our literature review and case study make it clear that, if we wish to understand how global change will affect phenotypic plasticity and its consequences for population biology, we need a deeper understanding of the environmental mechanisms shaping variation in plasticity within species.

Perhaps the most difficult and needed measurements concern spatio-temporal changes in phenotypic selection, which underlie the evolution of phenotypic cues for plasticity. There have been repeated calls for measuring the environmental sensitivity of selection, notably as a way to identify the causes of natural selection [7,87,88]. This becomes a necessity when investigating the adaptiveness and evolution of plasticity, but the available methods and their applications are still limited [21,89]. In particular, we are not aware of an attempt to use multiple environmental variables as predictors of changes in an optimum phenotype as a way to investigate selection on environmental cues for plasticity, consistent with predictions from theory [15,20]. Manipulative experimental approaches are also a powerful yet underused tool for measuring selection on phenotypic plasticity and understanding the adaptive role of environmental cues. For instance, Schmitt *et al.* [90] experimentally shut down plastic stem elongation in response to crowding in plants, by constructing genetically modified lines of *Brassica rapa* that lack the photoreceptor phytochrome A involved in the detection of the relevant cue (ratio of wavelength characteristic of shading by other plants). They showed that the resulting lack of plastically induced elongation is detrimental in a crowded environment, while constitutive expression of stem elongation is detrimental in uncrowded environments. Other experiments of this kind, where cue perception/use is disrupted, or decoupled from the selective pressure, would yield extremely useful information, but are still too rare.

Furthermore, evaluating whether phenotypic plasticity will remain adaptive in the face of global change requires an integrative approach at different levels. The first level of integration is across life stages. Environmental changes can affect phenotypic expression at different stages of the life cycle, so that the effects of global change can be mediated not only by current cues, but also by transgenerational, early-life and carry-over effects (figure 1). The investigation of how these mechanisms of response to the environment interact is just starting [66,91], but it will provide important results on the dynamics of expression of plasticity. Second, there is also a strong need for an integrative approach at the community and/or ecosystem level. Interactions among species are a major source of selection for adaptive plasticity (e.g. synchrony of phenology, antipredator defences, competitive interactions). For example, because the migrant pied and collared flycatchers display shallower reaction norms to temperature than blue tits, they breed later in warmer environments, and suffer from competition with resident tit species [92]. An important step would be to increase the number of studies comparing plasticity of interacting species in wild populations, notably examining how climate and environmental change are affecting cues and the expression of plasticity across trophic levels.

Comparing populations can provide insights as to how phenotypic plasticity and cue use are shaped by evolution. In our case study, geographically very close, and connected, populations occupying different habitats differed extensively in the cues affecting laying date plasticity, as well as the reliability of these cues as predictors of the putative selective pressure, namely the peak of abundance of the main food source (caterpillars). The populations from evergreen and deciduous habitats differed in the time windows—and to a lesser extent, in the environmental variables—that they use. The difference in time windows among populations is consistent with results from another study showing shorter windows for populations breeding in 'late' habitats, such as high latitudes [93]. This suggests that these differences in time windows can be adaptive. However, detection of cues in wild populations relies on a correlative approach, and we cannot completely exclude that another unmeasured environmental factor correlated to temperature drives the plasticity of laying date, as well as local variation of cue windows. The ecological reality of these populations is certainly highly complex, and more information on environmental heterogeneity would be needed to assess which aspect of environmental variability can be linked to the difference in cue use. For instance, the focal populations vary in the abundance of caterpillars, suggesting that the required use of additional prey may partly explain the apparent difference among populations in the reliability of cues for predicting the selective environment. Altogether, understanding the phenology of blue tits (and other insectivorous passerines in temperate forests) requires integrating knowledge on—at least—three trophic levels: an insectivorous bird, a herbivorous caterpillar and an autotroph tree. In temperate regions, spring temperature seems to be the main environmental factor influencing hatching and development period in insects [94], following a period of low metabolic rates caused by ambient temperature during winter (or even a diapause period mainly driven by photoperiod [95]). Similarly, tree phenology often includes a chilling period (i.e. a period of cold temperature required to lift dormancy after winter [25]). Chilling requirement and cold tolerance vary among species; more specifically, deciduous oaks seem more sensitive to cold temperatures and freezing stress than evergreen oaks [96,97]. Cold sensitivity of deciduous oaks suggests that winter temperature could partly predict tree and thus insect phenology, offering a potential explanation as to why winter temperatures are included in the cue window of birds breeding in deciduous oak forests. Finally, the use of extreme climatic events as an additional source of information in E-Muro (ECE) also requires further investigation before clear interpretations can be made. Our results overall highlight that ecological (biotic and abiotic components) variation can have strong effects on plasticity, but further empirical work is needed to be able to discuss our results from a more mechanistic point of view.

We find little evidence for multiple redundant climatic cues, but we cannot exclude that some other, unmeasured cues, such as tree phenology, could also be important in determining laying date [74]. Although partial redundancy should increase the reliability of the information [57], information acquisition is also expected to be costly [98]. An open remaining question is thus the circumstances under which we can expect organisms to use several, partly redundant sources of information, and whether this could mitigate the effects of global change. For example, while temperature in late winter/early spring may not remain a reliable cue, tree phenology could provide more robust information on the long term. Detecting redundant environmental cues is challenging because of collinearity among factors leading to statistical issues (as is probably the case in our analysis), especially in short time series (but see [99]).

If a cue is no longer informative, there could be evolution of cue use. In general, we know little about the evolutionary potential of cue use but a couple of studies suggest some genetic variation exists for this. For example, in *Daphnia magna*, the integration of different cues for plasticity of life-history traits varies among clones [100]. In *Arabidopsis thaliana*, the knowledge of genetic pathways involved in determining flowering time allows us to understand variability in plastic responses and how multiple cues are integrated, and thus to predict the effects of environmental changes on plasticity [101,102]. Similar approaches in the wild seem very challenging for now, but laboratory experiments could provide very useful results in this as yet little-explored area.

Ethics. The blue tit monitoring protocol was approved by the Animal Care and Use committee Languedoc-Rousillon (CEEA-LR-12066) as well as by regional institutions (bylaw issued by the Prefecture on 15 June 2012, no. 2012167-0003). Captures of breeding birds were performed under ringing permits delivered by the CRBPO (Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris; ringing permit number 1907 to A.C., program permit number 369).

Data accessibility. Phenological data are available on HAL repository (hal.archives-ouvertes.fr): hal-01899075. Meteorological data are accessible from https://donneespubliques.meteofrance.fr/

Authors' contributions. C.T., A.C., L.-M.C. and S.B. designed the research. A.C., C.T. and S.B. (and many other contributors) collected field data. S.B. conducted statistical analyses. C.T., L.-M.C., A.C. and S.B. wrote the paper.

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