



HAL
open science

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

Suzanne Bonamour, Luis-Miguel Chevin, A. Charmantier, Céline Teplitsky

► To cite this version:

Suzanne Bonamour, Luis-Miguel Chevin, A. Charmantier, Céline Teplitsky. Phenotypic plasticity in response to climate change: the importance of cue variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2019, 374 (1768), pp.20180178. 10.1098/rstb.2018.0178. hal-02326802

HAL Id: hal-02326802

<https://hal.science/hal-02326802>

Submitted on 22 Oct 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

Special issue:

“The role of plasticity in phenotypic adaptation to rapid environmental change”

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

Suzanne Bonamour¹, Luis-Miguel Chevin¹, Anne Charmantier¹ and Céline Teplitsky¹

Authors affiliations:

¹ CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE,
Campus CNRS, 1919 Route de Mende, 34293 Montpellier 5, France.

Author for correspondence:

Suzanne Bonamour

E-mail: suzanne.bonamour-du-tartre@cefe.cnrs.fr

20 Abstract

21

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

36

37

38

39 Keywords:

40 phenotypic plasticity, climate change, cue reliability, blue tits, laying date

41

42 1. Introduction

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

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

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

64 A core prerequisite for adaptive predictive plasticity is the existence of reliable cues, i.e.
65 accurate environmental information about future selection on the expressed plastic phenotype [11–
66 14]. While the definition of cues is fairly straightforward in theory, their empirical characterization may
67 be a very arduous task (electronic supplementary material, Box S1). Yet it is a crucial step in order to
68 understand how global change can affect adaptive plasticity and its consequences on population
69 biology. For instance, theory predicts that if cue reliability decreases, plasticity may be selected to
70 decrease [15], or else may drive populations to extinction by increasing the expected load caused by
71 phenotypic mismatch with the optimum in a fluctuating environment [16–18]. This is just one possible
72 scenario, but it illustrates the point that one of the most central tasks for understanding and predicting
73 the ecological and evolutionary roles of phenotypic plasticity under global change is to decipher which

74 environmental cues are used by organisms, why (i.e. which selective pressures), and the extent to
75 which global change is likely to affect cue reliability.

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

81 2. Nature and evolution of cues for phenotypic plasticity

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

104 The aspect of cue reliability that influences the evolution of plasticity (in models of linear
105 reaction norms) is the regression slope of the environment of selection on the environment of
106 development [15,28]. When the time lag between these two environments increases, cues are

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

130 Recently, there has been a growing interest in understanding theoretically how cue variability
131 and reliability at different time scales interact to shape plastic responses. Organisms are predicted to
132 integrate various sources of information, including cues from the current environment (for labile traits
133 that change continuously in life), earlier cues perceived during development (early-life or carry-over
134 effects), and transgenerational cues from the environment to which previous generations were
135 exposed (figure 1, [33]), including the parental phenotype itself [37]. The relative weight of these
136 different types of cues is expected to vary depending on their predictive power over different time
137 scales (related to the temporal autocorrelation of the environment), and the strength of selection
138 [32,33,37].

139 Cue variation through space and/or time can lead to variation in plasticity, with an alternation
140 of different ecotypes. A telling example of within-population variation in plasticity comes from the wild

141 mosquitofish (*Gambusia holbrooki*). Fish born in the early spring (development at cool temperature)
142 are expected to experience more variable environments than fish born in early summer (development
143 at warm temperature). Accordingly, metabolic rate is plastic in fish born in early spring, but not in early
144 summer fish [38]. Following on from such encouraging case studies, more work is needed to assess,
145 both theoretically and empirically, whether and how much variation in cue variability and predictability
146 drives within-species variation in plasticity.

147 3. How may global change influence cues and plasticity?

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

156 (a) Changes in the availability and reliability of cues

157 The simplest way environmental change may affect cue use is by disrupting their detection, either by
158 degrading the signal or by disturbing organisms' sensory abilities. For example, juvenile damselfish
159 (*Pomacentrus wardi*) no longer respond to predator cues in degraded environments (dead coral reefs),
160 and the likely mechanism is a degradation of the conspecific alarm cue [40]. Similarly, eutrophication
161 can impair visual signals, leading to maladaptive plasticity in male sticklebacks (*Gasterosteus*
162 *aculeatus*), as their increased investment in courtship behavior is not correlated with female interest
163 [41]. Pervasive electrosmog, i.e. human-made electromagnetic noise, completely disrupts the
164 magnetic compass orientation in the migratory European robin *Erithacus rubecula* [42].

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

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

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

200 Some mechanisms may mitigate the loss of reliability in some cues. First, the potentially
201 negative effects of loss of reliability of a particular environmental variable as a cue could be greatly
202 alleviated if organisms are using multiple cues, because partial redundancy in information from
203 different environmental sources may increase the robustness of the signal [57]. For example in the
204 above-mentioned case of the coral reef damselfish, the loss of olfactory cue in dead coral water can
205 be compensated by the use of visual cues [40]. Similarly, we could expect that the mismatch in trophic
206 webs could be alleviated if species are using each other's presence, abundance, or phenotype as cues

207 (as investigated empirically by Phillimore et al. [58] with butterflies and their host plants), rather than
208 using a unique climatic variable such as temperature alone. Second, the expression of maladaptive
209 responses to an unreliable cue could be reduced through learning, for example if females are able to
210 recalibrate their cue use based on past experience [59].

211 (b) Consequences on the expression and evolution of plasticity

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

227 Retaining partially adaptive plastic responses in novel environments also requires that cues
228 remain reliable. In the specific case of extreme climatic events, whether such cues exist is still
229 unknown. One recent study tackling this issue found no evidence that the Eurasian oystercatchers
230 (*Haematopus ostralegus*) uses cues (lunar cycle, past and current water height) to avoid flooding of
231 their nests during extreme precipitation events [61]. Furthermore, global change generally involves
232 variation of more than one environmental variable, and an alteration of the correlation structure of
233 these variables within and between times. This may trigger conflicting ecological demands on
234 organisms [24], such that new combinations of environmental variables become the best predictors of
235 the optimum phenotype. The ability of organisms to track these altered patterns of change in the
236 optimum phenotype is predicted to depend on their ability to evolve a new combination of
237 environmental variables used as a cue [20]. This theoretical prediction has not been tested yet, but a
238 couple of studies suggest that cue use can evolve relatively fast. A study in the pitcher plant mosquito
239 (*Wyeomia smithii*) suggests that the critical photoperiod for diapause induction has shifted in 5 years
240 towards shorter day length (i.e. later in the season) due to longer growing seasons [62]. Antipredator

241 responses of the Iberian waterfrog (*Pelophylax perezi*) tadpoles to an invasive species (crayfish,
242 *Procambarus clarkia*) is also a likely case of cue evolution. Tadpoles from this species have the ability
243 to build morphological defenses against native predators [63] but only tadpoles from populations
244 coexisting with *P. clarkia* since 10-15 generations display anti-predator response to this new predator
245 [64].

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

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

260 4. Case study: local variation of cues in Mediterranean blue tits and 261 their preys

262 Investigating the mechanisms of plastic response to climate change and their limits in the wild is
263 notoriously difficult (electronic supplementary material, Box S1). However, an exceptionally well-
264 characterized research model of adaptive plasticity in wild populations is the earlier egg-laying date of
265 temperate forest insectivorous passerines during warmer springs. This earlier breeding phenology
266 allows birds to track the phenology of the caterpillars they use as main food source for their offspring
267 [21,68]. In the following section, we investigate in some detail how plastic phenological change relates
268 to environmental cues and their reliability in four Mediterranean populations of blue tits (*Cyanistes*
269 *caeruleus*).

270 The four wild populations of blue tits have been monitored for 20 to 42 years (electronic
271 supplementary material, table S1). Two populations breed in forests dominated by the Deciduous
272 downy oak *Quercus pubescens* (the D-Rouvière and the D-Muro populations, in the French mainland

273 close to Montpellier and Corsica respectively, where ‘D’ stands for deciduous) and two in forests
274 dominated by the evergreen holm oak *Quercus ilex* (the E-Muro and the E-Pirio populations, both in
275 Corsica; ‘E’ stands for evergreen forest [69]). These ecological characteristics have induced local
276 adaptation in birds [70], particularly in their life-history traits. Average phenology of two of these
277 populations has been changing over time: mean laying date is increasingly early (more than three days
278 per decade) for the populations breeding in evergreen, but not in deciduous forests (figure 2a and
279 electronic supplementary material, table S2a), despite similar trends of climate warming in the four
280 sites (electronic supplementary material, table S2c and figure S1; note that table S1 reports trends in
281 temperature over the spring – from April to end-June – while figure S1 presents trends in temperature
282 over the entire year). This pattern is all the more striking as the E-Muro and D-Muro populations are
283 only 5.6 km apart [70], and connected by gene flow [71].

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

297 In three of the populations (D-Rouvière, D-Muro and E-Pirio), the climatic factor that most
298 influences variation of mean laying date is the mean temperature (electronic supplementary materials,
299 table S4) explaining between 54 and 75% of variability in laying date (table 1a). “Evergreen”
300 populations are also sensitive to the number of ECE. In E-Pirio, this effect is additive with the mean
301 temperature effect, but not highly robust. In turn, the number of ECE within a window is the best
302 predictor of average laying date in the E-Muro population (electronic supplementary materials, table
303 S4), but the simultaneous use of information from mean temperature cannot be excluded (mean
304 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
305 found no effect of other climate variables such as rainfall (electronic supplementary materials, table
306 S4). Hence, although some combination of other factors (e.g. bud development [74] or population

307 density [75]) likely play a role, temperature is a key driver behind the plasticity of laying date. This is in
308 line with other correlative studies in great tits, showing that the average spring temperature explains
309 more than 50% of the variability of laying date [68,76], and with experiments showing that laying date
310 responds to temperature treatments [77]. The underlying physiological mechanisms remain elusive,
311 as no effect of temperature on the neuroendocrine system linked to reproduction has been detected
312 yet [78,79]. Despite many studies on bird breeding phenology, knowledge about mechanisms driving
313 phenological plasticity are still scarce, and the relative roles of direct and indirect effects of
314 temperature (e.g. for the latter, a constraint on the timing of egg laying mediated by food abundance
315 or quality) are unknown [80].

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

327 The use of different time windows in the four bird populations leads to contrasted rates of
328 change of the cue over the study period. In the “Evergreen” populations, where the window includes
329 only spring temperature, the mean temperature inside the cue window increases over the 1991-2017
330 period (E-Muro: 0.4 ± 0.07 °C/decade, t-value = 6.18, p-value <0.0001; E-Pirio: 0.6 ± 0.08 , t-value =
331 7.81, p-value <0.0001, figure 2b), but there is no such increase in the two other sites where the
332 windows include information from spring and winter (D-Rouvière: 0.03 ± 0.3 °C/decade, t-value = 0.11,
333 p-value = 0.91; D-Muro 0.22 ± 0.12 , t-value = 1.76, p-value = 0.09). This is in line with the very slow or
334 absent rate of climate change in winter as compared to spring in these Mediterranean areas (electronic
335 supplementary material, figure S1). Climate change is also associated with increasing frequency of ECE,
336 and their number increases in the window used by the E-Muro population (0.49 ± 0.16 positive
337 ECE/decade, t-value = 2.98, p-value = 0.005, see electronic supplementary material table S6 for other
338 populations). Hence overall, even though spring warming has been pervasive in all populations
339 (electronic supplementary materials, table S2c, figure S1), we only detect climate warming during the
340 cue windows influencing bird phenology in E-Pirio and E-Muro. This difference of windows across

341 habitats explains laying dates are advancing in the evergreen avian populations but not in the
342 deciduous populations.

343 It is also possible to investigate the reliability of cues in this system. The fitness consequences
344 of phenological responses of blue tits depend on the phenology of caterpillars of *Tortrix viridana*, the
345 main food resource for nestlings [81], thought to influence reproductive success through offspring
346 survival. The synchronization of the nesting period (especially when nestlings reach the peak of their
347 energetic needs, around 9 days after hatching [82]) with date of peak abundance in caterpillars
348 depends on how reliably the environmental cue used by birds to modify their phenology predicts
349 caterpillar peak date. We can thus measure the linear regression slope of the environment affecting
350 selection on timing of breeding on the environment affecting timing of breeding itself, in order to
351 quantify the reliability of the cue used by birds in a way that matches theoretical predictions [e.g.
352 15,28]. Caterpillar phenology is studied in the four sites thanks to coprometers (i.e. 50*50 cm cloth
353 square collecting the frass of caterpillars under oak trees). The mass of frass collected during a given
354 time period allows us to estimate the abundance of caterpillars throughout the season. The peak date
355 of caterpillar abundance is the day with the highest collected quantity of caterpillar frass. To evaluate
356 the cue used by caterpillars, we used the same sliding window analysis as for birds. Dataset sizes allow
357 caterpillar sliding windows analyses only in E-Pirio and D-Muro (at least 20 years of data are required
358 [73]). Temperature explained ca. 60% of the variation in the date of caterpillar peak in both sites (table
359 1b, figure 3, electronic supplementary materials table S5). The reliability of the cue was high in both
360 populations: 1.02 ± 0.04 (t-value = 25.17, p-value < 0.0001) in D-Muro and 0.70 ± 0.08 in E-Pirio (t-
361 value = 9.071, p-value < 0.0001; with lower reliability in E-Pirio than D-Muro (negative blue tit cue*E-
362 Pirio interaction: -0.32 ± 0.09 , t-value = -3.62, p-value = 0.0005).

363 Another quantity of interest is how well the cue used by birds predict the food peak itself. The
364 slope of the regression of the caterpillar date on the cue used by blue tits is the reaction norm that is
365 favoured by natural selection, if caterpillar date is taken as the optimum phenotype each year. This
366 relationship is significantly negative in all sites (figure 2e, electronic supplementary material, table S7):
367 early prey abundance is associated with high temperature in the cue window. However, the proportion
368 of variation in the food peak that is captured by its relationship with the cue for plasticity is lower in E-
369 Pirio ($r^2 = 0.21$) than in D-Muro ($r^2 = 0.59$, see discussion), and also moderate in the two other
370 populations (D-Rouvière: $r^2 = 0.33$, E-Muro $r^2 = 0.29$). The strength of this relationship in D-Muro is
371 similar as that found for a Dutch great tit population in Hoge Veluwe [68]. If the food peak correctly
372 predicts the optimum laying date, this suggests that plasticity in response to temperature in the time
373 windows we identified only allows tracking a moderate proportion of temporal fluctuations in this
374 optimum. However, note that caterpillar abundance data in the D-Rouvière site should be used with

375 caution: data collection stopped in 2002 because of frequent rainfalls, and 10 years of data may not
376 be sufficient for analyses to be reliable.

377 A plasticity-mediated phenological mismatch between predators and their food source can
378 arise from use of different cues, or from different responses to the same cues. Regardless of the
379 mechanism, theory predicts that the slope of the consumer should be shallower than the slope of the
380 resource, because cue reliability is expected to be lower in consumers [55]. Accordingly, a wide scale
381 analysis over 812 taxa revealed that secondary consumers have lower climate sensitivity than other
382 groups (e.g. primary producers or consumers [54]). In line with expectations, in E-Pirio birds are less
383 sensitive to temperature than caterpillars (figure 2c,d, table 1, species*temperature interaction: -4.06
384 (± 1.28), t-value = -3.17, p-value = 0.002). However, in the D-Muro site, the slopes of the reaction norms
385 are similar in birds and caterpillars (figure 2c,d, table 1, species*temperature interaction: -1.32 (\pm
386 1.02), t-value = -1.29, p-value = 0.20). The abundance of caterpillars in D-Muro is (much) higher than
387 in the three other populations (electronic supplementary material, table S1). This make its likely that
388 in other sites such as E-Pirio, birds are exploiting other resources, especially when caterpillars are rare
389 [81,83]. When food sources are diversified, flatter reaction norms in birds than in caterpillars may not
390 imply that the reaction norms are not adaptive, but that birds are responding to a more
391 multidimensional environment [20]. An important next step would thus be to estimate how the cue
392 for avian phenology and the date of caterpillars jointly predict the annual optimum laying date [21].
393 However, this may not be sufficient to get a full understanding of the role of plasticity in adaptation in
394 this system. For example, even in D-Muro where average laying date is tracking the caterpillar date
395 accurately, birds are always late compared to the food peak (figure 2f, electronic supplementary
396 material table S8), and there is strong directional selection for earlier laying date [84]. An integrative
397 estimate of optimal laying date, using multiple components of fitness such as survival or recruitment
398 success (as in e.g. [85,86]), could help understand this lag, and whether or not it is adaptive.

399 5. Discussion and perspectives

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

403 Perhaps the most difficult and needed measurements concern spatio-temporal changes in
404 phenotypic selection, which underlie the evolution of phenotypic cues for plasticity. There have been
405 repeated calls for measuring the environmental sensitivity of selection, notably as a way to identify
406 the causes of natural selection [7,87,88]. This becomes a necessity when investigating the adaptiveness
407 and evolution of plasticity, but the available methods and their applications are still limited [21,89]. In

408 particular, we are not aware of an attempt to use multiple environmental variables as predictors of
409 changes in an optimum phenotype, as a way to investigate selection on environmental cues for
410 plasticity, consistent with predictions from theory [15,20]. Manipulative experimental approaches are
411 also a powerful yet underused tool for measuring selection on phenotypic plasticity and understanding
412 the adaptive role of environmental cues. For instance, Schmitt et al. [90] experimentally shut down
413 plastic stem elongation in response to crowding in plants, by constructing genetically modified lines of
414 *Brassica rapa* that lack the photoreceptor phytochrome A involved in the detection of the relevant cue
415 (ratio of wavelength characteristic of shading by other plants). They showed that the resulting lack of
416 plastically induced elongation is detrimental in a crowded environment, while constitutive expression
417 of stem elongation is detrimental in uncrowded environments. Other experiments of this kind, where
418 cue perception/use is disrupted, or decoupled from the selective pressure, would yield extremely
419 useful information, but are still too rare.

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

435 Comparing populations can provide insights as to how phenotypic plasticity and cue use are
436 shaped by evolution. In our case study, geographically very close, and connected, populations
437 occupying different habitats differed extensively in the cues affecting laying date plasticity, as well as
438 the reliability of these cues as predictors of the putative selective pressure, namely the peak of
439 abundance of the main food source (caterpillars). The populations from evergreen and deciduous
440 habitats differed in the time windows – and to a lesser extent, in the environmental variables – that
441 they use. The difference in time windows among populations is consistent with results from another

442 study showing shorter windows for populations breeding in “late” habitats, such as high latitudes [93].
443 This suggests that these differences in time windows can be adaptive. However, detection of cues in
444 wild populations relies on a correlative approach, and we cannot completely exclude that another
445 unmeasured environmental factor correlated to temperature drives the plasticity of laying date, as
446 well as local variation of cue windows. The ecological reality of these populations is certainly highly
447 complex, and more information on environmental heterogeneity would be needed to assess which
448 aspect of environmental variability can be linked to the difference in cue use. For instance, the focal
449 populations vary in the abundance of caterpillars, suggesting that the required use of additional preys
450 may partly explain the apparent difference among populations in the reliability of cues for predicting
451 the selective environment. Altogether, understanding the phenology of blue tits (and other
452 insectivorous passerines in temperate forests) requires integrating knowledge on – at least – three
453 trophic levels: an insectivorous bird, a herbivorous caterpillar and an autotroph tree. In temperate
454 regions, spring temperature seems to be the main environmental factor influencing hatching and
455 development period in insects [94], following a period of low metabolic rates caused by ambient
456 temperature during winter (or even a diapause period mainly driven by photoperiod [95]). Similarly,
457 tree phenology often includes a chilling period (i.e. a period of cold temperature required to lift
458 dormancy after winter [25]). Chilling requirement and cold tolerance vary among species, more
459 specifically deciduous oaks seem more sensitive to cold temperatures and freezing stress than
460 evergreen oaks [96,97]. Cold sensitivity of deciduous oaks suggest that winter temperature could
461 partly predict tree and thus insect phenology, offering a potential explanation as to why winter
462 temperatures are included in the cue window of birds breeding in deciduous oak forests. Finally, the
463 use of extreme climatic events as an additional source of information in E-Muro (ECE) also requires
464 further investigation before clear interpretations can be made. Our results overall highlight that
465 ecological (biotic and abiotic components) variation can have strong effects on plasticity, but further
466 empirical work is needed to be able to discuss our results from a more mechanistic point of view.

467 We find little evidence for multiple redundant climatic cues, but we cannot exclude that some
468 other, unmeasured cues, such as tree phenology, could also be important in determining laying date
469 [74]. Although partial redundancy should increase the reliability of the information [57], information
470 acquisition is also expected to be costly [98]. An open remaining question is thus the circumstances
471 under which we can expect organisms to use several, partly redundant sources of information, and
472 whether this could mitigate the effects of global change. For example, while temperature in late
473 winter/early spring may not remain a reliable cue, tree phenology could provide more robust
474 information on the long term. Detecting redundant environmental cues is challenging because of

475 collinearity among factors leading to statistical issues (as is probably the case in our analysis), especially
476 in short time series (but see [99]).

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

485

486

487 **References**

- 488 1. Gienapp P, Teplitsky C, Alho JS, Mills J a., Merilä J. 2008 Climate change and evolution:
489 disentangling environmental and genetic responses. *Mol. Ecol.* **17**, 167–178.
490 (doi:10.1111/j.1365-294X.2007.03413.x)
- 491 2. Merilä J, Hendry AP. 2014 Climate change, adaptation, and phenotypic plasticity: The problem
492 and the evidence. *Evol. Appl.* **7**, 1–14. (doi:10.1111/eva.12137)
- 493 3. Matesanz S, Gianoli E, Valladares F. 2010 Global change and the evolution of phenotypic
494 plasticity in plants. *Ann. N. Y. Acad. Sci.* **1206**, 35–55. (doi:10.1111/j.1749-6632.2010.05704.x)
- 495 4. Alberti M, Marzluff J, Hunt VM. 2017 Urban driven phenotypic changes: Empirical
496 observations and theoretical implications for eco-evolutionary feedback. *Philos. Trans. R. Soc.*
497 *B Biol. Sci.* **372**, 20160029. (doi:10.1098/rstb.2016.0029)
- 498 5. Davidson AM, Jennions M, Nicotra AB. 2011 Do invasive species show higher phenotypic
499 plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol. Lett.* **14**, 419–431.
500 (doi:10.1111/j.1461-0248.2011.01596.x)
- 501 6. Lande R. 2015 Evolution of phenotypic plasticity in colonizing species. *Mol. Ecol.* **24**, 2038–
502 2045. (doi:10.1111/mec.13037)
- 503 7. Chevin L-M, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing
504 environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357.
505 (doi:10.1371/journal.pbio.1000357)
- 506 8. Vedder O, Bouwhuis S, Sheldon BC. 2013 Quantitative assessment of the importance of
507 phenotypic plasticity in adaptation to climate change in wild bird populations. *PLoS Biol.* **11**,
508 e1001605. (doi:10.1371/journal.pbio.1001605)
- 509 9. Gienapp P, Lof M, Reed TE, McNamara JM, Verhulst S, Visser ME. 2013 Predicting
510 demographically sustainable rates of adaptation: can great tit breeding time keep pace with
511 climate change? *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **368**, 20120289.
512 (doi:10.1098/rstb.2012.0289)
- 513 10. Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007 Adaptive versus non-adaptive
514 phenotypic plasticity and the potential for contemporary adaptation in new environments.
515 *Funct. Ecol.* **21**, 394–407. (doi:10.1111/j.1365-2435.2007.01283.x)
- 516 11. Moran NA. 1992 The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139**,

- 517 971–989.
- 518 12. Tufto J. 2000 The evolution of plasticity and nonplastic spatial and temporal adaptations in
519 the presence of imperfect environmental cues. *Am. Nat.* **156**, 121–130. (doi:10.1086/303381)
- 520 13. Botero CA, Weissing FJ, Wright J, Rubenstein DR. 2015 Evolutionary tipping points in the
521 capacity to adapt to environmental change. *Pnas* **112**. (doi:10.1073/pnas.1408589111)
- 522 14. Scheiner SM. 2013 The genetics of phenotypic plasticity: XII: Temporal and spatial
523 heterogeneity. *Ecol. Evol.* **3**, 4596–4609. (doi:10.1002/ece3.792)
- 524 15. Gavrillets S, Scheiner SM. 1993 The genetics of phenotypic plasticity. V. Evolution of reaction
525 norm shape. *J. Evol. Biol.* **6**, 31–48. (doi:DOI 10.1046/j.1420-9101.1993.6010031.x)
- 526 16. Reed TE, Waples RS, Schindler DE, Hard JJ, Kinnison MT. 2010 Phenotypic plasticity and
527 population viability: the importance of environmental predictability. *Proc. R. Soc. B Biol. Sci.*
528 **277**, 3391–3400. (doi:10.1098/rspb.2010.0771)
- 529 17. Chevin L-M, Gallet R, Gomulkiewicz R, Holt RD, Fellous S. 2013 Phenotypic plasticity in
530 evolutionary rescue experiments. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **368**, 20120089.
531 (doi:10.1098/rstb.2012.0089)
- 532 18. Ashander J, Chevin L-M, Baskett ML. 2016 Predicting evolutionary rescue via evolving
533 plasticity in stochastic environments. *Proc. R. Soc. B Biol. Sci.* **283**, 20161690.
534 (doi:10.1098/rspb.2016.1690)
- 535 19. Griffith TM, Sultan SE. 2005 Shade tolerance plasticity in response to neutral vs green shade
536 cues in *Polygonum* species of contrasting ecological breadth. *New Phytol.* **166**, 141–148.
537 (doi:10.1111/j.1469-8137.2004.01277.x)
- 538 20. Chevin L-M, Lande R. 2015 Evolution of environmental cues for phenotypic plasticity.
539 *Evolution (N. Y.)* **69**, 2767–2775. (doi:10.1111/evo.12755)
- 540 21. Chevin L-M, Visser ME, Tufto J. 2015 Estimating the variation, autocorrelation, and
541 environmental sensitivity of phenotypic selection. *Evolution (N. Y.)* **69**, 2319–2332.
542 (doi:10.1111/evo.12741)
- 543 22. Westneat DF, Stewart IRK, Hatch MI. 2009 Complex interactions among temporal variables
544 affect the plasticity of clutch size in a multi-brooded bird. *Ecology* **90**, 1162–1174.
545 (doi:10.1890/08-0698.1)
- 546 23. Sgrò CM, Terblanche JS, Hoffmann AA. 2016 What can plasticity contribute to insect

- 547 responses to climate change? *Annu. Rev. Entomol.* **61**, 433–451. (doi:10.1146/annurev-ento-
548 010715-023859)
- 549 24. Valladares F, Gianoli E, Gómez JM. 2007 Ecological limits to plant phenotypic plasticity. *New*
550 *Phytol.* **176**, 749–763. (doi:10.1111/j.1469-8137.2007.02275.x)
- 551 25. Polgar CA, Primack RB. 2011 Leaf-out phenology of temperate woody plants: From trees to
552 ecosystems. *New Phytol.* **191**, 926–941. (doi:10.1111/j.1469-8137.2011.03803.x)
- 553 26. Black AR. 1993 Predator-induced phenotypic plasticity in *Daphnia pulex*: Life history and
554 morphological responses to *Notonecta* and *Chaoborus*. *Limnol. Oceanogr.* **38**, 986–996.
555 (doi:10.4319/lo.1993.38.5.0986)
- 556 27. Teplitsky C, Plénet S, Joly P. 2004 Hierarchical responses of tadpoles to multiple predators.
557 *Ecology* **85**, 2888–2894. (doi:10.1890/03-3043)
- 558 28. de Jong G. 1999 Unpredictable selection in a structured population leads to genetic
559 differentiation in evolved reaction norms. *J. Evol. Biol.* **12**, 839–851.
- 560 29. Bradshaw AD. 1965 Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* **13**,
561 115–155. (doi:10.1016/S0065-2660(08)60048-6)
- 562 30. Padilla DK, Adolph SC. 1996 Plastic inducible morphologies are not always adaptive: The
563 importance of time delays in a stochastic environment. *Evol. Ecol.* **10**, 105–117.
564 (doi:10.1007/BF01239351)
- 565 31. Mousseau TA, Fox CW. 1998 The adaptive significance of maternal effects. *Trends Ecol. Evol.*
566 **13**, 403–407. (doi:10.1016/S0169-5347(98)01472-4)
- 567 32. Leimar O, McNamara JM. 2015 The evolution of transgenerational integration of information
568 in heterogeneous environments. *Am. Nat.* **185**, E55–E69. (doi:10.1086/679575)
- 569 33. McNamara JM, Dall SRX, Hammerstein P, Leimar O. 2016 Detection vs. selection: integration
570 of genetic, epigenetic and environmental cues in fluctuating environments. *Ecol. Lett.* **19**,
571 1267–1276. (doi:10.1111/ele.12663)
- 572 34. Uller T. 2008 Developmental plasticity and the evolution of parental effects. *Trends Ecol. Evol.*
573 **23**, 432–438. (doi:10.1016/j.tree.2008.04.005)
- 574 35. Dey S, Proulx SR, Teotónio H. 2016 Adaptation to temporally fluctuating environments by the
575 evolution of maternal effects. *PLoS Biol.* **14**, 1–29. (doi:10.1371/journal.pbio.1002388)

- 576 36. Shama LNS, Strobel A, Mark FC, Wegner KM. 2014 Transgenerational plasticity in marine
577 sticklebacks: Maternal effects mediate impacts of a warming ocean. *Funct. Ecol.* **28**, 1482–
578 1493. (doi:10.1111/1365-2435.12280)
- 579 37. Kuijper B, Hoyle RB. 2015 When to rely on maternal effects and when on phenotypic
580 plasticity? *Evolution (N. Y.)*. **69**, 950–968. (doi:10.1111/evo.12635)
- 581 38. Seebacher F, Beaman J, Little AG. 2014 Regulation of thermal acclimation varies between
582 generations of the short-lived mosquitofish that developed in different environmental
583 conditions. *Funct. Ecol.* **28**, 137–148. (doi:10.1111/1365-2435.12156)
- 584 39. Ratajczak Z, Carpenter SR, Ives AR, Kucharik CJ, Ramiadantsoa T, Stegner MA, Williams JW,
585 Zhang J, Turner MG. 2018 Abrupt change in ecological systems: inference and diagnosis.
586 *Trends Ecol. Evol.* **33**, 513–526. (doi:10.1016/j.tree.2018.04.013)
- 587 40. Lönnstedt OM, McCormick MI, Chivers DP. 2013 Degraded environments alter prey risk
588 assessment. *Ecol. Evol.* **3**, 38–47. (doi:10.1002/ece3.388)
- 589 41. Candolin U. 2009 Population responses to anthropogenic disturbance: Lessons from three-
590 spined sticklebacks *Gasterosteus aculeatus* in eutrophic habitats. *J. Fish Biol.* **75**, 2108–2121.
591 (doi:10.1111/j.1095-8649.2009.02405.x)
- 592 42. Engels S *et al.* 2014 Anthropogenic electromagnetic noise disrupts magnetic compass
593 orientation in a migratory bird. *Nature* (doi:10.1038/nature13290)
- 594 43. Kriska G, Horváth G, Andrikovics S. 1998 Why do mayfly lay their eggs en masse on dry asphalt
595 roads? *J. Exp. Biol.* **201**, 2273–2286.
- 596 44. Hanazato T. 1991 Pesticides as chemical agents inducing helmet formation in *Daphnia*
597 *ambigua*. *Freshw. Biol.* **26**, 419–424. (doi:10.1111/j.1365-2427.1991.tb01408.x)
- 598 45. Riessen HP. 2012 Costs of predator-induced morphological defences in *Daphnia*. *Freshw. Biol.*
599 **57**, 1422–1433. (doi:10.1111/j.1365-2427.2012.02805.x)
- 600 46. Robertson BA, Rehage JS, Sih A. 2013 Ecological novelty and the emergence of evolutionary
601 traps. *Trends Ecol. Evol.* **28**, 552–560. (doi:10.1016/j.tree.2013.04.004)
- 602 47. Schlaepfer MA, Runge MC, Sherman PW. 2002 Ecological and evolutionary traps. *Trends Ecol.*
603 *Evol.* **17**, 474–480. (doi:http://dx.doi.org/10.1016/S0169-5347(02)02580-6)
- 604 48. Marrot P, Charmantier A, Blondel J, Garant D. 2018 Current spring warming as a driver of
605 selection on reproductive timing in a wild passerine. *J. Anim. Ecol.* **87**, 754–764.

- 606 (doi:10.1111/ijlh.12426)
- 607 49. Williams CM, Henry HAL, Sinclair BJ. 2015 Cold truths: How winter drives responses of
608 terrestrial organisms to climate change. *Biol. Rev.* **90**, 214–235. (doi:10.1111/brv.12105)
- 609 50. Inouye DW, Barr B, Armitage KB, Inouye BD. 2000 Climate change is affecting altitudinal
610 migrants and hibernating species. *Proc. Natl. Acad. Sci. U. S. A.* **97**, 1630–1633.
611 (doi:10.1073/pnas.97.4.1630)
- 612 51. Parmesan C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev.*
613 *Ecol. Evol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- 614 52. Visser ME, Both C. 2005 Shifts in phenology due to global climate change: the need for a
615 yardstick. *Proc. R. Soc. B Biol. Sci.* **272**, 2561–2569. (doi:10.1098/rspb.2005.3356)
- 616 53. Byers DL. 2017 Studying plant–pollinator interactions in a changing climate: A review of
617 approaches. *Appl. Plant Sci.* **5**, 1700012. (doi:10.3732/apps.1700012)
- 618 54. Thackeray SJ *et al.* 2016 Phenological sensitivity to climate across taxa and trophic levels.
619 *Nature* **535**, 241–245. (doi:10.1038/nature18608)
- 620 55. Gienapp P, Reed TE, Visser ME. 2014 Why climate change will invariably alter selection
621 pressures on phenology. *Proc. R. Soc. B Biol. Sci.* **281**, 20141611.
622 (doi:10.1098/rspb.2014.1611)
- 623 56. Doi H, Gordo O, Katano I. 2008 Heterogeneous intra-annual climatic changes drive different
624 phenological responses at two trophic levels. *Clim. Res.* **36**, 181–190. (doi:10.3354/cr00741)
- 625 57. Dore AA, Mcdowall L, Rouse J, Bretman A, Gage MJG, Chapman T. 2018 The role of complex
626 cues in social and reproductive plasticity. *Behav. Ecol. Sociobiol.* (doi:10.1007/s00265-018-
627 2539-x)
- 628 58. Phillimore AB, Stålhandske S, Smithers RJ, Bernard R. 2012 Dissecting the contributions of
629 plasticity and local adaptation to the phenology of a butterfly and its host plants. *Am. Nat.*
630 **180**, 655–670. (doi:10.1086/667893)
- 631 59. Grieco F, van Noordwijk AJ, Visser ME. 2002 Evidence for the effect of learning on timing of
632 reproduction in blue tits. *Science (80-.)*. **296**, 136–138. (doi:10.1126/science.1068287)
- 633 60. Chevin L-M, Hoffmann AA. 2017 Evolution of phenotypic plasticity in extreme environments.
634 *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160138. (doi:10.1098/rstb.2016.0138)

- 635 61. Bailey LD, Ens BJ, Both C, Heg D, Oosterbeek K, van de Pol M. 2017 No phenotypic plasticity in
636 nest-site selection in response to extreme flooding events. *Philos. Trans. R. Soc. B Biol. Sci.*
637 **372**, 20160139. (doi:10.1098/rstb.2016.0139)
- 638 62. Bradshaw WE, Holzapfel CM. 2001 Genetic shift in photoperiodic response correlated with
639 global warming. *Proc. Natl. Acad. Sci.* **98**, 14509–14511. (doi:10.1073/pnas.241391498)
- 640 63. Nunes AL, Orizaola G, Laurila A, Rebelo R. 2014 Morphological and life-history responses of
641 anurans to predation by an invasive crayfish: An integrative approach. *Ecol. Evol.* **4**, 1491–
642 1503. (doi:10.1002/ece3.979)
- 643 64. Nunes AL, Orizaola G, Laurila A, Rebelo R. 2014 Rapid evolution of constitutive and inducible
644 defenses against an invasive predator. *Ecology* **95**, 1520–1530. (doi:10.1890/13-1380.1)
- 645 65. Tufto J. 2015 Genetic evolution, plasticity, and bet-hedging as adaptive responses to
646 temporally autocorrelated fluctuating selection: A quantitative genetic model. *Evolution (N.*
647 *Y.)*. **69**, 2034–2049. (doi:10.1111/evo.12716)
- 648 66. Donelson JM, Salinas S, Munday PL, Shama LNS. 2018 Transgenerational plasticity and climate
649 change experiments: Where do we go from here? *Glob. Chang. Biol.* **24**, 13–34.
650 (doi:10.1111/gcb.13903)
- 651 67. Lande R. 2009 Adaptation to an extraordinary environment by evolution of phenotypic
652 plasticity and genetic assimilation. *J. Evol. Biol.* **22**, 1435–1446. (doi:10.1111/j.1420-
653 9101.2009.01754.x)
- 654 68. Visser ME, Holleman LJM, Gienapp P. 2006 Shifts in caterpillar biomass phenology due to
655 climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**,
656 164–172. (doi:10.1007/s00442-005-0299-6)
- 657 69. Blondel J, Thomas D, Charmantier A, Perret P, Bourgault P, Lambrechts MM. 2006 A thirty-
658 year study of phenotypic and genetic variation of Blue tits in Mediterranean habitat mosaics.
659 *Bioscience* **56**, 661–673. (doi:10.1641/0006-3568(2006)56[661:ATSOPA]2.0.CO;2)
- 660 70. Charmantier A, Doutrelant C, Dubuc-Messier G, Fargevieille A, Szulkin M. 2016 Mediterranean
661 blue tits as a case study of local adaptation. *Evol. Appl.* **9**, 135–152. (doi:10.1111/eva.12282)
- 662 71. Szulkin M, Gagnaire PA, Bierne N, Charmantier A. 2016 Population genomic footprints of fine
663 scale differentiation between habitats in Mediterranean blue tits. *Mol. Ecol.* **25**, 542–558.
- 664 72. Bailey LD, van de Pol M. 2016 climwin : An R toolbox for climate window analysis. , 1–27.

- 665 (doi:10.1371/journal.pone.0167980)
- 666 73. van de Pol M, Bailey LD, McLean N, Rijdsdijk L, Lawson CR, Brouwer L. 2016 Identifying the best
667 climatic predictors in ecology and evolution. *Methods Ecol. Evol.* **7**, 1246–1257.
668 (doi:10.1111/2041-210X.12590)
- 669 74. Bourgault P, Thomas D, Perret P, Blondel J. 2010 Spring vegetation phenology is a robust
670 predictor of breeding date across broad landscapes: A multi-site approach using the Corsican
671 blue tit (*Cyanistes caeruleus*). *Oecologia* **162**, 885–892. (doi:10.1007/s00442-009-1545-0)
- 672 75. Bourret A, Bélisle M, Pelletier F, Garant D. 2015 Multidimensional environmental influences
673 on timing of breeding in a tree swallow population facing climate change. *Evol. Appl.* **8**, 933–
674 944. (doi:10.1111/eva.12315)
- 675 76. Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC. 2008 Adaptive
676 phenotypic plasticity in response to climate change in a wild bird population. *Science (80-.)*.
677 **320**, 800–803. (doi:10.1126/science.1157174)
- 678 77. Visser ME, Holleman LJM, Caro SP. 2009 Temperature has a causal effect on avian timing of
679 reproduction. *Proc. R. Soc. B Biol. Sci.* **276**, 2323–2331. (doi:10.1098/rspb.2009.0213)
- 680 78. Schaper S V., Dawson A, Sharp PJ, Caro SP, Visser ME. 2012 Individual variation in avian
681 reproductive physiology does not reliably predict variation in laying date. *Gen. Comp.*
682 *Endocrinol.* **179**, 53–62. (doi:10.1016/j.ygcen.2012.07.021)
- 683 79. Caro SP, Schaper S V., Dawson A, Sharp PJ, Gienapp P, Visser ME. 2013 Is microevolution the
684 only emergency exit in a warming world? Temperature influences egg laying but not its
685 underlying mechanisms in great tits. *Gen. Comp. Endocrinol.* **190**, 164–169.
686 (doi:10.1016/j.ygcen.2013.02.025)
- 687 80. Caro SP, Schaper S V., Hut RA, Ball GF, Visser ME. 2013 The Case of the Missing Mechanism:
688 How Does Temperature Influence Seasonal Timing in Endotherms? *PLoS Biol.* **11**.
689 (doi:10.1371/journal.pbio.1001517)
- 690 81. Bañbura J, Blondel J, de Wilde-Lambrechts H, Galan MJ, Maistre M. 1994 Nestling diet
691 variation in an insular Mediterranean population of blue tits *Parus caeruleus*: effects of years,
692 territories and individuals. *Oecologia* **100**, 413–420. (doi:10.1007/BF00317863)
- 693 82. Dias PC, Blondel J. 1996 Local specialization and maladaptation in the Mediterranean blue tit
694 (*Parus caeruleus*). *Oecologia* **107**, 79–86. (doi:10.1007/BF00582237)

- 695 83. Tremblay I, Thomas DW, Blondel J, Perret P, Lambrechts MM. 2005 The effects of habitat
696 quality on foraging patterns, provisioning rate and nestling growth in corsican blue tits *Parus*
697 *caeruleus*. *Ibis (Lond. 1859)*. **147**, 17–24. (doi:10.1111/j.1474-919x.2004.00312.x)
- 698 84. Porlier M, Charmantier A, Bourgault P, Perret P, Blondel J, Garant D. 2012 Variation in
699 phenotypic plasticity and selection patterns in blue tit breeding time: between- and within-
700 population comparisons. *J. Anim. Ecol.* **81**, 1041–1051. (doi:10.1111/j.1365-
701 2656.2012.01996.x)
- 702 85. Price TD, Kirkpatrick M, Arnold SJ. 1988 Directional selection and the evolution of breeding
703 date in birds. *Science (80-)*. **240**, 798–799. (doi:10.1126/science.3363360)
- 704 86. Reed TE, Grøtan V, Jenouvrier S, Saether B-E, Visser ME. 2013 Population Growth in a Wild
705 Bird Is Buffered Against Phenological Mismatch. *Science (80-)*. **340**, 488–491.
706 (doi:10.1017/CBO9781107415324.004)
- 707 87. Wade MJ, Kalisz S. 1990 The causes of natural selection. *Evolution (N. Y)*. **44**, 1947.
708 (doi:10.2307/2409605)
- 709 88. MacColl ADC. 2011 The ecological causes of evolution. *Trends Ecol. Evol.* **26**, 514–522.
710 (doi:10.1016/j.tree.2011.06.009)
- 711 89. Hunter DC, Pemberton JM, Pilkington JG, Morrissey MB. 2018 Quantification and
712 decomposition of environment-selection relationships. *Evolution (N. Y)*. **72**, 851–866.
713 (doi:10.1111/evo.13461)
- 714 90. Schmitt J, McCormac AC, Smith H. 1995 A test of the adaptive plasticity hypothesis using
715 transgenic and mutant plants disabled in phytochrome-mediated elongation responses to
716 neighbors. *Am. Nat.* (doi:10.1086/285832)
- 717 91. Beaman JE, White CR, Seebacher F. 2016 Evolution of Plasticity: Mechanistic Link between
718 Development and Reversible Acclimation. *Trends Ecol. Evol.* **31**, 237–249.
719 (doi:10.1016/j.tree.2016.01.004)
- 720 92. Samplonius JM *et al.* 2018 Phenological sensitivity to climate change is higher in resident than
721 in migrant bird populations among European cavity breeders. *Glob. Chang. Biol.* , 3780–3790.
722 (doi:10.1111/gcb.14160)
- 723 93. Phillimore AB, Leech DI, Pearce-Higgins JW, Hadfield JD. 2016 Passerines may be sufficiently
724 plastic to track temperature-mediated shifts in optimum lay date. *Glob. Chang. Biol.* **22**, 3259–
725 3272. (doi:10.1111/gcb.13302)

- 726 94. van Asch M, Visser ME. 2007 Phenology of Forest Caterpillars and Their Host Trees: The
727 Importance of Synchrony. *Annu. Rev. Entomol.* **52**, 37–55.
728 (doi:10.1146/annurev.ento.52.110405.091418)
- 729 95. Tauber CA, Tauber MJ. 1981 Insect seasonal cycles: genetics and evolution. **12**, 281–308.
- 730 96. Cavender-Bares J, Holbrook NM. 2001 Hydraulic properties and freezing- induced cavitation in
731 sympatric evergreen and deciduous oaks with contrasting habitats. *Plant, Cell Environ.* **24**,
732 1243–1256.
- 733 97. Cavender-Bares J, Cortes P, Rambal S, Joffre R, Miles B, Rocheteau A. 2005 Summer and
734 winter sensitivity of leaves and xylem to minimum freezing temperatures: A comparison of co-
735 occurring Mediterranean oaks that differ in leaf lifespan. *New Phytol.* **168**, 597–612.
736 (doi:10.1111/j.1469-8137.2005.01555.x)
- 737 98. DeWitt TJ, Sih A, Wilson DS. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.*
738 **13**, 77–81. (doi:10.1016/S0169-5347(97)01274-3)
- 739 99. Morrissey MB, Ruxton GD. 2018 Multiple Regression Is Not Multiple Regressions: The
740 Meaning of Multiple Regression and the Non-Problem of Collinearity. *Philos. Theory, Pract.*
741 *Biol.* **10**. (doi:10.3998/ptpbio.16039257.0010.003)
- 742 100. Harney E, Paterson S, Plaistow SJ. 2017 Offspring development and life-history variation in a
743 water flea depends upon clone-specific integration of genetic, non-genetic and environmental
744 cues. *Funct. Ecol.* **31**, 1996–2007. (doi:10.1111/1365-2435.12887)
- 745 101. Wilczek AM, Burghardt LT, Cobb AR, Cooper MD, Welch SM, Schmitt J. 2010 Genetic and
746 physiological bases for phenological responses to current and predicted climates. *Philos.*
747 *Trans. R. Soc. B Biol. Sci.* **365**, 3129–3147. (doi:10.1098/rstb.2010.0128)
- 748 102. Wilczek AM *et al.* 2009 Effects of genetic perturbation on seasonal life history plasticity.
749 *Science (80-.).* **323**, 930–935.

750

751

753 *Table 1*

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

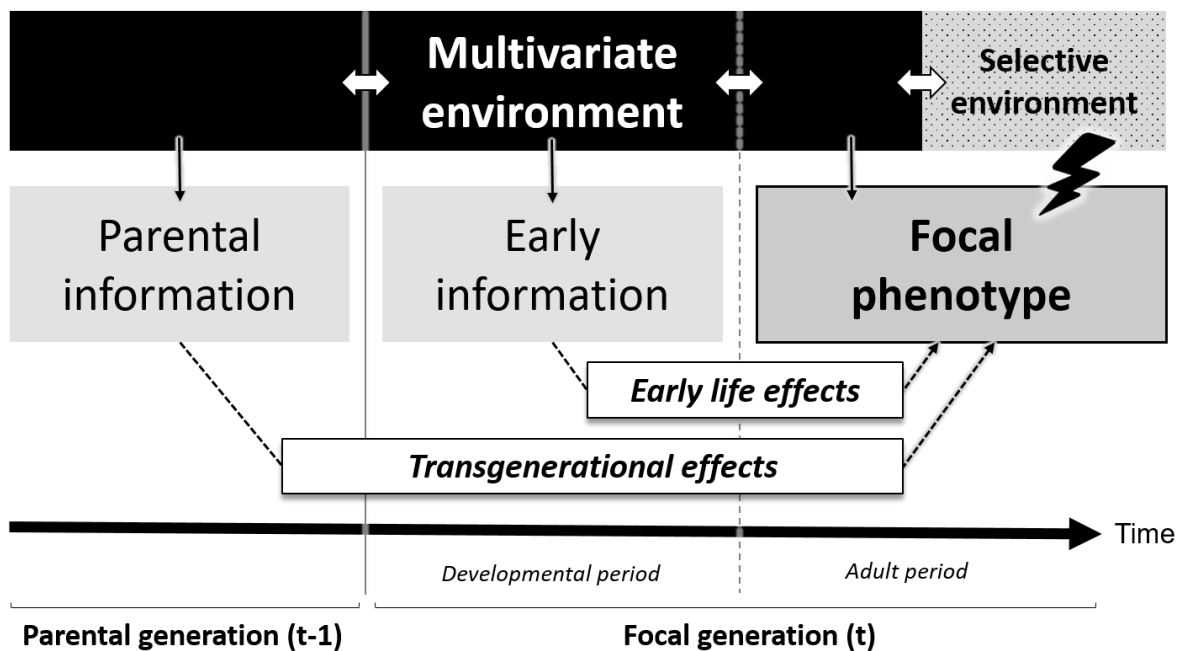
759

a)	Cue	Intercept			Slope			r^2
		Estimates (\pm se)	t-value	p-value	Estimates (\pm se)	t-value	p-value	
<i>D-Rouvière</i>	MeanT	131.78	34.51	<0.0001	-4.42	-8.91	<0.0001	0.75
	(17 th Jan. – 1 st April)	(\pm 3.82)			(\pm 0.50)			
<i>D-Muro</i>	MeanT	137.61	20.31	<0.0001	-3.67	-5.92	<0.0001	0.59
	(4 th Feb. – 7 th April)	(\pm 6.78)			(\pm 0.62)			
<i>E-Muro</i>	MeanT	175.33	1.14	<0.0001	-5.13	-5.11	<0.0001	0.57
	(15 th March – 27 th April)	(\pm 13.34)			(\pm 1.00)			
<i>E-Pirio</i>	ECE	112.21	92.90	<0.0001	-2.41	-4.95	0.0001	0.55
	(23 th March – 15 th April)	(\pm 1.21)			(\pm 0.49)			
<i>E-Pirio</i>	MeanT	200.53	16.82	<0.0001	-5.10	-6.07	<0.0001	0.54
	(31 th March – 7 th May)	(\pm 11.92)			(\pm 0.84)			
b)								
<i>D-Muro</i>	MeanT	171.22	19.01	<0.0001	-5.00	-6.15	<0.0001	0.61
	(11 th Feb. – 7 th April)	(\pm 9.01)			(\pm 0.81)			
<i>E-Pirio</i>	MeanT	283.38	14.14	<0.0001	-8.47	-6.46	<0.0001	0.58
	(13 th March – 7 th June)	(\pm 20.04)			(\pm 1.31)			

760

761 *Figure 1*

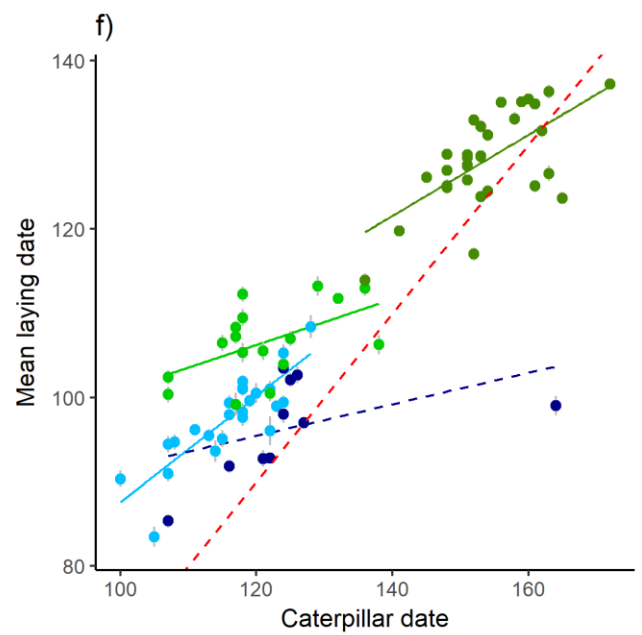
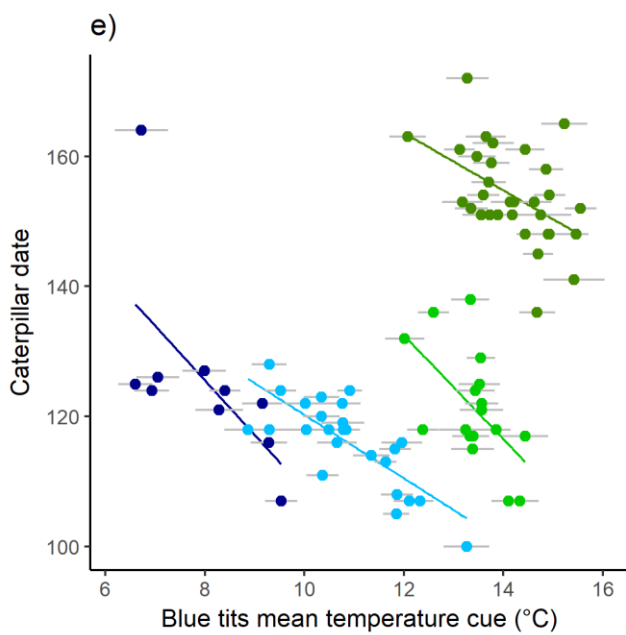
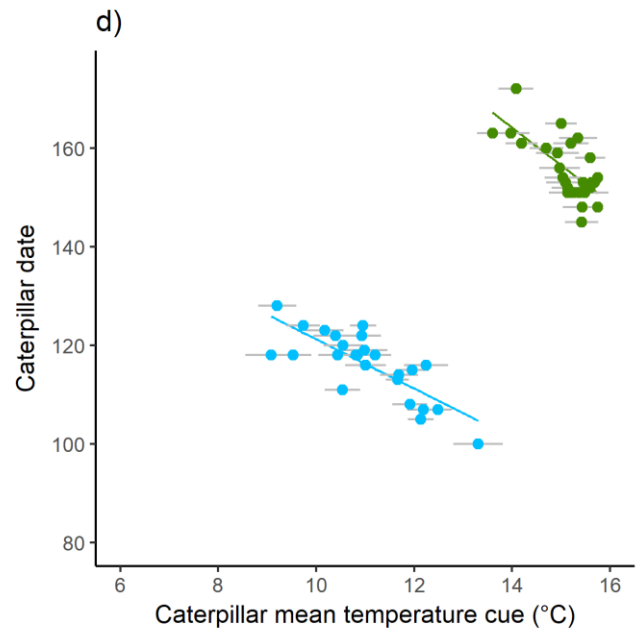
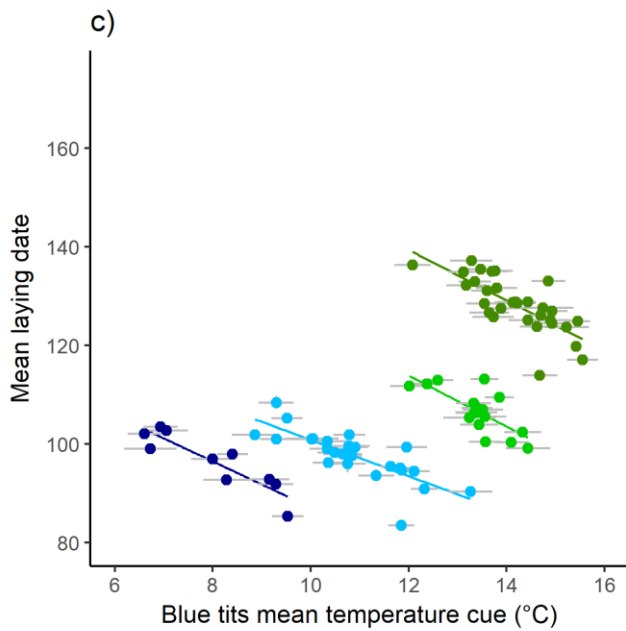
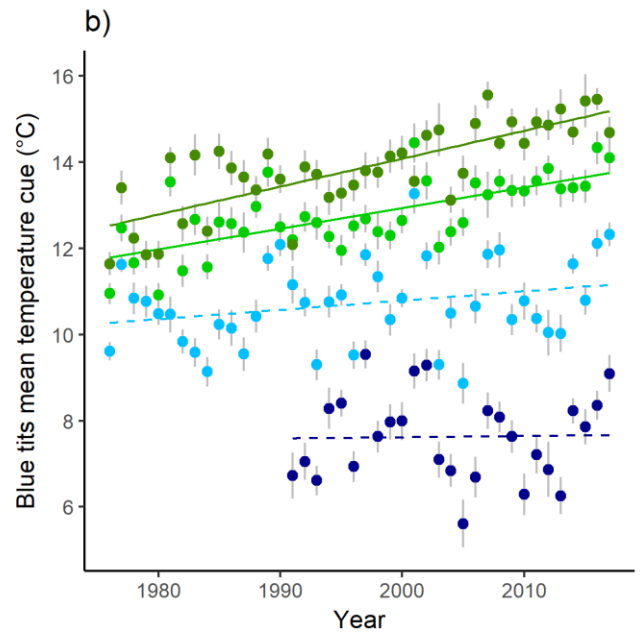
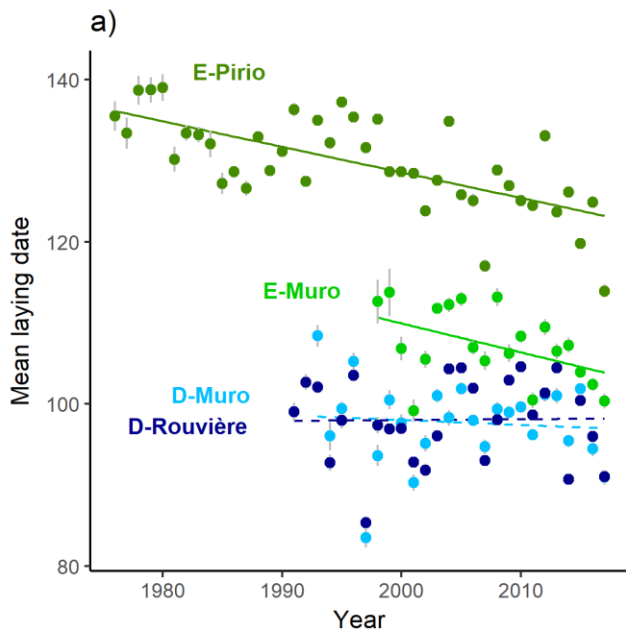
762 Summarized diagram of the relationships between the environment, cues, and phenotypes in the
763 framework of phenotypic plasticity. The multivariate environment can be used as a cue to initiate a
764 plastic response in an individual (thin black arrows). The focal phenotype (on which selection is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



770

771 *Figure 2*

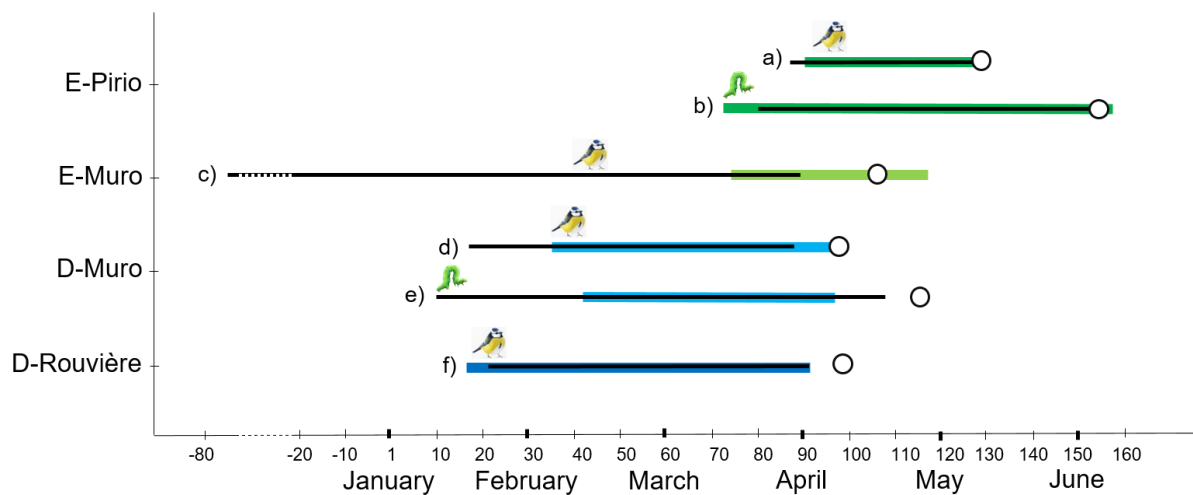
772 a) Temporal trends in annual mean laying dates in the four Blue tit populations (mean \pm se); b)
773 Temporal trends in mean temperature (in $^{\circ}\text{C} \pm$ se) for the cue windows used by each population; c)
774 Blue tit reaction norms: annual mean laying date (\pm se) as a function of the estimated cue (in $^{\circ}\text{C} \pm$ se);
775 d) Caterpillar reaction norm (only for E-Pirio and D-Muro): annual caterpillar peak date as a function
776 of the estimated cue ($^{\circ}\text{C} \pm$ se); e) Cue reliability for blue tits measured as the correlation between the
777 caterpillar peak date and the cue (table S7); f) Synchrony between blue tits and caterpillars illustrated
778 as the correlation between mean laying date of blue tits (\pm se) and caterpillar peak date (see table S8).
779 In all panels, the “Evergreen” sites are in green (dark green for E-Pirio, light green for E-Muro), and
780 “Deciduous” sites are in blue (dark blue for D-Rouvière, light blue for D-Muro). All dates are ordinal
781 dates with 1= 1st January. In panel f, the red dashed line represents the expected optimal relationship
782 between laying date and caterpillar date. In some cases, error bars are not visible because they are
783 very small compared to the figure scale.



785

786 *Figure 3*

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



794

795

796 Ethics

797 The blue tit monitoring protocol was approved by the Animal Care and Use committee Languedoc-
798 Rousillon (CEEA-LR-12066) as well as by Regional Institutions (bylaw issued by the Prefecture on
799 15/06/2012 n° 2012167-0003). Captures of breeding birds were performed under ringing permits
800 delivered by the CRBPO (Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris; ringing
801 permit number 1907 to AC, program permit number 369).

802 Data accessibility

803 Data will be available from the Dryad Digital Repository after acceptance of the article.
804 Meteorological data are accessible from <https://donneespubliques.meteofrance.fr/>

805 Author's contributions

806 C.T., A.C., L.M.C., S.B. designed the research. A.C., C.T. and S.B. (and many other contributors) collected
807 field data. S.B. conducted statistical analyses. C.T., L.M.C., A.C., and S.B. wrote the paper.

808 Competing interests

809 We have no competing interests.

810 Acknowledgments

811 We thank Ally Phillimore and an anonymous reviewer for their constructive comments on the
812 manuscript. We also thank Anssi Laurila, Samuel Caro and Pierre-Yves Henry for discussions, and
813 Martijn van de Pol and Liam Bailey for useful advice about windows comparison. We thank all the
814 people who helped maintain the study site and conduct the blue tit monitoring, in particular Jacques
815 Blondel, Philippe Perret, Christophe de Franceschi, Annick Lucas, Pablo Giovannini, Samuel Caro, Claire
816 Doutrelant and Marcel Lambrechts.

817 Funding

818 This project was funded by the CNRS and the European Research Council (Starting grant ERC-2013-StG-
819 337365-SHE to A.C., and starting grant StG-678140-FluctEvol to L.M.C.).