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1 Climate-induced phenology shifts linked to range
2 expansions in species with multiple reproductive cycles
3 per year

4
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26

27 **Advances in phenology (the annual timing of species' life-cycles) in response to**
28 **climate change are generally viewed as bioindicators of climate change, but have not**
29 **been considered as predictors of range expansions. Here, we show that phenology**
30 **advances combine with the number of reproductive cycles per year (voltinism) to**
31 **shape abundance and distribution trends in 130 species of British Lepidoptera, in**
32 **response to ~0.5 °C spring-temperature warming between 1995 and 2014. Early adult**
33 **emergence in warm years resulted in increased within- and between-year population**
34 **growth for species with multiple reproductive cycles per year ($n = 39$ multivoltine**
35 **species). By contrast, early emergence had neutral or negative consequences for**
36 **species with a single annual reproductive cycle ($n = 91$ univoltine species), depending**
37 **on habitat specialisation. We conclude that phenology advances facilitate polewards**
38 **range expansions in species exhibiting plasticity for both phenology and voltinism,**
39 **but may inhibit expansion by less flexible species.**

40

41 **Introduction**

42

43 Climate change is resulting in changes in the size, latitudinal range^{1,2}, and elevational extent³
44 of species' distributions. However, distribution changes are highly variable among species,
45 and rates of polewards expansion often fail to track the climate³⁻⁵. Range expansions are
46 dependent on stable or increasing abundance trends⁶, and hence understanding the effects
47 of climate change on species' abundances is crucial in order to understand variation in range
48 shifts. A potentially-important contributing factor is phenological advancement⁷⁻⁹, with many
49 species now undertaking life-cycle events earlier in the year. However, it is unclear whether
50 such phenology advances are beneficial or detrimental for populations of species¹⁰⁻¹⁴.

51

52 We used British Lepidoptera to examine this question, because long-term phenological,
53 population and distribution data are all available spanning several decades. We focus on two

54 traits in which Lepidoptera can display phenotypic plasticity (whereby environmental cues
55 directly alter the physical or behavioural phenotype of individuals¹⁵): voltinism and
56 phenology. Lepidoptera include species that are obligately univoltine (i.e. all individuals pass
57 a winter in diapause), and species in which every individual makes a plastic developmental
58 'decision' whether to undergo diapause or to directly develop, based on environmental cues.
59 Populations of such species may therefore undergo multiple generations per year depending
60 on the length of the local growing season annually, and in cooler regions may be functionally
61 univoltine.

62

63 Many Lepidoptera have also advanced their phenology, with adults emerging earlier in
64 recent, warmer years¹⁶ because the growth rate of immature stages increases at warmer
65 temperatures (although photoperiod may regulate phenology in some species¹⁷). Such
66 phenology advances could be either detrimental or beneficial to species, depending on the
67 outcomes of longer or more favourable growing seasons¹⁸⁻²¹ and potential temporal
68 decoupling from host-plants or natural enemies²²⁻²⁴. Overall, it is currently unclear whether
69 phenology advances will result in increases or declines in annual abundance, and whether
70 species with different life-histories differ in the consequences of phenology advances.

71

72 Here, we show that phenology advances have resulted in increased abundance trends and
73 range expansions in species with multiple reproductive cycles per year (i.e. multivoltine
74 species). Early emergence permits the number of individuals of these species to increase
75 faster in second and subsequent generations within the year, generating positive overall
76 abundance and distribution trends. However, phenology advances do not correlate with
77 abundance trends or range expansions in species with a single annual reproductive cycle
78 (i.e. univoltine species), and are associated with abundance declines in the subset of
79 univoltine species that are also habitat specialists.

80

81 **Results**

82 *Interspecific relationships between phenology and demography*

83 We analysed trends in the phenology, abundance, and distribution of 130 species of
84 Lepidoptera (29 butterflies and 101 moths) for which trends could be robustly estimated over
85 a 20-year period (1995-2014) during which mean spring temperatures warmed by
86 approximately 0.5 °C (Supplementary Figure 1). We compared functionally univoltine
87 species ($n = 91$; defined as those that rarely undergo more than one generation per year
88 anywhere in their British range, e.g. Silver-studded Blue *Plebejus argus*; Figure 1c) with
89 multivoltine species ($n = 39$; those that regularly undergo two or more generations in part or
90 all of their British range, e.g. Small Blue *Cupido minimus*; Figure 1d). Both univoltine and
91 multivoltine species significantly advanced their adult emergence dates over the study
92 period, with the first annual emergence peak for multivoltines (~ 3 days/decade, range -23.8–
93 16.7) advancing significantly faster than univoltines (~ 1.5 days/decade, range -4.8–6.2;
94 Supplementary Table 2).

95

96 We found that phenology advances led to positive abundance trends for multivoltine species,
97 but not for univoltine species (Likelihood Ratio Test (LRT), $\chi^2 = 8.23$, d.f. = 1, $P = 0.004$;
98 Table 1). Multivoltine species showed greater increases in abundance if they had advanced
99 their phenology, but there was no clear relationship between phenology advances and
100 abundance trends among univoltine species (Figure 2). We found that phenology advances
101 did not directly correlate with change in distribution size (LRT, $\chi^2 = 0.07$, d.f. = 1, $P = 0.792$)
102 or change in range margin latitude (LRT, $\chi^2 = 1.29$, d.f. = 1, $P = 0.256$). However,
103 abundance trends were themselves significantly, positively related to trends in both
104 distribution size (LRT, $\chi^2 = 52.3$, d.f. = 1, $P < 0.001$) and range margin (LRT, $\chi^2 = 8.82$, d.f. =
105 1, $P = 0.003$) for all species, regardless of voltinism (Supplementary Figure 2). To test the
106 indirect relationship between distribution and phenology moderated by abundance, we
107 predicted species' abundance trends from our models of the relationship between phenology
108 advances, voltinism and abundance trends (Table 1), yielding an estimate of the specific
109 component of abundance change that was driven by phenology advances. We found that

110 these model-predicted abundance trends were significantly related to trends in range margin
111 (LRT, $\chi^2 = 5.16$, d.f. = 1, $P = 0.023$), but marginally not distribution size (LRT, $\chi^2 = 3.17$, d.f.
112 = 1, $P = 0.075$). Hence, we conclude that climate-linked shifts in range margin latitudes are
113 indirectly driven by phenology advances, mediated by effects of abundance (Figure 1).
114 These results were robust to phylogeny, to the designation of some species ($n = 36$) whose
115 voltinism patterns were hard to categorise because they have both univoltine and bivoltine
116 populations in Britain and/or mainland Europe, and to our selection of a relatively short 20-
117 year study period (Tables S3-4).

118

119 *Intraspecific relationships between phenology and demography*

120 To understand whether links between phenology advances and abundance trends were
121 causally related both between and within species, or solely correlated at species-level, we
122 calculated trends in phenology and abundance independently for every population (i.e.
123 recording site) in our dataset ($n = 3$ -104 populations per species) and assessed the
124 intraspecific relationships between the two variables at population-level. These analyses
125 confirmed our previous findings, revealing that multivoltine species showed greater
126 increases in abundance in populations that had advanced their phenology, but no such
127 effect in populations of univoltine species (Table 2). Among multivoltine species, 8/39
128 (20.5%) species showed individually significant, positive population-level relationships
129 between phenology advances and abundance trends (eight times higher than the two-tailed
130 chance expectation), no species displayed a significant negative relationship, and the
131 average relationship across all 39 multivoltine species was significantly positive (LRT, $\chi^2 =$
132 57.50, d.f. = 1, $P < 0.001$; Figure 2d). These positive population-level relationships were
133 evident in both the subset of multivoltine species that are, on average, increasing nationally,
134 as well as the multivoltine species that are declining nationally (Supplementary Figure 3),
135 suggesting that phenology shifts could be locally adaptive by limiting population-level rates
136 of decline in species that are declining nationally. By contrast, among univoltine species,
137 only 3/91 (3.3%, c.f. null expectation of 2.5%) species displayed a significant positive

138 relationship between phenology advance and abundance trends at population-level, with
139 3/91 (3.3%) showing a negative relationship, and the average relationship across all 91
140 univoltine species was not significantly different from zero (Figure 2c).

141

142 *Annual phenological variation*

143 To gain insight into why multivoltine species benefitted from phenology advances, but
144 univoltine species did not, we examined the effects of annual variation in emergence dates
145 on a sequence of Lepidopteran life-cycle events (Table 1). Both univoltine and multivoltine
146 species emerged significantly earlier in years when spring temperatures were warmer
147 (Figure 3a), but with a significantly larger effect in multivoltine than univoltine species. Earlier
148 emergence in multivoltine species was associated with greater population growth between
149 the first and second generations (Figure 3b), and consequently, earlier emergence by
150 multivoltine species led to increased abundance, in both years t and $t+1$ (Figure 3c-d).
151 However, earlier emergence in univoltine species was significantly associated with reduced
152 abundance in year $t+1$ (Figure 3).

153

154 *Role of habitat specialisation*

155 Habitat availability can be an important predictor of range expansion^{6,25}, and we found that
156 including habitat specialisation in our statistical models revealed further distinctions between
157 habitat specialist species ($n = 21$) and wider-countryside generalist species ($n = 109$). Most
158 notably, phenology advances led to abundance declines among univoltine habitat
159 specialists, but there was no relationship among univoltine wider-countryside generalists
160 (Table 1). After refining our models by including habitat specialisation, species' model-
161 predicted abundance trends were significantly related to trends in distribution size (LRT, $\chi^2 =$
162 14.49, d.f. = 1, $P < 0.001$) as well as range-margin latitude (LRT, $\chi^2 = 5.90$, d.f. = 1, $P =$
163 0.015).

164

165 **Discussion**

166

167 Our results demonstrate that positive demographic responses to climate change are only
168 evident in the subset of species which are multivoltine and have advanced their phenology,
169 thereby showing plasticity in both phenology and voltinism. This combination provides a
170 pathway by which benefits can be gained from earlier emergence in warmer springs, yielding
171 increasing abundance in the second annual generation associated with these phenology
172 advances. Such benefits are not experienced by the subset of multivoltine species that have
173 not advanced their phenology, whilst univoltine species are constrained to develop through
174 only one generation per year (by innate factors or by climate, in the case of species that are
175 functionally univoltine under cool British conditions, even if they have the potential to be
176 multivoltine elsewhere).

177

178 Phenology advances are associated with declines in abundance among univoltine habitat
179 specialists, which might experience direct costs associated either with phenology advances
180 themselves, or with warmer winter or spring temperatures (e.g. extended periods of delayed
181 sexual maturity²⁷, diapause, or larval²⁸ or adult aestivation²⁹), before suitable conditions for
182 emergence/reproduction arise the following year. These factors may potentially lead to
183 greater reproductive success in years of later emergence (i.e. phenology delays; Figure 3c-
184 d), even though abundance was higher in individual years of earlier emergence (Table 1). In
185 particular, univoltine habitat specialists (whose host-plant niche is often narrow) may
186 experience phenological mismatches with host-plants³⁰, from which generalist species may
187 be buffered. Host-plants may also be advancing their phenology⁸, so it is possible that such
188 univoltine species might have declined even more without phenology advances. As with
189 plasticity in both phenology and voltinism, spatiotemporal variation in habitat and host-plant
190 associations (and hence specialisation) may also include an element of plasticity, whereby
191 individuals can make behavioural decisions to occupy favourable habitats under specific
192 environmental conditions²⁶; but genotypic diversity among populations and individuals may
193 also contribute to habitat and host-plant selection.

194

195 Despite this, we found no significant differences between univoltine and multivoltine species
196 in their overall abundance or distribution trends, potentially because emergence dates did
197 not advance for all multivoltine species, or for all populations of species that have advanced
198 their phenology overall (Supplementary Figure 3). Identifying the factors that drive or
199 constrain phenology advances will therefore be important. These factors might include local
200 adaptation to photoperiod signals^{31,32}, physiological barriers limiting increases in
201 development rate³³, or availability of suitable habitat or microclimatic conditions to otherwise
202 mitigate the effects of climate change through behavioural responses²⁶. In particular,
203 understanding drivers of detrimental phenology advances in populations of univoltine habitat
204 specialists may be important for their conservation, particularly as this group includes many
205 UK conservation-priority species (e.g. High Brown Fritillary *Argynnis adippe*). Our findings
206 show that the effects of climate-driven phenology advances have the potential to be
207 detrimental in univoltine habitat specialists, but some of these species might benefit from
208 gaining a second generation in Britain under future climate change (those which are
209 functionally univoltine in Britain but have the capacity to be multivoltine; e.g. *P. argus*, Figure
210 1). This may be more likely to occur if emergence dates continue to advance in much
211 warmer years. Given that there is not a consistent outcome of phenology advances among
212 species, strategies for conservation management under climate change should employ
213 approaches that generate local conditions for a diverse range of phenological strategies
214 across species at different trophic levels, such as approaches that maximise habitat,
215 microclimate and host-plant heterogeneity^{34,35}.

216

217 In conclusion, our study shows that range expansions in response to climate change^{3,5} are
218 influenced by phenology advances, through their effect on population abundance. However,
219 the nature of the relationship between phenology advances and abundance depends on life-
220 cycle plasticity in voltinism. Species with multiple reproductive cycles per year may be able
221 to capitalise on warmer springs by advancing their phenology, thus increasing the total

222 number of reproductive cycles per year^{19,20} and/or increasing reproductive success within
223 each cycle¹⁸, with consequent population growth and expanding distributions. By contrast,
224 univoltine habitat specialists experience apparent costs when they advance their phenology,
225 resulting in population declines and retracting distributions, although these costs are not
226 evident in univoltine generalists. These variable demographic consequences of phenology
227 advances may help to explain why some species' distributions have not expanded quickly
228 enough to track temperature changes^{3,5}.

229

230

231 **Methods**

232

233 **Datasets**

234

235 We used data obtained by four recording schemes to assess changes in phenology,
236 abundance, distribution size and latitude of the northern range margin over a 20-year period
237 (1995-2014). Specifically, we used data from two population-monitoring schemes that
238 contained abundance records, with high spatial and temporal resolution over many years for
239 fixed sampling locations, to measure phenology and abundance (butterflies: the United
240 Kingdom Butterfly Monitoring Scheme (UKBMS); moths: the Rothamsted Insect Survey
241 (RIS) Light-Trap Network). We also used data from two distribution recording schemes that
242 contained annual presence records summarised at hectad (10 × 10 km) level for the whole
243 of Great Britain to measure distribution size and range margin (butterflies: Butterflies for the
244 New Millennium (BNM); moths: the National Moth Recording Scheme (NMRS)).

245

246 In the UKBMS, data is collected annually over a 26-week period (1st April - 29th
247 September). Weekly transects are walked along a fixed route, following a standard method³⁶
248 to count the abundance of each species present. In the RIS, night-flying and crepuscular

249 moths are attracted to a 200 W tungsten bulb installed within a standard light-trap design,
250 operated in the same location on every night of the year between dusk and dawn³⁷. Sampled
251 moths are collected daily or every few days, and the abundance of each species counted.
252 Thereby, both recording schemes generate abundance data for a fixed site, with a temporal
253 resolution of one week or better, over a long period of time (in many cases continuously for
254 2-4 decades). This allows for reliable estimation of changes in site-level abundance and
255 phenology over time.

256

257 In both the BNM and the NMRS, data are contributed with high spatial resolution by
258 volunteer recorders as a form of citizen science, and summarised to produce annual
259 distribution maps at hectad resolution. The BNM was established in 1995³⁸ but builds upon a
260 previous atlas project³⁹, whilst the NMRS officially commenced in 2007; both recording
261 schemes include historical records dating back to the 17th and 18th centuries, respectively.
262 Both schemes comprise mainly records of adult Lepidoptera, either observed during the
263 daytime or captured in light-traps, but also include other recording methods (e.g. pheromone
264 lures) and records of immature life-stages. The annual number of hectad-level species
265 presences recorded by the BNM has remained roughly stable in each year since its
266 commencement in 1995 (with fewer records from earlier years), despite growth in the total
267 number of records submitted to the scheme. Both the number of hectad-level species
268 presences recorded by the NMRS, and the number of records submitted, continue to grow⁴⁰.
269 Not all datasets had been updated beyond 2014 at the time of analysis; therefore, we
270 selected the 20-year study period 1995-2014 in order to contain the maximum informational
271 content across the four datasets.

272

273 **Data selection**

274

275 To obtain consistent estimates of variables across datasets, unbiased by increased
276 recording in later years, we restricted each dataset according to uniform criteria for both

277 butterflies and moths. We grouped subspecies at specific level by reference to a recent
278 checklist of British Lepidoptera⁴¹, and treated species complexes as a single taxonomic
279 entity equivalent to one species (the only such aggregate included our final dataset was
280 Common/Lesser Common Rustic *Mesapamea secalis/didyma*). We initially excluded from
281 the study: (i) species that were obligatory migrants, or for which a substantial proportion of
282 records represent immigrant individuals; and (ii) species for which new methods of recording
283 have been developed within the study period (e.g. Sesiidae, now mainly recorded using
284 pheromone lures).

285

286 For the population monitoring schemes, we first restricted each dataset to include a
287 population (defined as one species at one transect/trap location) in each year only if (i) there
288 were at least 10 recording events in that year during which any species was recorded (even
289 if the focal species was not) and (ii) the focal species was itself recorded during at least
290 three of those recording events. For all remaining combinations of population × year, we
291 fitted a generalized additive model (GAM) to all abundance records (including zeroes), with a
292 Poisson error distribution and using a Restricted Maximum Likelihood approach to
293 estimation of smoothing. We followed a series of logical steps (Supplementary Figure 7) to
294 exclude GAMs which were deemed not to have fitted successfully; GAMs were discarded if
295 their predicted abundance on 1st January was > 1, or failed to reach at least one peak
296 (defined as a day on which model-predicted abundance was greater than both the preceding
297 and following days) before 31st December. These rules excluded populations in each year
298 from which first-generation individuals were recorded on the first or last day of recording
299 (UKBMS: April - September; RIS: January - December), preventing reliable estimation of
300 phenology. We then further restricted the dataset to include only populations that had
301 successfully-fitted GAMs for at least (i) 15 years of the 20-year study period, and (ii) one
302 year in the period 1980-1990 (to exclude sites that were recently colonised at the start of the
303 study period, potentially influencing abundance trends⁴²). Finally, from the remaining
304 populations, we included only species for which (i) at least three populations matched the

305 criteria above, and (ii) records existed in each of the 20 years of the study period from at
306 least one population, even if no single population had been recorded for 20 years. For some
307 butterflies which may be active before the commencement of UKBMS monitoring (e.g.
308 Peacock *Aglais io*), a sufficient proportion of GAMs fitted unsuccessfully that too little data
309 remained for the species' inclusion in the study, despite being common and widespread;
310 others (e.g. Orange-tip *Anthocharis cardamines*) are represented by only a few populations.
311 It is possible that these early-emerging species may have experienced some of the largest
312 phenology advances²².

313

314 For the distribution recording schemes, we first restricted each dataset separately to include
315 only hectads that were heavily-recorded, following previous studies^{1,2}, in order to be
316 confident that species not recorded in a hectad were truly absent. Specifically, we first
317 excluded hectads unless they had a presence record (of any species) in both the first and
318 second halves of the study period (i.e. 1995-2004 and 2005-2014 respectively). For each
319 remaining hectad, we calculated annual species richness of the hectad itself and of the 100
320 nearest neighbouring hectads combined (i.e. the surrounding region), and from these, the
321 annual percentage of regional species richness that had been recorded in each hectad. We
322 excluded all hectads for which the median annual percentage of regional species richness
323 recorded (across all 20 years) was < 25%. This left 1639 heavily-recorded hectads in the
324 BNM dataset and 475 heavily-recorded hectads in the NMRS dataset (Supplementary Table
325 1). Using distributions from within the remaining hectads, we excluded: (i) species which had
326 been recorded in < 20 heavily-recorded hectads across the full study period (e.g. Lulworth
327 Skipper *Thymelicus acteon*, Dark Bordered Beauty *Epione vespertaria*), as these
328 distributions were too small to reliably estimate change in distribution size; and (ii) species
329 for which the mean elevation of all recorded hectads was > 200 m (using elevation data from
330 Farr *et al.*⁴³; e.g. Scotch Argus *Erebia aethiops*, Scotch Annulet *Gnophos obfuscata*), as
331 responses to climate change in upland species might involve elevational shifts rather than
332 changes in distribution or abundance³. Finally, we assessed which species reached their

333 range margin > 100 km south of the northernmost point of mainland Great Britain (latitude
334 58° 38' 14" N), following Hickling *et al.*¹. We excluded these northerly or ubiquitous species
335 (e.g. Meadow Brown *Maniola jurtina*, Dark Arches *Apamea monoglypha*) from a subset of
336 data for the specific analysis of range margin trends, but retained them in the main dataset.

337

338 The remaining, final dataset contained 130 species for which we had retained reliable data
339 from both population and distribution recording schemes, including 29 butterflies and 101
340 moths, which represents approximately 50% and 15% respectively of all resident British
341 butterfly and macro-moth species (moths are probably more likely to go unrecorded at a site
342 in any given year, despite continuous presence, leading to a lower proportion of populations
343 meeting the requirement for having been recorded in 15/20 years). Of these species, 12
344 butterflies (41%) were habitat specialists, but only 9 moths (9%), probably because UKBMS
345 transects are more likely to be established on priority habitats occupied by habitat specialists
346 (e.g. calcareous grassland) than RIS traps. For the population monitoring schemes, our
347 dataset comprised 425,087 abundance records of 3,484,983 individual Lepidoptera,
348 spanning 1,685 populations at 141 different sites (Supplementary Table 1). From the
349 distribution recording schemes, it comprised 913,037 hectad-level presence records from
350 heavily-recorded hectads.

351

352 **Generation of variables**

353

354 We generated two categorical variables to describe each species' life-cycle plasticity, by
355 reference to commonly-used identification resources^{44–48}. First, we described species'
356 functional voltinism: species were classified as univoltine if they rarely or never undergo
357 more than one generation per year anywhere in any part of their range within Great Britain,
358 even if they have the capacity to do so elsewhere in their global range (e.g. Silver-studded
359 Blue *Plebejus argus*, Figure 1c), or otherwise multivoltine if they regularly undergo a
360 substantial second generation in any part of their British range (e.g. Small Blue *Cupido*

361 *minimus*, Figure 1d). In total we categorised 91 species as univoltine and 39 species as
362 multivoltine. We additionally recorded whether this categorisation was considered to be
363 representative of all populations in all years. Second, we described species' habitat
364 specialisation: species were classified either as habitat specialist or wider-countryside
365 generalist. Butterfly assignments were drawn directly from an established set of habitat
366 specialisation classifications⁴⁸, and moths were assigned by expert opinion, using the same
367 criteria (Supplementary Table 5). In total we categorised 109 species as wider-countryside
368 generalists and 21 species as habitat specialists. The majority of habitat specialist species
369 were butterflies, despite most species in the overall dataset being moths (Supplementary
370 Table 6), reflecting a greater tendency for UKBMS transects to be established in protected
371 areas (with associated habitat specialists)⁴⁹ than for RIS traps.

372

373 For all species, we generated four annual variables: first-generation emergence date
374 (phenology), abundance, occupied distribution size and range margin latitude. Phenology
375 and abundance were calculated separately for every population, using population monitoring
376 scheme data. Single national values for distribution and range margin were calculated in
377 each year, using distribution recording scheme data.

378

379 Abundance of each population was the total number of individuals recorded in each year,
380 divided by the number of recording events (transects walked or trap samples collected) in
381 that year, and therefore represented mean abundance per recording event. To estimate the
382 annual phenology of each population, we used the GAM fitted to abundance data (as
383 described above). We used a series of logical steps (Supplementary Figure 4) to identify the
384 most plausible date for the first peak in abundance; phenology therefore refers to the
385 emergence of the first generation in each year, regardless of each species' voltinism. We
386 used this approach to estimating phenology because it is more robust to the influence of
387 variation in abundance than other approaches (e.g. first appearance date)⁵⁰.

388

389 For multivoltine species, we additionally estimated the ratio between abundance in the first
390 generation and all subsequent generations for multivoltine species (intergenerational
391 abundance ratio). We used logical steps again (Supplementary Figure 4) to identify the most
392 plausible date for the trough of minimum abundance between the first and second
393 generations, and calculated the ratio between the sum of daily abundances (predicted from
394 the GAM) before and after this trough.

395

396 To calculate each species' annual distribution size, we calculated the number of heavily-
397 recorded hectads in which the focal species was recorded, and the total annual number of
398 heavily-recorded hectads in which any species was recorded. From these, we calculated the
399 percentage of the maximum possible distribution size that was occupied by the focal species
400 in each year (distribution). This accounts for an increase in the number of heavily-recorded
401 hectads that were recorded in later years of the study period. To calculate the annual latitude
402 of each species' range margin, we identified the 10 most northerly occupied hectads
403 (including all hectads that were tied for 10th place) in each year, and calculated the mean
404 northing of these hectads.

405

406 We then calculated rates of change over 20 years in phenology, abundance, distribution and
407 range margin for each species (Supplementary Data 1). Change in distribution was
408 calculated as the slope of a linear regression between distribution and year, and was
409 therefore the annual change in the percentage of hectads that were occupied. Likewise,
410 change in range margin was calculated as the slope of a linear regression between range
411 margin and year, and was the annual northwards advance in the latitude of the range
412 margin, in km (a negative value indicated a southwards retraction). Change in abundance
413 was calculated as the slope of a generalised linear mixed-effects model (GLMM) between
414 the logarithm of mean abundance (per recording event) and year, with site as a random
415 effect and a Gaussian error distribution, and was therefore the annual change in abundance
416 as the logarithm of the odds-ratio. Finally, change in phenology was calculated as the slope

417 of a GLMM between phenology and year (with the same structure as above), and was
418 therefore the annual change in phenology in days. We reversed the sign of this slope, so
419 that a positive number indicated an advance in phenology (emerging earlier in the year). For
420 the variables generated from population monitoring scheme data (phenology advance and
421 abundance trend), we additionally calculated the rate of change separately for each
422 population. These were calculated as above, except that they were the slope of a linear
423 regression rather than a GLMM. For change in abundance and change in phenology, we
424 also calculated rates of change (as above) over the full time period of available data for each
425 species (31-44 years per species, between 1973 and 2017).

426

427 We tested the relevance of our species-level trends, based on a subset of data-rich
428 populations, to national trends, using abundance as a case study. Our estimated abundance
429 trends were significantly correlated to long-term national abundance trends from the
430 UKBMS⁵¹ (1967-2016; F-test, adjusted $R^2 = 30.0\%$, $F = 12.97$, $P = 0.001$) and RIS⁵² (1976-
431 2016; F-test, adjusted $R^2 = 31.2\%$, $F = 46.29$, $P < 0.001$). For the UKBMS, we also
432 calculated national trends for the study period only; these correlated even more strongly with
433 our estimated trends (1995-2014; F-test, adjusted $R^2 = 49.3\%$, $F = 28.25$, $P < 0.001$).

434

435 Finally, for each of the 141 sites from which we had population monitoring scheme data
436 included in the final dataset, we calculated annual spring temperatures, as the number of
437 growing degree days above a 5 °C threshold (GDD5) from 1st March to 31st May inclusive,
438 for the 5 × 5 km grid square containing the site centroid, using gridded data from the UK
439 Meteorological Office⁵³.

440

441 **Statistical analysis**

442

443 We used GLMMs to test relationships between change in phenology, abundance,
444 distribution and range margin. In each case, we initially constructed two models on the full

445 dataset ($n = 130$ species), testing the fixed effects respectively of a two-way interaction
446 between the independent variable and voltinism, and of a three-way interaction between the
447 independent variable, voltinism and habitat specialisation class. We used Gaussian error
448 distributions because our dependent variables were all approximately normally-distributed
449 (Supplementary Figures 5-7), and included taxon group (butterfly or moth) as a random
450 effect (allowing random intercepts). We tested significance of fixed effects in each model
451 using Likelihood Ratio Tests; where interaction terms were non-significant, we retested
452 models with them removed and their constituent parts included, first as two-way interaction
453 terms and if still non-significant, as single main effects. If the final model contained a
454 significant interaction term, we split the dataset into subcategories as indicated by the
455 interaction term, and tested whether the relationship between independent and dependent
456 variables was significantly different to zero separately for each subcategory except
457 multivoltine habitat specialist species, because the subset of data for this category was too
458 small ($n = 3$ species).

459

460 Using this approach, we first tested the interspecific effect of change in phenology on all
461 three main dependent variables, calculated at species-level: change in abundance,
462 distribution, and range margin. We additionally repeated these analyses using two subsets
463 of data, first excluding species for which the voltinism classification might not be
464 representative of some populations, and second only including such species. Next, we
465 repeated the initial analyses, using a three-level categorical variable to describe voltinism
466 (obligate univoltine, functionally univoltine, and multivoltine), where species which have the
467 capacity to be multivoltine but are functionally univoltine throughout Britain were assigned to
468 a separate category from species which are univoltine throughout their global range. Finally,
469 we retested the relationship between change in phenology and change in abundance, using
470 trends in each variable calculated over the full time period of available data.

471

472 Next, we tested the direct effects of change in abundance on change in distribution and
473 range margin, because earlier studies suggest that distribution expansions are dependent on
474 stable or positive abundance trends⁶. We also hypothesized that the effects of change in
475 emergence date might indirectly explain change in distribution, mediated by change in
476 abundance, so we used our earlier models to predict the expected change in abundance of
477 each species, based on (i) its voltinism and observed change in phenology, and (ii) voltinism,
478 habitat specialisation, and observed change in phenology. We tested the relationship
479 between these model-predicted changes in abundance, and change in distribution and range
480 margin.

481

482 To check for the possible influence of phylogenetic relatedness on our results, we re-tested
483 these interspecific relationships using phylogenetic generalized least squares (PGLS)
484 models. For this purpose, we constructed a phylogeny of all 130 study species
485 (Supplementary Data 2), using the marker *cytochrome c oxidase subunit I* (COI). We visually
486 confirmed that (i) relationships between families within our phylogeny broadly matched a
487 recent published phylogeny of the Lepidoptera⁵⁴ and (ii) congeneric species were always
488 grouped in monophyletic taxa within our phylogeny.

489

490 Thirdly, we tested the intraspecific effect of change in phenology on change in abundance,
491 calculated at population-level, using species as a random effect in place of taxon group.
492 Finally, we used the annual estimates of spring temperature, phenology, mean abundance
493 per recording event, and intergenerational abundance ratio, to conduct several further tests,
494 using the same approach as above except with species and year as crossed random effects.
495 When analysing mean abundance and the intergenerational abundance ratio as dependent
496 variables, we used the logarithm of each variable. Specifically, we analysed: (i) the effect of
497 spring temperature upon phenology; and the effect of phenology upon (ii) mean abundance
498 in the same year and (iii) in the following year; and (iv) the intergenerational abundance ratio

499 (for multivoltine species only, because this variable could not be estimated for univoltine
500 species).

501

502 All statistical analyses were conducted in R version 3.5.0⁵⁵, except construction of the
503 phylogeny for PGLS, which was conducted in Geneious version 11.1.4⁵⁶. We used the
504 following R packages: mgcv⁵⁷ to fit GAMs, lme4⁵⁸ to construct and test GLMMs, caper⁵⁹ to
505 construct and test PGLSs, ggplot2⁶⁰ to prepare figures, and blighty⁶¹ to plot maps of the UK
506 shown in Figure 1.

507

508 **Data availability**

509

510 Datasets were obtained respectively from the UKBMS, Rothamsted Research (RIS) and
511 Butterfly Conservation (BNM and NMRS), and may be requested from the same sources.

512

513 **Code availability**

514

515 All R scripts, from initial processing of datasets to final analyses, are archived online at
516 Zenodo (doi: [10.5281/zenodo.3351514](https://doi.org/10.5281/zenodo.3351514)).

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518

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534 **Author contributions**

535

536 This study was instigated by C.J.M., C.D.T. and J.K.H. The study was primarily designed by
537 C.J.M., C.D.T., D.B.R. and J.K.H., in discussion with M.A.B., J.R.Be, T.B., J.R.Br, R.F.,
538 G.M., I.M., P.J.P., R.R., I.S. and R.V. The statistical analysis was conducted by C.J.M.,
539 using data provided by J.R.Be, R.F. and D.B.R.; and C.J.M. prepared the first draft of the
540 manuscript. The study forms part of a wider program of research which was originally
541 designed by M.A.B., J.R.Be, J.R.Br, C.D., R.F., K.G., J.K.H., A.A.H., G.M., S.N., D.B.R., I.S.,
542 C.D.T. and C.W.W. All authors contributed substantially to revising the manuscript.

543 **Competing interests**

544

545 The authors declare no competing interests.

546

547 **Materials & Correspondence** should be addressed to C.J.M.

548

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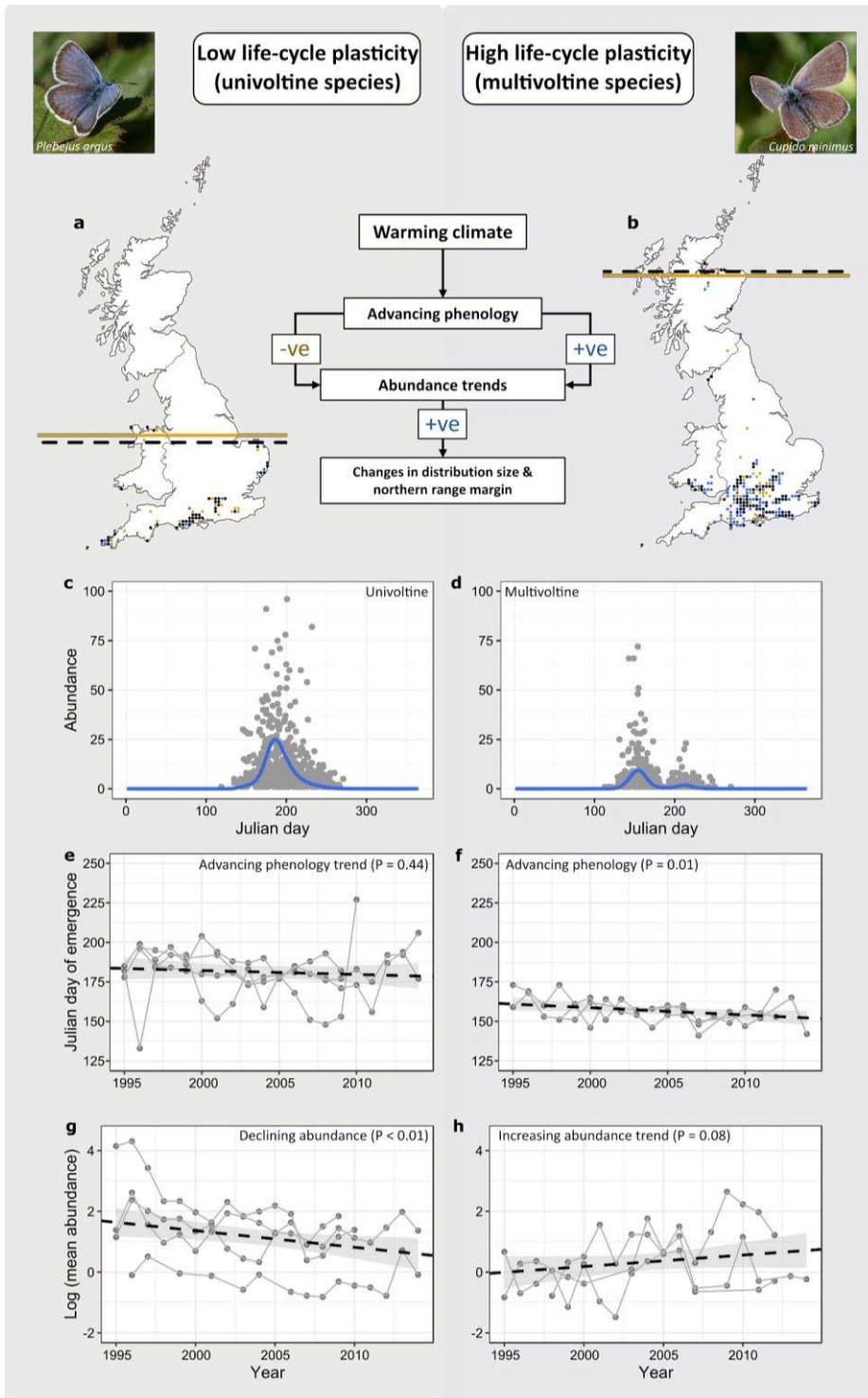
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685



689 **Figure 1| Effects of phenology advances on abundance and distribution trends**

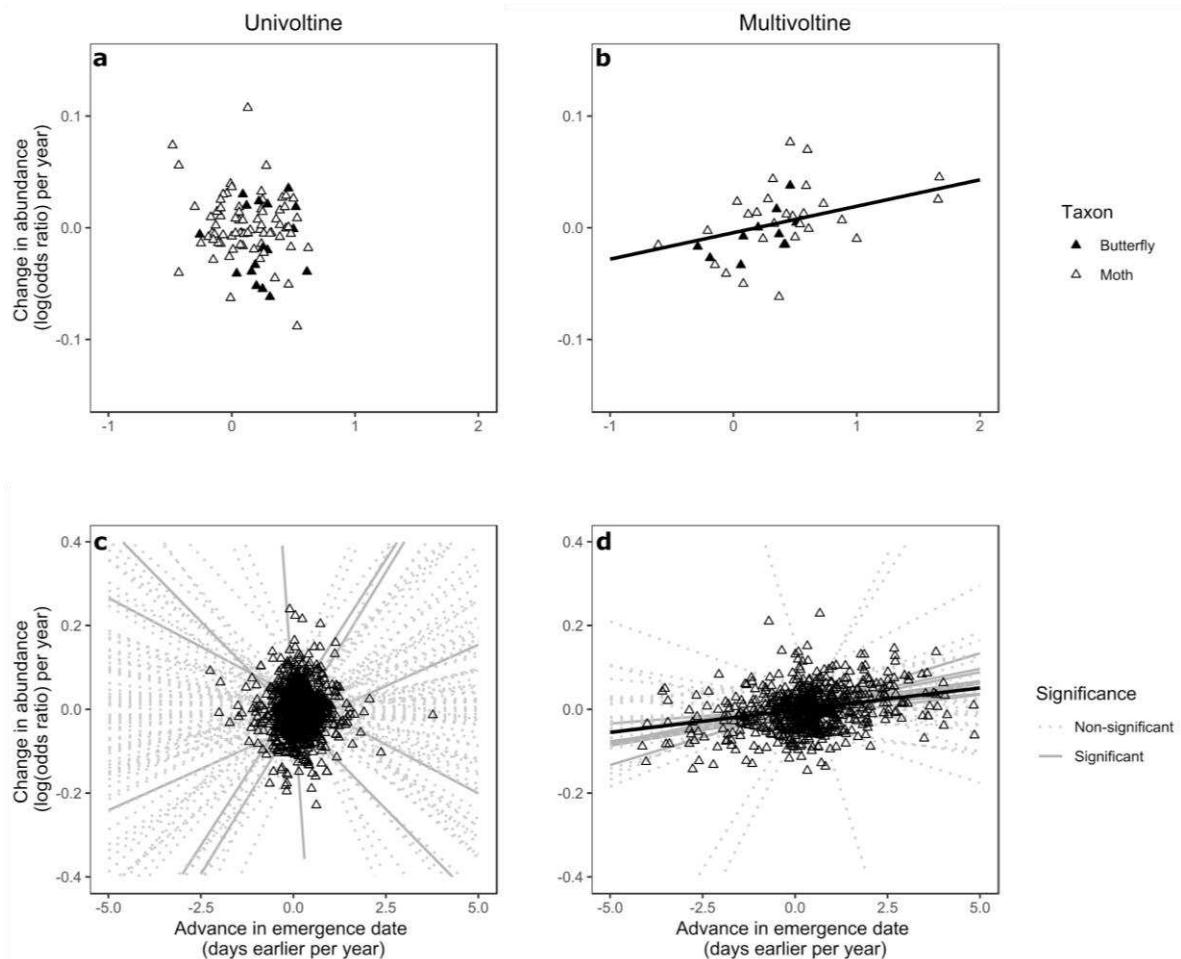
690 **depend on voltinism, illustrated with example species.** The flow chart describes the

691 main conclusions of this study: climate-driven phenology advances have a positive effect on

692 abundance trends in multivoltine species, but a neutral or negative effect on abundance
693 trends in univoltine species (depending on habitat specialisation). In turn, abundance trends
694 have a positive effect on trends in distribution size and northern range margin, regardless of
695 voltinism. Trends in emergence date, abundance, distribution size, and northern range
696 margin are depicted for two butterflies: Silver-studded Blue *Plebejus argus*, and Small Blue
697 *Cupido minimus*. **a,b**, *P. argus* has retracted in distribution size (-0.2 %/yr) and range margin
698 (-1.8 km/yr), whereas *C. minimus* has expanded in distribution size (1.3 %/yr) and range
699 margin (7.4 km/yr). Distribution size depicted as no. occupied hectads in 1995-2014 (black
700 circles), 1995-2004 only (orange circles), and 2005-2014 only (blue circles). Range margins
701 are depicted for 1995 (orange lines) and 2014 (dashed black lines). **c,d**, voltinism of
702 univoltine *P. argus* and multivoltine *C. minimus*, shown by observed abundance on transect
703 counts across all sites and years (grey circles; counts >100 omitted) and GAM-fitted curves
704 (blue lines). **e-h**, both *P. argus* and *C. minimus* have advanced their phenology (0.25 days/yr
705 and 0.46 days/yr respectively); *P. argus* has declined in abundance (-5.5 %/yr) but *C.*
706 *minimus* has increased in abundance (3.8 %/yr). Observed peak day of first-generation
707 emergence (**e,f**) and mean abundance per recording event (**g,h**) in each year is shown (grey
708 circles), and points at the same site are connected (grey lines); overall trend across the
709 duration of the study period (Supplementary Data 1) is shown (black dashed line) with 95%
710 confidence intervals (grey shading).

711

712



714

715

716 **Figure 2 | Phenology advances and voltinism drive abundance trends in multivoltine**717 **species.** Advancing phenology correlates with increasing abundance at species- and718 population-level for multivoltine species ($n = 39$), but not univoltine species ($n = 91$). Lines

719 depict model-predicted relationships between phenology and abundance trends, from

720 generalized linear mixed-effects models. **a,b**, points show changes in phenology and

721 abundance over the study period (1995-2014) at species-level for univoltine and multivoltine

722 species respectively. Point colour indicates taxonomic group (butterflies: filled, moths: open).

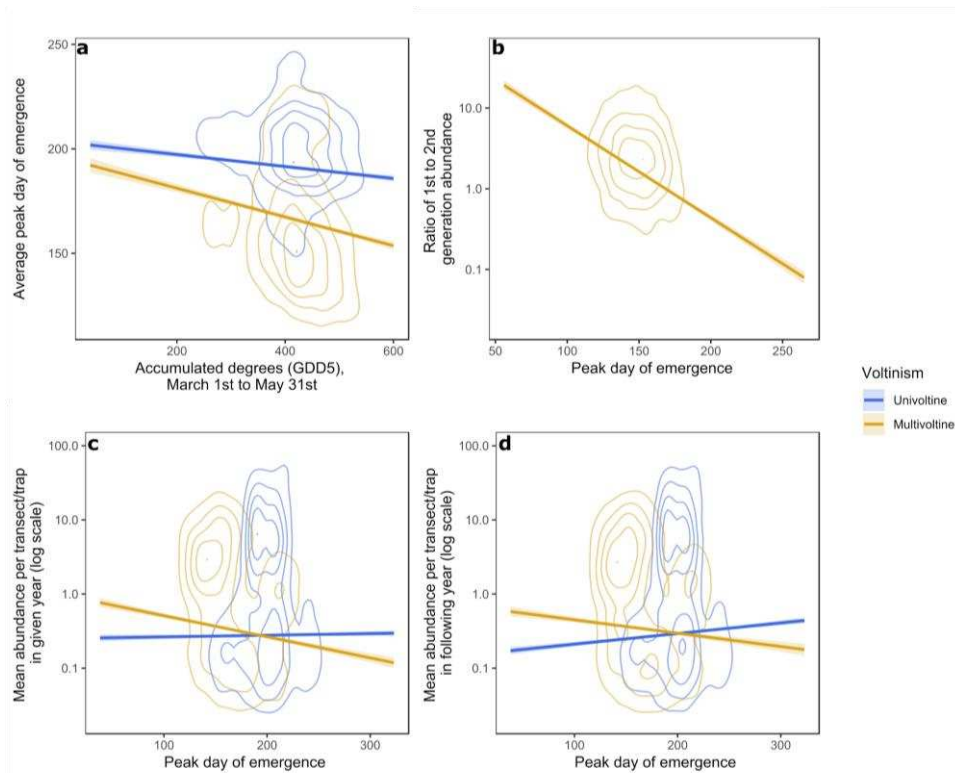
723 Lines show significant ($P < 0.05$) relationships. **c,d**, points show changes in phenology and

724 abundance over the study period at population-level. Grey lines show relationships

725 calculated independently for each species; lines are solid if the relationship is significantly

726 different to zero ($P < 0.05$), or otherwise are dotted. Solid black lines indicate the overall

727 relationship across species, and are plotted only if significant ($P < 0.05$). Among univoltine
728 species (**c**), 3/91 (3.3%) show a significant positive relationship, and 3/91 (3.3%) a
729 significant negative relationship, between phenology and abundance change; the average
730 relationship across species is not significant (Table 2). Among multivoltine species (**d**), 8/39
731 (20.5%) show a significant positive relationship between phenology and abundance change,
732 and none show a significant negative relationship; the average relationship across species is
733 also significantly positive (Table 2).
734



736

737

738 **Figure 3 | Species' responses to annual variation in spring temperature depend on**
 739 **voltinism.** Lines depict model-predicted relationships \pm 95% confidence interval, from
 740 generalized linear mixed-effects models fitted to annual population-level estimates of
 741 emergence date and abundance for all univoltine and multivoltine species. The relative
 742 density of underlying data points is represented by contour lines. Colour indicates voltinism
 743 (blue: univoltine species, orange: multivoltine species). **a**, average peak day of first-
 744 generation emergence is earlier in years with warmer springs (measured as the accumulated
 745 growing degrees-days above 5 °C (GDD5) between 1st March and 31st May) for both
 746 univoltine and multivoltine species, and the effect is significantly stronger for multivoltine
 747 species. **b**, in multivoltine species, abundance in second and subsequent generations is
 748 proportionally larger compared to the first generation (as indicated by a larger
 749 intergenerational abundance ratio) in years when peak day of first-generation emergence
 750 was earlier. **c**, abundance of multivoltine species (measured as the mean number of

751 individuals recorded per transect/trap) is greater in years when peak day of first-generation
752 emergence was earlier, but there is no relationship for univoltine species. **d**, abundance of
753 multivoltine species is greater when peak day of first-generation in the previous year was
754 earlier, but abundance of univoltine species is greater when peak day of first-generation
755 emergence in the previous year was later.
756

757 **Tables**

758

759 **Table 1 | Statistical tests of interspecific relationships between phenology, demography**
 760 **and spring temperature.**

761

		Overall model				Univoltine species: Overall effect			Univoltine habitat specialists			Univoltine wider countryside generalists			Multivoltine species: Overall effect			Multivoltine habitat specialists			Multivoltine wider countryside generalists				
Dependent variable	Independent variable	Interacting covariates	n	AIC	Marginal R ²	Effect size (s.e.)	χ^2 (P)	n	Effect size (s.e.)	χ^2 (P)	n	Effect size (s.e.)	χ^2 (P)	n	Effect size (s.e.)	χ^2 (P)	n	Effect size (s.e.)	χ^2 (P)	n	Effect size (s.e.)	χ^2 (P)	n	Effect size (s.e.)	χ^2 (P)
Change in abundance	Change in emergence date	Voltinism	130	-539.8	0.083	-	8.23 (0.004)	91	-0.02 (0.01)	2.37 (0.124)	-	-	-	-	39	0.02 (0.01)	10.60 (0.001)	-	-	-	-	-	-	-	-
		Voltinism * Class	130	-550.3	0.171	-	4.54 (0.033)	-	-	-	18	-0.09 (0.03)	5.90 (0.015)	73	-0.00 (0.01)	0.08 (0.784)	-	3	-	-	36	0.02 (0.01)	11.25 (0.001)	-	-
Change in occupied distribution		Voltinism	130	588.9	0.004	0.13 (0.49)	0.07 (0.792)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Voltinism * Class	130	582.4	0.058	-	2.83 (0.093)	-	-	-	18	-4.55 (2.44)	3.81 (0.051)	73	-0.62 (0.99)	0.42 (0.517)	-	3	-	-	36	0.49 (0.48)	1.07 (0.301)	-	-
Change in NRM		Voltinism	38	220.1	0.068	1.80 (1.62)	1.29 (0.256)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Voltinism * Class	38	222.0	0.339	-	6.26 (0.012)	-	-	-	9	-1.35 (4.74)	0.10 (0.748)	21	-0.17 (3.49)	0.00 (0.980)	-	2	-	-	6	4.13 (0.62)	9.44 (0.002)	-	-
Change in occupied distribution	Change in abundance	Voltinism	130	587.9	0.178	43.07 (5.42)	52.3 (<0.001)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Voltinism * Class	130	537.4	0.198	-	4.26 (0.039)	-	-	-	18	43.71 (10.58)	12.77 (<0.001)	73	37.12 (7.93)	19.68 (<0.001)	-	3	-	-	36	37.35 (9.55)	13.31 (<0.001)	-	-
Change in NRM		Voltinism	38	220.1	0.233	51.39 (17.48)	8.82 (0.003)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Voltinism * Class	38	212.9	0.414	-	1.94 (0.164)	-	-	-	9	46.49 (30.95)	5.21 (0.113)	21	44.17 (21.81)	4.11 (0.043)	-	2	-	-	6	86.02 (58.71)	1.28 (0.258)	-	-
Change in occupied distribution	Model-predicted change in abundance	Voltinism	130	587.1	0.013	37.70 (21.86)	3.17 (0.075)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Voltinism * Class	130	587.1	0.059	56.20 (14.57)	14.49 (<0.001)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Change in NRM		Voltinism	38	220.5	0.133	152.99 (68.87)	5.16 (0.023)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Voltinism * Class	38	220.5	0.138	89.71 (38.56)	5.90 (0.015)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Annual peak day of emergence	Annual spring temperature (GDD5)	Voltinism	2942	260780	0.066	-	175.14 (<0.001)	18436	-0.03 (0.00)	314.08 (<0.001)	-	-	-	-	10990	-0.07 (0.01)	175.72 (<0.001)	-	-	-	-	-	-	-	-
		Voltinism * Class	2942	260611	0.065	-	0.31 (0.576)	-	-	-	1726	-0.03 (0.00)	52.49 (<0.001)	16710	-0.03 (0.00)	277.68 (<0.001)	-	243	-0.07 (0.01)	13.79 (<0.001)	10747	-0.07 (0.01)	172.43 (<0.001)	-	-
Abundance in given year	Annual peak day of emergence	Voltinism	2978	117.9	0.009	-	117.9 (<0.001)	18571	0.00 (0.00)	0.64 (0.424)	-	-	-	-	11214	-0.01 (0.00)	432.83 (<0.001)	-	-	-	-	-	-	-	-
		Voltinism * Class	2978	145.13	0.053	-	145.13 (<0.001)	-	-	-	1741	-0.02 (0.00)	43.79 (<0.001)	16830	0.002 (0.001)	8.91 (0.003)	-	243	-0.01 (0.00)	6.21 (0.013)	10971	-0.01 (0.00)	429.31 (<0.001)	-	-
Abundance in following year		Voltinism	2602	72934	0.009	-	113.8 (<0.001)	16365	0.004 (0.001)	37.77 (<0.001)	-	-	-	-	26884	-0.004 (0.000)	153.37 (<0.001)	-	-	-	-	-	-	-	-
		Voltinism * Class	2602	72763	0.057	-	5.20 (0.023)	-	-	-	1501	-0.01 (0.00)	20.96 (<0.001)	14864	0.005 (0.001)	62.95 (<0.001)	-	210	-0.009 (0.005)	3.23 (0.072)	9447	-0.004 (0.000)	149.92 (<0.001)	-	-
Intergenerational abundance ratio		Voltinism	6800	23086	0.124	-0.03 (0.00)	737.97 (<0.001)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Class	6800	22351	0.130	-	10.82 (0.001)	-	-	-	-	-	-	-	-	-	-	220	-0.06 (0.01)	41.76 (<0.001)	6580	-0.03 (0.00)	701.77 (<0.001)	-	-

762

763 Relationships were tested (i) between change in emergence date and changes in abundance, occupied distribution,
 764 and northern range margin (NRM), over the full study period (1995-2014); (ii) between changes in abundance (both
 765 as observed, and as modelled by the interaction of change in emergence date, voltinism and habitat specialisation
 766 class) and changes in occupied distribution and northern range margin, over the full study period; and (iii) between
 767 annual spring temperature (GDD5), peak day of emergence, and various descriptors of abundance. An overall
 768 model was constructed in each case and its significance tested using a Likelihood Ratio Test (LRT); therefore d.f.
 769 = 1 for all χ^2 values. If so indicated, this model included voltinism and habitat specialisation class as covariates
 770 interacting with the independent variable in a three-way interaction (retention or exclusion of interaction terms was
 771 determined using AIC values and LRTs); for such models, the dataset was split and separate models constructed
 772 for all four combinations of voltinism and habitat specialisation, in order to test the significance of the relationship
 773 for each set of species to zero. Tests that had statistical significance ($P < 0.05$) are indicated in bold.
 774 Intergenerational abundance ratio could only be estimated for multivoltine species, and therefore analysis of this
 775 variable did not include voltinism as a fixed effect.

776

777 **Table 2 | Statistical tests of intraspecific relationships between phenology and**
 778 **abundance change.**
 779

Dependent variable	Independent variable	Data subset	Interacting covariates	n	AIC	Marginal R ²	Effect size (s.e.)	X ² (P)
Change in abundance	Change in emergence date	Full dataset	Voltinism	1677	-5255.4	0.028	-	9.18 (0.002)
			Voltinism * Class	1677	-5261.4	0.032	-	0.17 (0.679)
		Univoltine species	-	1038	-3182.7	0.000	-0.00 (0.00)	0.02 (0.886)
			Class	1038	-3179.4	0.002	-	0.81 (0.368)
		Univoltine habitat specialists	-	99	-254.9	0.007	0.01 (0.02)	0.59 (0.441)
		Univoltine wider countryside generalists	-	939	-2933.2	0.0001	-0.00 (0.00)	0.13 (0.723)
		Multivoltine species	-	639	-2029.7	0.074	0.01 (0.00)	57.50 (<0.001)
			Class	639	-2086.9	0.084	-	0.006 (0.938)
		Multivoltine habitat specialists	-	14	-32.46	0.002	0.01 (0.04)	0.06 (0.800)
		Multivoltine wider countryside generalists	-	625	-1995.7	0.078	0.01 (0.00)	58.63 (<0.001)
		Multivoltine species (increasing abundance)	-	295	-903.9	0.068	0.01 (0.00)	21.46 (<0.001)
		Multivoltine species (declining abundance)	-	344	-1162.7	0.091	0.01 (0.00)	33.80 (<0.001)

780
 781 An overall model was constructed in each case with species as a random effect, and with voltinism as an interacting
 782 covariate if indicated. Significance of each model was tested using a Likelihood Ratio Test, and tests that had
 783 statistical significance ($P < 0.05$) are indicated in bold.
 784