Climate-driven variation in biotic interactions provides a narrow and variable window of opportunity for an insect herbivore at its ecological margin

James E. Stewart1, Ilya M. D. Maclean2, Gara Trujillo3, Jon Bridle4,5 and Robert J. Wilson1,2,6

1College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PS, UK
2Environment & Sustainability Institute, University of Exeter, Penryn Campus, Exeter TR10 9FE, UK
3International Institute for Industrial Environmental Economics (IIIIEE), Lund University, P.O. Box 196, 22100 Lund, Sweden
4School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK
5Department of Genetics, Evolution, and Environment, University College London, London WC1E 6BT, UK
6Departmento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, Madrid E28006, Spain

Climate-driven geographic range shifts have been associated with transitions between dietary specialism and generalism at range margins. The mechanisms underpinning these often transient niche breadth modifications are poorly known, but utilization of novel resources likely depends on phenological synchrony between the consumer and resource. We use a climate-driven range and host shift by the butterfly Aricia agestis to test how climate-driven changes in host phenology and condition affect phenological synchrony, and consider implications for host use. Our data suggest that the perennial plant that was the primary host before range expansion is a more reliable resource than the annual Geraniaceae upon which the butterfly has become specialized in newly colonized parts of its range. In particular, climate-driven phenological variation in the novel host Geranium dissectum generates a narrow and variable ‘window of opportunity’ for larval productivity in summer. Therefore, although climatic change may allow species to shift hosts and colonise novel environments, specialization on phenologically limited hosts may not persist at ecological margins as climate change continues. We highlight the potential role for phenological (a)synchrony in determining lability of consumer–resource associations at range margins and the importance of considering causes of synchrony in biotic interactions when predicting range shifts.

This article is part of the theme issue ‘Species’ ranges in the face of changing environments (Part II)’.

1. Introduction

Climate change is causing widespread shifts in species’ geographic range limits [1–3]. The extent of such shifts depends on species’ life histories, potential for plastic responses and the quality of available habitat at the expanding margin [4–6]. Habitat availability may itself be determined by the process of range expansion: range shifts have recently been identified as a cause, rather than consequence, of increased dietary generalism at poleward range margins in herbivorous insects [7,8]. However, dietary generalism and incorporation of novel host plants can be transient in such systems, and the mechanisms underlying gain or loss of hosts from insect diets are poorly known [7–9]. Here, we highlight phenological (a)synchrony between insects and unpredictable host

© 2022 The Author(s) Published by the Royal Society. All rights reserved.
resources as a potential mechanism for lability in insect–host associations at range margins.

The phenology of many consumers is closely synchronized with the development and availability of their resources, and their interactions occur within an often narrow ‘window of opportunity’ for the consumer defined by the phenology of both partners [10–14]. For herbivorous insects, the length of the phenological window of opportunity will be partly determined by the specificity of its interaction with the host, the host’s growth form and the broader environmental context. For example, the window of opportunity for herbivory is typically longer on perennials than on short-lived annual plants, the availability of which may be defined by environmental drivers of their germination and senescence [15,16]. The window is also typically longer for polyphagous than obligately monophagous species (which can exploit fewer distinct phenological windows) and for populations inhabiting topographically variable landscapes in which heterogeneous microclimates provide diverse phenological windows [16,17]. Differences in synchrony among nearby microclimates may also cause local variation in host condition, quality and profitability for the herbivore, thereby influencing local patterns of host selection and opportunities for dietary change [7,8,18–20].

Robust evidence is therefore required on the drivers and vulnerability of host–herbivore phenological synchrony (which may scale up to emergent patterns of herbivore range and host shifts [10,19,21]), including the role of microclimate in consumer persistence by potentially buffering asynchrony in biotic interactions [18,20]. Here, we address this knowledge gap, using as an exemplar the brown argus butterfly (Aricia agestis; Lepidoptera: Lycaenidae) at its range margin in the UK. In doing so, we highlight how phenological (a)synchrony could provide an underlying mechanism for apparently high rates of host shifting near range margins [7,22]. Brown argus butterflies have two generations per year; larval offspring of the second generation emerge from mid-August and feed on leaves of the host plant before overwintering [23]. The brown argus’ UK range was historically largely restricted to calcareous grassland where its host, the perennial Helianthemum nummularium (Malvales: Cistaceae; hereafter Helianthemum), grows. However, since the 1990s, the brown argus has undergone a climate-driven range expansion associated with rapid evolution of biotic interactions, including specialization on annual Geraniaceae species (Erodium cicutarium, Geranium dissectum and G. molle; Geranieae: Geraniaceae) mainly in regions beyond the former range limit [21,24–27].

In this study, we test expectations of (a) greater temporal variation in the condition of the annual versus perennial host plants and (b) more opportunity for asynchrony between the consumer and its annual hosts than its perennial host, as a consequence of (a). We expect asynchrony with the less-predictable hosts to be more pronounced under warm, dry summer conditions, and we test for such effects on the condition and phenology of the annual Geraniaceae hosts that have enabled the range expansion. We conduct these tests (c) across sites and years, and (d) across microclimates within a site. We then consider the implications of asynchrony for host use, shifting host associations at range margins and the range dynamics of host-limited herbivores.

Figure 1. Map of study sites in England: + denotes Helianthemum sites (H1–H5, electronic supplementary material, table S1); × denotes Geraniaceae sites (Geranium, G1–G3; Erodium, E1–E2; electronic supplementary material, table S1).

2. Methods

(a) Study system

Brown argus butterflies prefer to lay their eggs on Geraniaceae, on which larvae grow 10% larger and faster than on Helianthemum (the ancestral host at the range margin in Britain), and prefer to lay on better condition leaves regardless of host species [19,21,24–26,28,29]. However, the annual, more ephemeral growth of the Geraniaceae host plants may make them less reliable as a food source than the evergreen perennial Helianthemum, especially under more variable climatic conditions at the range margin [16]. To investigate this, we surveyed 10 sites fortnightly–monthly between July 2016 and October 2017, to monitor phenology and condition of three host plant species. Helianthemum was the dominant host at five calcareous grassland sites, while Geraniaceae (G. dissectum and E. cicutarium; hereafter Geranium and Erodium) were dominant at five grassland/dune sites (figure 1). The number of sites and quadrats was chosen to maximize spatial coverage and replication within logistical constraints. See electronic supplementary material, S1.1 and 1.2 for survey dates and site profiles.

(b) Quadrat surveys and analyses

Using an average of 33.7 (0.25 m²) quadrats per survey (electronic supplementary material, S1.3 for quadrat placement), we recorded percentage cover (see electronic supplementary material, S1.3.2), phenophase (phenological stage) and condition of each host species. Host phenophase and condition underpin brown argus egg-laying site choice in the field [19,30]. Phenophase was estimated on a four-point scale (in leaf L, bud B, flower F or had set seed S). Condition was visually assessed on a scale of 0–3 (poor–high quality for egg-laying, following [19,26]; see electronic supplementary material, S1.3.3 for details and justification). We also measured mean sward height and percentage cover of bare ground (electronic supplementary material, S1.3), which can alter local microclimates [31,32].

Quadrat-level phenophase and condition were estimated based on the average for each host species in each quadrat. This approach can mask fine-scale changes in phenophase and
host condition, particularly for the annual hosts, so we also recorded plant-level phenophase and condition of the smallest, earliest phenophase Geraniaceae plant in each quadrat. This approach allows inference as to whether new germination has occurred, and of the age/condition of the plant material likely to be available to overwintering larvae. By September, Geraniaceae plants in later phenophases are typically senescent, in poor condition and expected to die before the autumn, making them a poor resource for larvae [30].

(c) Quantifying variation in host plant condition and phenophase
To test expectation (a), for greater temporal variation in the condition of the annual than perennial hosts, we used a Kruskal-Wallis (KW) test for each sampling period to compare quadrat-level condition between host species. Bonferroni-corrected Dunn’s tests were then used to identify which hosts differed significantly from one another in condition score within each sampling period. We then conducted interannual comparisons of Geraniaceae host condition (Mann–Whitney U (MHU) tests) and phenophase (χ² tests): these compared 2016 data with 2017 data, separately for each month between July and October. These months are the most relevant for host choice and larval feeding by second-generation brown argus and their offspring.

(d) Assessing plant–herbivore (a)synchrony
To contextualize host condition with reference to herbivore phenology and address question (b), we overlaid plots of site-specific host condition indices (calculated using survey data, electronic supplementary material, S1.5.1) from all July–October surveys with emergence phenology curves of adult second-generation brown argus and their larval offspring. Adult phenology was described as site-specific Gaussian curves for 2016 and 2017, based on the output of phenomenological models following [30,33] (see below and electronic supplementary material, S1.6). The larval phenology curves track the adult curves, with an estimated 11-day lag to account for mating and egg-laying (4 days post-emergence) and larval emergence (one week) [24]. Therefore, the larval emergence curves are presented as indicators rather than precise evaluations of appearance or abundance at each site.

The overlap between plotted condition indices and brown argus phenology curves was used to generate an area under the curve (AUC) metric of site- and year-specific synchrony between brown argus and the host plants (electronic supplementary material, S1.7). These AUC metrics were then modelled in a beta regression (logit link; electronic supplementary material, S1.7) to test for effects of site latitude, host plant, year and a host–year interaction on synchrony.

The phenomenological models used to generate phenology estimates account for variation in phenology between sites and years based on differences in latitude and temperature (electronic supplementary material, S1.6). In summary, brown argus second brood phenology in Britain varies with latitude (earlier further north) and between-brood temperature (earlier under warmer conditions between the first and second brood) and is related to the (latitude-dependent) phenology of the first brood [30,33]. See electronic supplementary material, S1.6 for more information.

(e) Testing climatic predictors of Geraniaceae recruitment and condition
To address our third question (c), using data on the youngest host within each quadrat, we tested for climatic drivers of recruitment and condition of each Geraniaceae species in early September, when most larval offspring were expected to have emerged to feed. We defined recruitment as the presence of at least one young, leaf-stage host plant in the focal quadrat. Plants in condition categories 1 and 2 were rarely observed during September surveys. We therefore reclassified condition 0/1 plants as poor condition (0) and condition 2/3 plants as good condition (1).

To test predictors of recruitment and condition, we used logistic regression with the following putative predictors: year, site, northing, easting, vegetation height, bare ground cover and (linear and quadratic terms for) local weather estimates based on the UK Meteorological Office’s 5 km gridded weather data [34]. Using daily weather data [34], we calculated the minimum, mean and maximum temperature, and mean rainfall for three periods in each year (justified in electronic supplementary material, S1.8): July, July–September and August–September (only including weather data up to the day of quadrat sampling at each site in early September). We also used daily weather data to calculate the Gaussean Aridity Index (GAI; precipitation/(2 × temperature)) for each period (e.g. [35]). Higher GAI values indicate cooler, wetter conditions. Day of year was tested both as a putative fixed effect predictor and as an offset term to account for the day of sampling.

All continuous predictors were standardized and site (n ≤ 5 per host plant) was included as a fixed effect (following [36]). We constructed candidate models by considering all plausible parameter combinations (including temperature–rainfall interactions), estimated parameters using maximum likelihood and used AIC-based model selection to establish the most parsimonious model(s) (see electronic supplementary material, S1.9–1.10 for details of model selection, validation and diagnostics).

(f) Testing microclimate effects on Geraniaceae phenology and condition
We calculated condition and phenophase indices (electronic supplementary material, S1.5.2) for each of 31 quadrats at site G1 in September 2017, using the phenophase (L, B, F and S) and condition (0–3) of all Geranium plants in each quadrat. The indices range between 0 (quadrats contain only plants at condition 0/seed set stage) and 1 (plants at condition 3/leaf stage). To test expectation (d), we modelled the indices (logistic regression) as a function of putative quadrat-specific predictors: microclimate (mean, maximum and minimum temperatures and soil moisture; electronic supplementary material, S1.11), percentage cover of bare ground and mean sward height. We also considered plausible temperature–moisture interactions.

3. Results
(a) Variation in host plant condition and phenophase
There was a substantial decline in quadrat-level condition of the annual host Geranium over summer 2016 that was not observed in the perennial Helianthemum or to the same extent in Exsium (figure 2a; KW tests, electronic supplementary material, table S4). However, by early November 2016, senesced Geranium had mostly been replaced by recently germinated, better condition recruits, and the quadrat-level condition was at least as high as that of Helianthemum (figure 2a–c; KW tests, electronic supplementary material, table S4).

Overall, in summer 2016, both Geraniaceae species showed substantial evidence of leaf senescence, including wilting and abscission, and little germination or seedling establishment until early October (JE Stewart 2016, personal observations).
By contrast, in 2017, there were many more seedlings and good-condition plants throughout the summer months and into the main sampling period in September (JE Stewart 2017, personal observations) (Geranium, figure 2b, c; Erodium, electronic supplementary material, figure S3). The condition of the youngest Geranium plant in each quadrat was significantly higher in all 2017 survey periods compared to 2016 (figure 2b; MWU tests, electronic supplementary material, table S5). Geranium phenophases differed significantly between years ($X^2$ tests, electronic supplementary material, table S5): in 2016, the youngest plant in each Geranium quadrat was typically an older plant in the seed set stage (figure 2c) and new plants in the leaf stage did not dominate until October; however, this younger form was dominant throughout summer 2017 (figure 2c).
Erodium showed similar patterns, though condition was equivalent between years for the August and September surveys (electronic supplementary material, figure S3; MWU tests, electronic supplementary material, table S5). Erodium quadrats were also dominated by young, leaf-stage plants in 2017: significantly more so than in 2016 during July and August (electronic supplementary material, figure S3; \( \chi^2 \) tests, electronic supplementary material, table S5). The observed quadrat-level patterns of Geraniaceae phenophase and condition were similar to these plant-level assessments (electronic supplementary material, figures S4 and S5).

(b) Plant–herbivore (a)synchrony
We assessed potential for asynchrony between the butterfly and its hosts (question (b)) by overlaying plots of site-specific host condition indices with curves representing brown argus phenology (figure 3), and performing beta regressions on derived synchrony estimates. The beta regressions of AUC synchrony estimates demonstrate that synchrony was lowest for brown argus on Geranium in 2016 (low AUC overlap: AUC range 0.51–0.73), but very high for other hosts and for Geranium in 2017 (high AUC overlap: AUC range 0.92–1.00) (figure 3, table 1; electronic supplementary material, table S6). Synchrony was lower for larvae than adults, especially on Geranium in 2016 (electronic supplementary material, table S6). There was no detectable effect of site latitude on adult or larval AUC overlap (electronic supplementary material, table S12.4).

In 2016, Geranium condition declined over the peak of adult brown argus emergence and was lowest during the period in which most larvae would be beginning to feed (figure 3a–c). By contrast, at their respective sites, good-condition Erodium and Helianthemum hosts were available throughout egg-laying and early larval feeding periods of the brown argus butterfly, with little variation between two climatically different years (2016 and 2017), or among sites at each sampling period (figure 3d–j). Among-site variation in condition is more pronounced for Geranium, but this does not mask the temporal variation within and between years (figure 3; electronic supplementary material, table S4). Among-site variation likely results from local variation in temperature and water relations linked to factors including weather, topography and geology.

(c) Climatic predictors of Geraniaceae condition and recruitment
We integrated climate data with in-field host plant surveys to investigate potential drivers of condition and phenology across the Geranium sites, addressing question (c). The probability of the youngest Geranium plants being in good condition increased with summer rainfall (MC_lad, figure 4a, table 2a). There was limited evidence that moister, cooler conditions in areas with shorter vegetation were associated with better condition (electronic supplementary material, table S8). Forcing models of Geranium condition to include an effect of year resulted in higher AIC values, and inflated parameter estimates and standard errors by several orders of magnitude, so these are reported only in the electronic supplementary material, for context (electronic supplementary material, S1.12.5 and table S8), and there are no effects of year in the final model set. The evidence suggests that probability of new Geranium recruitment was higher in 2017 (MC_lad, electronic supplementary material, S1.12.5; table S9) and lower following higher mean daily temperatures during August–September (MR_final, figure 4b, table 2b). There were no detectable effects of site northing or easting, or day of sampling, on condition or recruitment.

We had low statistical power to detect relationships between weather and the condition and recruitment of Erodium, models for which are outlined in the electronic supplementary material, S1.12.5.

(d) Microclimate effects on Geraniaceae phenology and condition
To address question (d), we assessed Geranium phenology and condition across a range of microclimates at site G1 in September 2017. At this site, areas of moister soil (where plants are less likely to dry out) were associated with Geranium plants in better condition and earlier phenophases (figure 4c,d; table 3). Candidate models suggested such plants were also more prevalent in areas with warmer, moister microclimates (electronic supplementary material, S1.12.6).

4. Discussion
Here, we describe temporal variation in condition and phenology of three plant species and highlight the implications for their use as larval host plants by a butterfly species that has recently expanded its geographic range. Our data, from multiple sites across 2 years, suggest that the annual host Geranium dissectum varies more in condition and availability than both Erodium cicutarium and Helianthemum nummularium, the species that have been used as long-standing hosts at the range margin, and does so in a way that differs between years and with (micro-)climatic conditions. Such variation in condition and availability likely generates narrow and unpredictable phenological ‘windows of opportunity’ for exploitation of ephemeral annual species that vary among sites and years under the conditions of variable population sizes or phenology observed near the limits of species’ geographic ranges [37]. Though we recognize differences in the hosts other than their perennation strategy, in this case the perennial plant that was used as the main pre-expansion host appears to be a more reliable resource, where present, than the more widespread annual Geranium species that has acted as a primary host during the climate-associated range expansion. Erodium is typically found on sandy soils, is relatively drought-tolerant compared to other Geraniaceae hosts, and appears to respond to a wider range of phenological cues than Geranium, which may improve its relative condition and availability as a host under the conditions we observed [30]. Our results suggest that climatic effects on the phenological synchrony of biotic interactions could act as a mechanism generating transient patterns of host associations at range margins, and consequently of habitat availability in the landscape and patterns of range shifting.

(a) (Micro-)climatic variation and host plant phenology
Our data indicate that the phenology of Geranium, a widespread annual host plant used by the brown argus
butterfly, is sensitive to weather variability. Greenhouse experiments and field observations suggest that summer temperatures and moisture thresholds are crucial to dormancy breaking and germination in *Geranium* [38,39]. A complementary interpretation of these data is that *Geranium* plants may germinate early following a cool spell and early summer rain, but will suffer high seedling mortality where the summer is subsequently hot and dry (e.g. [40,41]). For example, our data show that hot, dry conditions in 2016 were associated with early and pronounced senescence of plants in July, as well as delayed germination and/or early seedling mortality. By contrast, our study sites received relatively high rainfall throughout summer 2017 [30], which is likely to have overcome moisture-dependency in dormancy breaking and/or promoted seedling survival. *Geranium* condition was also higher following wetter (2017) summer conditions, which supports evidence that drought and thermal stress cause premature senescence and declines in

**Figure 3.** Plant condition index in 2016 and 2017 for *Geranium* at sites G1–G3 (a–c), *Erodium* at sites E1–E2 (d–e) and *Helianthemum* at sites H1–H5 (f–j), indicating the timing of host condition changes relative to the year- and site-specific emergence of second-generation brown argus adults and their larvae. Butterfly phenology curves typically overlap at each site; (k) summarizes larval AUC synchrony metrics for each host–year combination, summarized from site-specific metrics each calculated as the full area of the phenology curve minus that which lies above the corresponding host condition line. The equivalent plot for adult AUC is shown in electronic supplementary material, S1.12.4. Ec, *E. cicutarium*; Gd, *G. dissectum*; Hn, *H. nummularium*.
Table 1. Parameter estimates (with errors) for Bayesian beta regression of adult and larval AUC synchrony metrics, also showing the lower (L95) and upper (U95) credible intervals for each estimate. Predictors include year, host and host–year interaction. Estimates for *Erodium* and Year2016 are not shown here as they are the base level for each predictor and are therefore included in the intercept term.

|                  | adults          |          |          | larvae         |          |          |
|------------------|-----------------|----------|----------|----------------|----------|----------|
|                  | estimate        | L95      | U95      | estimate       | L95      | U95      |
| intercept        | 2.89 (0.44)     | 2.03     | 3.77     | 2.8 (0.4)      | 1.99     | 3.55     |
| year2017         | 1.61 (0.65)     | 0.38     | 2.93     | 1.69 (0.65)    | 0.46     | 3.01     |
| host*Geranium*   | −2.01 (0.48)    | −2.94    | −1.07    | −2.23 (0.45)   | −3.07    | −1.32    |
| host*Helianthemum* | 0.02 (0.48) | −0.94    | 0.97     | 0.01 (0.37)    | −0.7     | 0.73     |
| year2017 : host*Geranium* | 2.87 (0.73) | 1.43     | 4.29     | 3.06 (0.74)    | 1.58     | 4.5      |

Figure 4. (a,b) Predicted probabilities with 95% confidence intervals (dashed lines) of (a) a state of good condition in the youngest *Geranium* in each quadrat and (b) recruitment of *Geranium* in each quadrat. The probabilities (a) increase as a function of late summer rainfall and (b) decrease as a function of late summer temperature (MRfinal, table 2). Some points offset in x and y planes to show the raw data; mean daily rainfall ranges between −1.76 and 2.18 (1.29–2.87 mm) and temperature ranges between −1.16 and 1.85 (15.61–18.11°C). The condition (c) and phenophase (d) indices of *Geranium* at site G1 increase as a function of soil moisture. Quadrats with higher soil moisture are more likely to contain high proportions of good-condition new recruits, and low proportions of poor-condition, reproductive *Geranium*. Soil moisture ranges between −1.58 and 1.83 (14.6–34.4%).
the quality (for consumers) of herbaceous plants [42,43]. A higher proportion of younger and better-condition Erodium were available in 2017 than in 2016, although we lacked statistical power to associate this with climatic variables (electronic supplementary material, tables S9–S10). Our analysis was unable to detect a clear geographic gradient in (a)synchrony, which may limit the predictability of the window of opportunity for brown argus to interact more with its host-specialist herbivores such as the brown argus [19,22,26,46,47]. By reducing temporal overlap between suitable resources and key herbivore life stages (e.g. adult egg-laying and early larval stages), adverse (micro-)climatic conditions may limit egg-laying and feeding opportunities and reduce larval survival, particularly where plants with limited temporal availability (such as the annual Geraniaceae studied here) are the main hosts [18,48]. Climatic conditions that are set to become more common (i.e. variable rainfall and longer, hotter summers [49,50]) may therefore narrow or close the phenological window of opportunity for this host-specialist herbivore to exploit these ephemeral annual resources in late summer [46,47].

Our analysis was unable to detect a clear geographic gradient in (a)synchrony, which may limit the predictability of the window of opportunity for brown argus to interact

| model parameters | model | $\beta_0$ | $S_1$ | $S_2$ | $R$ | $T$ | $k$ | $LL$ | $\Delta$AIC |
|------------------|-------|-----------|-------|-------|-----|-----|-----|------|-----------|
| (a) condition of youngest G. dissectum | $MC_{final}$ | 2.053 (0.535) | 5.749 (0.985) | $-1.590$ (0.551) | 5.871 (0.891) | | 4 | $-61.17$ | 0.13 |
| | $MC_0$ | 0.545 (0.141) | | | | | 1 | $-143.30$ | 168.38 |
| | $MC_1$ | 1.565 (0.622) | 5.071 (1.116) | $-1.305$ (0.630) | 5.611 (1.128) | | 4 | * | * |
| (b) probability of G. dissectum recruitment | $MR_{final}$ | 0.310 (0.354) | 4.366 (0.794) | $-3.558$ (0.718) | | | | $-3.872$ (0.555) | 4 | $-49.07$ | 1.43 |
| | $MR_0$ | 0.352 (0.138) | | | | | 1 | $-147.78$ | 192.84 |
| | $MR_1$ | $-0.044$ (0.495) | 4.770 (1.126) | $-4.120$ (1.017) | | | | $-4.096$ (0.792) | 4 | * | * |

| model parameters | model | $\beta_0$ | $M$ | $k$ | $LL$ | $\Delta$AIC |
|------------------|-------|-----------|-----|-----|------|-----------|
| (a) quadrat-specific condition indices | $MC_{final}$ | 0.496 (0.413) | 0.810 (0.448) | 2 | $-15.59$ | 1.88 |
| | $MC_0$ | 0.428 (0.380) | | | 1 | $-19.69$ | 8.07 |
| (b) quadrat-specific phenophase indices | $MP_{final}$ | 0.366 (0.412) | 0.889 (0.453) | 2 | $-14.84$ | 1.57 |
| | $MP_0$ | 0.307 (0.376) | | | 1 | $-19.98$ | 9.85 |
with Geraniaceae across its range. The widespread annual Geraniaceae are the hosts primarily used by brown argus at the expanding front of its recent range in Britain, whereas Helianthemum represents the apparent ancestral host at most sites where the species has been present for the past century or longer [26,30]. Therefore, while there is variation among sites, variation in butterfly-host synchrony (and the success of this relatively novel interaction) may be especially pronounced and unpredictable near the range limits, particularly if abiotic conditions are marginal and population sizes small [22]. In this respect, our results suggest that the range limit may be set not via broad environmental gradients in synchrony, but via shifting availability of sites where herbivore-host synchrony is sufficient. Through a process of ecological fitting at the novel range margin, populations interact with the resources that they happen to be synchronous with [51].

The relationships between weather, plant condition and phenology, which we identify here for Geranium, are therefore crucial in mediating how climate change, variability and unpredictability will affect synchrony in biotic interactions. Given that climate change is causing widespread changes in phenological synchrony, both existing and novel host interactions may be vulnerable under climate change. However, recent evidence suggests that at least as many biotic interactions are becoming more synchronous as are becoming less synchronous [22]. This evidence therefore also highlights the potential for novel biotic interactions to emerge and further supports a role for spatio-temporal variation in synchrony underlying transient host interactions.

Spatio-temporal variation in the synchrony of biotic interactions is likely to generate transient mosaics of selection pressures for different diets, and thereby influence patterns of dietary specialization/generalization that recent research has shown to be an emergent and surprisingly common property of range dynamics [7,8,21,24]. In range expansions, many new consumer–resource interactions form and some may be lost [7,8]. For example, diet breadths in populations of Edith’s checkerspot butterfly (Euphydryas editha) increased after colonization events as individual host preferences diversified, but populations subsequently reverted to monophagy [8].

Spatio-temporal variation in phenological synchrony may prove to be an underlying mechanism not only for lability in insect–host associations at range margins, but also for range limit stability under scenarios of temporal environmental variability. In particular, existing phenological plasticity can increase fitness costs where environments become more unpredictable [52] and range limits are more stable (expansions less likely) where environmental variance is too large for adaptation and colonization [53]. Therefore, increasing environmental variance may preclude colonization events that depend on predictably synchronous biotic interactions.

(c) Evolution during range expansion
Following the recent range expansion and incorporation of Geraniaceae into the diet of the brown argus, Geraniaceae-feeding populations that were able to persist became specialized on the novel hosts, losing the adaptive capacity to use Helianthemum [21,24]. Though specialization on Geraniaceae appears to have become more reliable on average [29], our data suggest that interannual variation in phenology could still alter the success of this interaction, which may prove to be locally transient in the face of phenological asynchrony.

In a comparable example from Scandinavia, narrow oviposition preferences of the Glanville fritillary (Melitaea cinxia) for phenologically limited hosts risks high larval mortality under severe drought conditions in some years [20,54].

Conversely, phenological asynchrony at recently colonized Geraniaceae sites could lead to variable population dynamics and selection favouring continued dispersal from the natal site in search of suitable egg-laying locations [55,56]. During the range expansion, selection has apparently favoured more dispersive phenotypes that have increased flight capacity and more readily accept the geographically widespread Geraniaceae hosts [24,27,28]. Consequently, under certain (micro-)climatic conditions, the dispersive, Geraniaceae-favouring phenotype may represent an alternative life-history strategy that drives expansion at range margins and in-filling of the core range. Subsequent migrants that colonize Helianthemum sites may need to regain the ability to use Helianthemum (as shown in [21]; see also [8]) in order to benefit from the stability of (and phenological synchrony with) the host resource.

(d) Conservation and management implications
Understanding constraints and opportunities for species’ distributions is central to successful conservation practices. Our results highlight the importance of considering drivers of synchrony and the outcomes of biotic interactions when examining climate-driven range shifts, and recognizing the crucial roles of microclimate and individual behaviour in mediating these interactions [19]. Conservation strategies could seek to maximize habitat and microclimatic heterogeneity to promote diversity in local phenologies across trophic levels [57,58]. In some cases, microclimatic variation may generate sufficient fine-scale spatial heterogeneity in relative phenology and host condition to buffer local herbivore populations against phenological asynchrony [10,18,59,60]. However, to improve our predictions of ecological responses to climate change, and of the critical levels of environmental change likely to cause a rapid loss of ecosystem outputs, more empirical data are needed on shifts in biotic interactions across populations, climates and species ranges, their effects on demography, and their rates and patterns of evolution. In the present case, we have highlighted what might be typical variation in phenological synchrony across 2 years, which emphasizes the potentially large indirect impacts of climate change on herbivore success. However, it would be beneficial to expand sampling across both time and space to better understand general patterns of interannual variation and gain a more holistic understanding of the phenomena discussed.

5. Conclusion
Our results place a novel emphasis on the interactions between phenology, resource use and climate change in a range-expanding herbivore whose sensitivity to small changes in temperature might otherwise predict a positive range expansion response under future climates. Instead, small changes in temperature and moisture regime have the potential to disrupt the range expansion, mediated by physiological and physiological changes in the herbivore’s larval resource that essentially fragment the herbivore’s potential range. This suggests that novel host interactions may only remain as transient resources at shifting range margins. The mechanisms underlying insect–plant interactions, and their responses to climate change, are likely to be more complex...
References

1. Louthan AM, Doak DF, Angert AL. 2015 Where and when do species interactions set range limits? Trends Ecol. Evol. 30, 780–792. (doi:10.1016/j.tree.2015.09.011)

2. Nadeau CP, Urban MC, Bridle JR. 2017 Coarse climate change projections for species living in a fine-scaled world. Glob. Change Biol. 23, 12–24. (doi:10.1111/gcb.13475)

3. Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009 Structuring patterns of variability in species distributions. Nat. Commun. 10, 1–10. (doi:10.1038/s41467-019-12479-w)

4. Platt PJ, Mason SC, Palmer G, Hill JK, Oliver TH, Powney GD, Fox R, Thomas C. 2019 Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. Sci. Rep. 9, 15039. (doi:10.1038/s41598-019-15182-2)

5. Eriksson M, Rafajlović et al. 2021 Evolutionary change associated with the recent range expansion of the British butterfly, Euphydryas editha agestis. Mol. Ecol. 30, 792–804. (doi:10.1111/mec.12440)

6. Asher J, Warren MS, Fox R, Harding P, Jeffcoate G, Jeffcoate S. 2001 The millennium atlas of butterflies in Britain and Ireland. Oxford, UK: Oxford University Press.

7. Lancaster LT. 2020 Host use diversification during range shifts shapes global variation in Lepidopteran dietary breadth. Nat. Ecol. Evol. 4, 963–969. (doi:10.1038/s41559-020-1199-1)

8. Singer MC, Parmesan C. 2017 Colonizations cause diversification of host preferences: a mechanism explaining increased generalization at range boundaries expanding under climate change. Glob. Change Biol. 23, 3505–3518. (doi:10.1111/gcb.15656)

9. de la Paz Celorio-Mancera M, Wheat CW, Vogel H, Söderlund L, Jantz N, Nylin S. 2013 Mechanisms of macroevolution: polyphagous plasticity in butterfly larvae revealed by RNA-Seq. Mol. Ecol. 22, 4884–4895. (doi:10.1111/mec.12440)

10. Ward SE, Moon RD, Herms DA, Aukema BH. 2019 Determinants and consequences of plant–insect phenological synchrony for a non-native herbivore on a deciduous conifer: implications for invasion success. Oecologia 190, 867–878. (doi:10.1007/s00442-019-04465-2)

11. Visser ME, Holleman LM, Gienapp P. 2006 Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172. (doi:10.1007/s00442-005-0299-6)

12. Fuentelbaul A, Pureswaran D, Bause E, Despland E. 2017 How does synchrony with host plant affect the performance of an outbreaking insect defoliator? Oecologia 184, 847–857. (doi:10.1007/s00442-017-3914-4)

13. Posoldovitch D, Toffegaard T, Wiklund C, Ehrén J, Gotthard K. 2018 Phenological synchrony between a butterfly and its host plants: experimental test of effects of spring temperature. J. Anim. Ecol. 87, 150–161. (doi:10.1111/1365-2656.12677)

14. Toffegaard T, Posoldovitch D, Navarro-Cano JA, Wiklund C, Gotthard K, Ehrén J. 2018 Butterfly–host plant synchrony determines patterns of host use years and regions. Oikos 128, 493–502. (doi:10.1111/oik.05720)

15. Schoonhoven LM, van Loon JJA, Dicke M. 2005 Insect–plant biology. Second edition. Oxford, UK: Oxford University Press.

16. Kemp RJ, Hardy PB, Roy DB, Dennis RH. 2008 The relative exploitation of annuals as larval host plants by European butterflies. J. Natural Hist. 42, 1079–1093. (doi:10.1080/00222930801937608)

17. Ward SE, Schulze M, Roy B. 2018 A long-term perspective on microclimate and spring plant phenology for a non-native herbivore. Insect Sci. 25, 1093–1116. (doi:10.1111/1365-2672.12770)

18. Hellmann JJ, Weiss SB, McLaughlin JF, Ehrlich PR, Allen JM, Travers SE, Woltzvik EM. 2018 Global shifts in the phenological synchrony of species interactions over recent decades. Proc. Natl Acad. Sci. USA 115, 5211–5216. (doi:10.1073/pnas.1714511115)

19. Asher J, Warren MS, Fox R, Harding P, Jeffcoate G, Jeffcoate S. 2001 The millennium atlas of butterflies in Britain and Ireland. Oxford, UK: Oxford University Press.

20. Bridle JR, Buckle J, Bodsworth EJ, Thomas CD. 2014 Evolution on the move: specialization on widespread resources associated with rapid range expansion in response to climate change. Proc. R. Soc. B 281, 20131800. (doi:10.1098/rspb.2013.1800)

21. Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L. 2001 Ecological and evolutionary processes at expanding range margins. Nature 411, 577–581. (doi:10.1038/35079066)

22. Boum NAD, Thomas JA. 1993 The ecology and conservation of the brown argus butterfly Aricia agestis in Britain. Biol. Conserv. 63, 67–74. (doi:10.1016/0006-3207(93)90075-C)

23. Buckle J, Butlin RK, Bridle JR. 2012 Evidence for evolutionary change associated with the recent range expansion of the British butterfly, Aricia agestis, in response to climate change. Mol. Ecol. 21, 267–280. (doi:10.1111/j.1365-294X.2011.05388.x)
28. Bodsworth EJ. 2002 Dispersal and behaviour of butterflies in response to their habitat. PhD thesis, University of Leeds, Leeds, UK.

29. Pateman RM. 2012 Climate change and habitat associations at species’ range boundaries. PhD thesis, University of York, York, UK.

30. Stewart JE. 2020 Linking phenology to population dynamics and distribution change in a changing climate. PhD Thesis, University of Exeter, Exeter, UK.

31. Suggitt AJ, Gillingham FK, Hill JK, Huntley B, Kunin WE, Roy DB, Thomas JA. 2012 The autumn effect: timing of physical dormancy break in seeds of two winter annual species of Geraniaceae by a stepwise process. Oikos 120, 1–8. (doi:10.1111/j.1600-0706.2010.18270.x)

32. Bramer I et al. 2018 Advances in monitoring and modelling climate at ecologically relevant scales. New Gen. Biomonitoring, part 7 58, 101–161. (doi:10.1016/bsearc.2017.12.005)

33. Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, Robinson BS, Hodgson DJ, Inger R. 2018 A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6, e4794. (doi:10.7717/peerj.4794)

34. Oliver TH, Roy DB, Bretonet T, Thomas CD. 2010 Heterogeneous landscapes promote population stability. Ecol. Lett. 13, 473–484. (doi:10.1111/j.1461-0248.2010.01441.x)

35. Aguillo MC, Edwards BR, Donohue K. 2019 Can the environment have a genetic basis? A case study of seedling establishment in Arabidopsis thaliana. J. Hered. 110, 467–478. (doi:10.1093/hered/esz019)

36. Sade N, del Mar Rubio-Wilhelmi M, Urmajkitkorn K, Blumwald E. 2018 Stress-induced senescence and plant tolerance to abiotic stress. J. Exp. Bot. 69, 845–853. (doi:10.1093/jxb/erx235)

37. Abarca M, Spahn R. 2021 Direct and indirect effects of altered temperature regimes and phenological interactions provides a narrow and variable window for plant establishment in semi-arid Argentina. J. Arid Environ. 33, 409–416. (doi:10.1006/jare.1996.0076)

38. Cox JA, Conran JG. 1996 The effect of water stress on the life cycles of Erodium cicutarium and Erodium cicutarium (Geraniaceae). Austral. J. Ecol. 21, 235–240. (doi:10.1111/j.1442-9993.1996.tb00694.x)

39. D’Aquilio MC, Edwards BR, Donohue K. 2019 Can the environment have a genetic basis? A case study of seedling establishment in Arabidopsis thaliana. J. Hered. 110, 467–478. (doi:10.1093/hered/esz019)

40. Baskin JM, Baskin CC. 1971 Germination of winter annuals in July and survival of the seedlings. Bull. Torrey Bot. Club 98, 272–276. (doi:10.2307/2483627)

41. Hamann E, Blevins C, Franks SJ, Jameel MI, Pachauri RK, Meyer LA. 2014 The effects of host plant phenology on the population dynamics of insect herbivores. Aust. J. Ecol. 39, 189–190. (doi:10.1111/1442-9993.12213)

42. Kemp R. 1998 Importance of larval foodplant preferences, adult size and microhabitat choice of the Glanville fritillary butterfly. Funct. Ecol. 12, 143–1444. (doi:10.1111/1461-0248.12069.x)

43. Chan AM, Spahn R. 2021 Direct and indirect effects of altered temperature regimes and phenological mismatches on insect populations. Curr. Opin. Insect Sci. 47, 67–74. (doi:10.1016/j.cois.2021.04.008)

44. Harwood J, Baskin JM. 2012 The germination pattern of three winter annuals. Bullet. Torrey Bot. Club 95, 331–335. (doi:10.2307/2483867)

45. Gama-Archicige NS, Baskin JM, Geneve RL, Baskin CC. 2012 The autumn effect: timing of physical dormancy break in seeds of two winter annual species of Geraniaceae by a stepwise process. Ann. Bot. 110, 637–651. (doi:10.1093/abob/mcs122)

46. Baskin JM, Baskin CC. 2012 Climate change and habitat associations at species’ range boundaries. PhD thesis, University of York, York, UK.

47. Hoffmann AA, Brodie J. 2021 The dangers of irreversibility in an age of increased uncertainty: rethinking plasticity in invertabrateb. Oikos (doi:10.1111/1100.oi8715)

48. Benning JW, Hufbauer RA, Weiss-Lehman C. 2021 Increasing temporal variance leads to stable species range limits. BioRxiv 2021.08.09.455156. (doi:10.1101/2021.08.09.455156)

49. Salgado AL, DeLeys ME, Saastamoinen M. 2020 Narrow oviposition preference of an insect herbivore risks survival under conditions of severe drought. Funct. Ecol. 34, 1358–1369. (doi:10.1111/1365-2435.13587)

50. Bennett NL, Severns PM, Parmesan C, Singer MC. 2018 Genetics of dispersal. Biol. Rev. Cambridge Philos. Soc. 93, 574–599. (doi:10.1111/brv.12336)

51. Hankins IA. 2011 Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly. Proc. Natl Acad. Sci. USA 108, 1397–1404. (doi:10.1073/pnas.110020108)

52. Hoffmann AA, Bridle J. 2021 The dangers of irreversibility in an age of increased uncertainty: rethinking plasticity in invertabrateb. Oikos (doi:10.1111/1100.oi8715)

53. Connor EF, Adams-Manson RH, Carr TG, Beck MW. 2018 Incorporation of climate observations into climate change is reduced by microclimatic buffering. Nat. Clim. Change 8, 713–717. (doi:10.1038/s41558-018-0231-9)

54. Oliver T, Roy DB, Hill JK, Bretonet T, Thomas CD. 2010 Heterogeneous landscapes promote population stability. Ecol. Lett. 13, 473–484. (doi:10.1111/j.1461-0248.2010.01441.x)

55. Connor EF, Adams-Manson RH, Carr TG, Beck MW. 1994 The effects of host plant phenology on the demography and population dynamics of the leaf-mining moth, Cameraria hamadryadella (Lepidoptera: Gracillariidae). Ecol. Entomol. 19, 111–120. (doi:10.1111/j.1365-2311.1994.tb00400.x)

56. Bennett NL, Severs PM, Parmesan C, Singer MC. 2015 Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. Oikos 124, 41–53. (doi:10.1111/1100.oi490)

57. Stewart JE, Maclean IMD, Trujillo G, Bridle J, Wilson RI. 2022 Climate-driven variation in biotic interactions provides a narrow and variable window of opportunity for an insect herbivore at its ecological margin. Figshare.