Journal of Insect Conservation (2025) 29:62
https://doi.org/10.1007/s10841-025-00697-1

ORIGINAL PAPER

Trait-mediated phenological shifts in moths under climate change: evidence for alternative response strategies

Markus Franzén[1,2] · Yannick Francioli[2,3] · Göran Sjöberg[4] · Anders Forsman[2]

Received: 15 March 2025 / Accepted: 9 July 2025 / Published online: 2 August 2025

Abstract

Introduction Climate warming has shifted the timing of many insect life-history events; yet, the links between these shifts, ambient temperature exposure, and species' traits remain unclear.

Aims and methods We quantified seasonal and trait-mediated changes in moth phenology and temperature exposure by comparing nightly light trap data for 15,451 individuals representing 96 univoltine species collected in central Sweden in 1975 and 2019. Across the community, 35 species advanced their activity periods, while 23 delayed them. Spring species advanced consistently (median = −5.2 days), while summer species showed heterogeneous responses. Autumn species either delayed activity into cooler intervals or advanced into warmer ones. Phenological advancement was greater in species overwintering as pupae than in those overwintering as eggs or larvae (Δ = 4.7 days) and in adult-feeding species relative to non-feeding species (Δ = 3.9 days). Advancement was also correlated with larger body size and lower intraspecific variation in colour patterns. Shifts in timing were closely mirrored by corresponding changes in median temperature exposure, indicating that phenological responses rather than plastic adjustments in activity temperature underpin most observed thermal shifts.

Discussion The heterogeneous, trait-linked responses observed here counter the notion of uniform phenological advancement across taxa. The overwintering stage, adult feeding, body size, and colour pattern variability appear to mediate the capacity of species to track or avoid warming temperatures through phenological change.

Implications for insect conservation Incorporating life-history traits into phenological assessments can identify species most at risk of climate-driven mismatches, thereby improving prioritisation in conservation planning.

Keywords Climate change · Insect phenology · Lepidoptera · Life-history traits · Temperature exposure · Thermal niche · Timing of flight

Introduction

Global climate change fundamentally alters the timing of biological events, with profound implications for species interactions and ecosystem functioning (Parmesan and Yohe 2003). With temperatures rising at unprecedented rates (Pörtner et al. 2022), phenological shifts represent one of the most visible and widespread biological responses to climate change, affecting taxa across trophic levels and geographic regions (Thackeray et al. 2016; Cohen et al. 2018). While phenological advances have been documented across diverse organisms, the magnitude and direction of these shifts vary substantially among species, suggesting that intrinsic traits may mediate responses to climate warming (Scranton and Amarasekare 2017; Habel et al. 2024; Hickinbotham et al. 2024). This variation is particularly evident in insects,

Adult-feeding

✉ Markus Franzén
markus.franzen@liu.se

1 Department of Physics, Chemistry and Biology (IFM), Linköping University, Linköping SE-581 83, Sweden

2 Center for Ecology and Evolution in Microbial Model Systems, Department of Biology and Environmental Science, Linnaeus University, EEMiS, Kalmar SE-391 82, Sweden

3 Department of Biology, The University of Texas at Arlington, 701 S. Nedderman Drive, Arlington, TX 76019, USA

4 Avellaneda Museum, Furängsvägen 56, Gävle 805 98, Sweden

where species exhibiting different life-history strategies show contrasting phenological responses (Altermatt 2010; Teder 2020). Understanding how species-specific traits influence these responses is crucial for predicting community-level impacts, identifying species at risk of phenological mismatches (Miller-Rushing et al. 2010), and developing effective conservation strategies under climate change.

To adapt to changing climates, species may (1) shift their phenology to track favourable conditions, (2) modify their realized thermal activity niche—defined here as the range of ambient temperatures experienced during their flight period—while maintaining their phenological rhythms, or (3) shift their geographic range to track optimal climates (Macgregor et al. 2019). These responses are not mutually exclusive but can be interdependent. For example, specialist species with narrow thermal niches often show more pronounced phenological shifts than thermal generalists (Buckley and Kingsolver 2021). This suggests a potential trade-off, where a significant change in phenology allows a species to conserve its thermal niche. In contrast, a lack of phenological plasticity may necessitate physiological or behavioural adjustments to cope with new thermal conditions. While some taxa shift phenology to conserve their thermal niche, as observed in birds and butterflies (Socolar et al. 2017; Gutiérrez and Wilson 2021), others like boreal Lepidoptera employ combined strategies of phenological and range shifts (Hällfors et al. 2021).

A species' capacity to respond phenologically is shaped by a suite of life-history traits that influence its sensitivity and plasticity. These traits can be broadly grouped by their functional roles. Traits related to developmental cues and constraints, such as the overwintering stage, are critical, as they determine when development can resume in response to spring warming; species overwintering as pupae, for instance, often show stronger phenological advancement (Altermatt 2010). Traits governing energy balance and metabolic rates, such as body size and colouration, are also key. Body size relates to thermal inertia and development time, with smaller species typically responding more rapidly to temperature changes (Connoy et al. 2020), while colouration directly impacts thermoregulatory capacity, with darker morphs absorbing more solar radiation (Zeuss et al. 2014). Finally, traits reflecting ecological specialisation influence a species' flexibility. Diet breadth reflects resource specialisation, with monophagous species facing greater constraints due to dependence on specific host plants (Chmura et al. 2019). Similarly, habitat preference influences microclimate exposure, with forest-dwelling species experiencing buffered thermal regimes compared to open-habitat species (Zografou et al. 2021). We also consider colour-pattern variation, which can be linked to a species' ecological generalism, as polymorphic populations may tolerate a broader range of environmental conditions (Forsman et al. 2008, 2020; Forsman and Wennersten 2016). Understanding these trait-mediated responses is essential for predicting species-specific vulnerabilities to climate change.

Here, we investigate how moths respond to warming through shifts in phenology and their realized thermal activity niche, leveraging a unique long-term dataset from Sweden that compares two distinct time periods (1975 and 2019). We test three hypotheses. First, we predict that phenological responses are season-dependent, with spring species advancing and autumn species delaying their activity periods under warming conditions (Frei et al. 2014). Second, we hypothesise that moths demonstrate alternative response strategies, modifying either their phenology or their realised thermal activity niche, but rarely both simultaneously (Urban et al. 2016). Third, we propose that the magnitude and direction of these responses depend on the species' life-history traits, including taxonomic affinity, range size, overwintering stage, diet breadth, habitat preference, body size, and colour-pattern variation (Forsman et al. 2008; Kharouba et al. 2014).

To test these hypotheses, we analysed nightly moth captures (15,451 individuals, 96 species) from a single location in central Sweden, comparing activity patterns that were quantified with high temporal resolution in the mid-1970s and again in 2019, a period during which regional temperatures increased by 1.5 °C (SMHI 2024). This dataset enables a robust assessment of phenological and thermal niche shifts, providing insights into the mechanisms underlying species' responses to climate change and their implications for biodiversity conservation (Forrest and Miller-Rushing 2010).

Methods

Study area

We collected data from a light trap placed north of Gävle in central Sweden (60°45'4.34"N, 17°6'28.08"E). The study site, located at the intersection of the boreo-nemoral zone, offers a unique opportunity to investigate moth phenologies due to the unusually high species richness at this latitude in Europe (Antão et al. 2020). The surrounding landscape comprises diverse habitats, including semi-dry hay meadows, scattered bedrocks, and mixed forests dominated by pine and spruce.

The study area has a humid continental climate (Köppen-Geiger classification: Dfb), characterised by warm summers and cold winters. The mean annual temperature is 5.3 °C, with January averaging −5.1 °C and July averaging 16.4 °C. Annual precipitation averages 683 mm, distributed relatively evenly throughout the year, with slightly higher rainfall in summer months. The growing season typically extends from mid-April to early October (approximately 170 days), with snow cover usually persisting from December through March (average 120 days annually). Habitat composition has remained relatively stable at the immediate trap location.

Data collection

Moth data were collected using a single light trap operated by one of the authors (Sjöberg) across two periods: the 1970s (primarily 1975) and 2019. The light trap was positioned at the same location throughout both sampling periods. Data from 1975 spanned 9 April to 21 July and 26 August to 5 November, with supplementary sampling from 21 July to 13 August 1978 to compensate for an electrical failure in 1975. The period 13–26 August, missing from the 1970s, was excluded from the 2019 dataset to ensure identical sampling effort between periods. While time series interpolation could potentially reconstruct activity during this gap, we chose to exclude it to maintain symmetrical sampling effort and avoid introducing model-based artefacts into our phenological estimates. Data were collected continuously from 9 April to 5 November 2019. We hereafter refer to the mid-1970s period as the historical period and 2019 as the contemporary period.

The light trap operated automatically, using a twilight sensor that switched it on at dusk and off at dawn. We employed the same trap design across sampling periods, using mercury vapour (125 W HG) light bulbs to ensure consistent attraction efficiency. However, there were modifications in collection methods between sampling periods: in the historical period, moths were manually collected from illuminated white sheets surrounding the light source, whereas in the contemporary period, we employed a standardised Ryrholm trap design with the same light source. The automated trap system in the contemporary period enabled continuous overnight collection without manual attendance, with specimens counted the following morning. While this could potentially affect the catches, thereby influencing duration estimates, we expect its effect on the timing of peak activity to be minimal. The trap was emptied daily, and captured moths were identified, counted, and recorded.

Data processing

Our total dataset comprised over 250 species. After filtering, we analysed trait data and phenological responses for 96 moth species (Lepidoptera: Macroheterocera), consisting of a total of 15,451 individuals. The dataset comprised 3,773 individuals from the historical period and 11,678 individuals from the contemporary period (Supplementary Material 1 Supplementary Table 1). Species were included if they had a minimum of five individuals sampled and activity durations ranged from 5 to 70 days. This duration constraint effectively filters out species with sparse data and multivoltine species. This threshold was determined based on an exploratory analysis of flight period distributions in our data and established life-history knowledge for the regional fauna, allowing us to conservatively exclude species with bimodal or excessively extended flight periods, which are indicative of multiple generations.

All selected species were Macrolepidoptera, encompassing the families Noctuidae ($n=45$), Geometridae ($n=31$), Erebidae ($n=9$), Notodontidae ($n=4$), and Lasiocampidae ($n=4$), as well as single species from Drepanidae, Endromidae, and Sphingidae.

Morphological, ecological, and life-history traits were collected from the literature (Skou 1984, 1991; Hydén 2007). Male wingspan, used as a proxy for body size, averaged 37.41 ± 11.00 mm (mean ± SD). Species were categorised by colour pattern variation (non-variable: $n=52$; variable: $n=29$; highly variable: $n=15$) (Forsman et al. 2020). Geographic distribution was quantified as the number of European countries in which a species was present (mean $= 27.54 \pm 4.45$ countries) (Karsholt and Razowski 1996). We acknowledge that this metric is a coarse proxy for geographic range size, but it provides a standardised measure of distribution breadth across all species.

Species were further classified by habitat preference (forest: $n=20$; open: $n=15$; generalist: $n=61$), diet specialisation (specialist: $n=16$; oligophagous/generalist: $n=80$), adult feeding capability (feeding: $n=84$; non-feeding: $n=12$), overwintering life stage (egg: $n=25$; larva: $n=50$; pupa: $n=21$) (Skou 1984, 1991; Hydén 2007), and seasonal activity based on our data (spring: $n=15$, peak before 1 June; summer: $n=62$, peak between 1 June and 26 August; autumn: $n=19$, peak after 26 August).

Thermal niche and phenological metrics

The realised thermal activity niche was determined using median activity temperatures, with temperature data sourced from SMHI (10 km from the trap site) (SMHI 2024). This metric represents the temperatures at which individuals were observed to be active under local environmental conditions, reflecting their realised activity patterns rather than their fundamental physiological thermal limits. Consequently, each species is represented by a single value for the historical and another for the contemporary period, forming paired observations in subsequent analyses. To describe phenology, we calculated three percentile-based measures of flight activity for each species in each sampling period: the 5th percentile ("start"), the median ("peak"), and the 95th percentile ("end"). We then defined duration as the difference (in days) between the 5th and 95th percentiles, thus capturing the core flight window (90% of captures) rather than the entire calendar range. This percentile approach reduces the impact of outlying observations.

To quantify the potential influence of thermal plasticity on phenology, we compared the temperature profiles of 1975 and 2019. We used daily mean temperature data from SMHI weather station in Gävle, Sweden (Latitude: 60.67°N, Longitude: 17.13°E). For each year, we calculated daily degree-days (DD) using a base temperature of 5 °C, a standard threshold for temperate insect development. Cumulative degree-days (CDD) were calculated by summing the daily DD values.

Statistical analyses

We conducted all statistical analyses in R version 4.4.3 (R Core Team 2024). Visualisations were generated using ggplot2 version 3.5.1 (Wickham and Wickham 2007). Because our study design involved a single light trap at a single site, with data from two focal periods, species-level comparisons provided the primary source of replication ($n = 96$ species). To investigate phenological and thermal niche shifts, we first employed paired sample t-tests to compare species-specific patterns between historical and contemporary periods. We then used one-sample t-tests to evaluate whether the mean shifts across all species deviated significantly from zero.

To examine the drivers of phenological shifts (the change in peak activity day), we developed a set of generalised linear models (GLMs) using glmmTMB version 1.1.10 (Brooks et al. 2023) with a Gaussian error structure. We employed three separate models to mitigate issues with multicollinearity and to test our distinct hypotheses clearly.

The first model tested our hypothesis about seasonal and thermal trade-offs, assessing the shift in peak phenology as a function of season (spring, summer, autumn), the shift in the realised thermal niche, and their interaction. The second model tested the influence of multiple life-history traits simultaneously, including diet specialisation, habitat preference, European range size, wingspan, and colour-pattern variation as predictors. The third model analysed the effect of the adult feeding strategy (feeding vs. non-feeding) separately due to its correlation with other traits.

We assessed multicollinearity among predictors using variance inflation factors (VIF) via the car package version 3.1-3 (Fox et al. 2019) and ensured all predictors in a given model had VIF values below 3. Following theoretical frameworks that caution against stepwise model selection (Whittingham et al. 2006; Grueber et al. 2011), we retained all biologically informed predictors in our final models. Model interpretation utilised marginal effects calculated using the ggeffects package version 2.0.0 (Lüdecke 2018), with the significance of model terms assessed through Type II likelihood ratio tests implemented via the car package's Anova function.

To determine if the thermal profiles were statistically different based on the SMHI data 1975 and 2019, we performed a two-sample Kolmogorov-Smirnov (K-S) test on the distributions of daily DD values.

Results

On average, the flight period duration for moth species was 23.21 ± 0.94 days (mean ± SE), calculated as the interval between the 5th and 95th percentiles of activity. Between the historical and contemporary periods, the timing of peak flight activity advanced by 2.34 ± 0.89 days (mean ± SE), while the realised thermal activity niche shifted towards cooler conditions by 2.22 ± 0.29 °C (mean ± SE). Phenological shifts differed markedly among seasons ($\chi^2 = 22.39$, $df = 2$, $p < 0.001$), and this seasonal effect was modulated by the magnitude of thermal niche change (season × thermal niche shift interaction: $\chi^2 = 9.43$, $df = 2$, $p = 0.009$). The main effect of thermal niche shift alone was not significant ($\chi^2 = 0.35$, $df = 1$, $p = 0.552$), indicating that the relationship between thermal and phenological responses depends on season of activity. Spring species consistently advanced their activity independently of temperature changes, initiating and concluding their flying periods earlier in the contemporary period (Figs. 1 and 2; Table 1). Summer species showed heterogeneous responses with no clear directional trend. Autumn species exhibited a distinct pattern characterised by delayed activity, with earlier initiation of activity but unchanged end dates, resulting in extended flight periods (Figs. 2C, D).

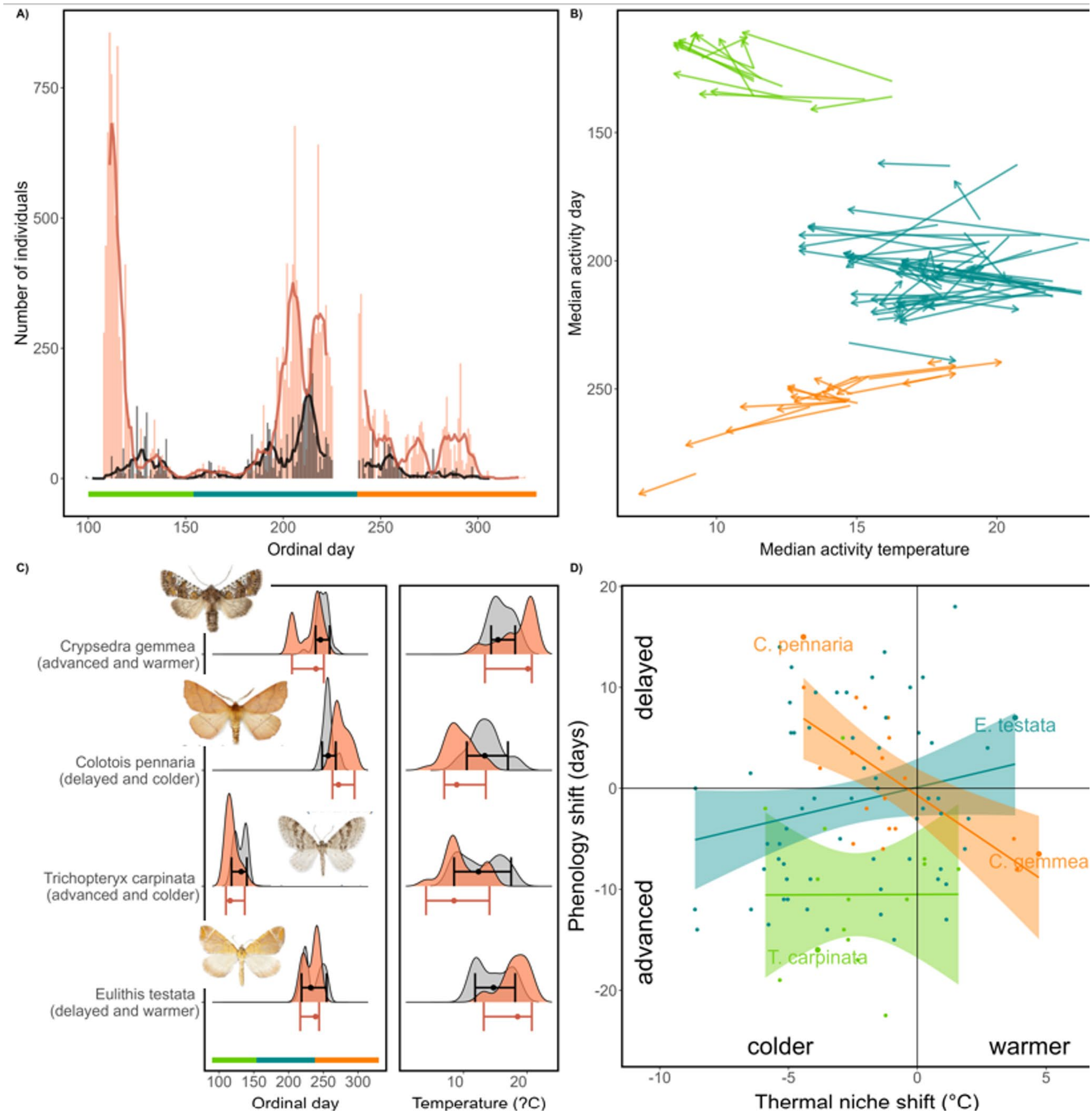

Fig. 1 Phenology and thermal niche shifts between historical and contemporary periods for 96 moth species. **A**) The number of moth individuals (pooled across species) recorded per night. Historical records are shown in black, and contemporary records are in orange, with seven-day moving averages represented by lines. The bottom ribbon denotes the three seasons: spring (green), summer (blue), and autumn (orange). **B**) Bidirectional species-specific shifts in phenology and thermal niche, with arrows starting in the historical period and pointing to the contemporary position. Arrow colours indicate the species' season: green (spring), blue (summer), and orange (autumn). **C**) Examples of four species demonstrating combinations of shifts in activity timing and temperature while active, corresponding to the four quadrants of panel D. Each curve represents the distribution of individuals in time (right panel) and temperature (left panel). Colours represent periods: grey for historical and orange for contemporary. Horizontal bars indicate the 5th and 95th percentiles, and dots mark medians (black for historical, orange for contemporary). **D**) Association between phenology shifts and thermal niche shifts across the studied species. Colours represent the season during the historical period: green (spring), blue (summer), and orange (autumn). Linear regression lines are displayed for each season with 95% confidence intervals. The plot is divided into four quadrants representing combinations of delayed/advanced phenology and colder/warmer thermal niches (e.g. delayed and colder or advanced and warmer)

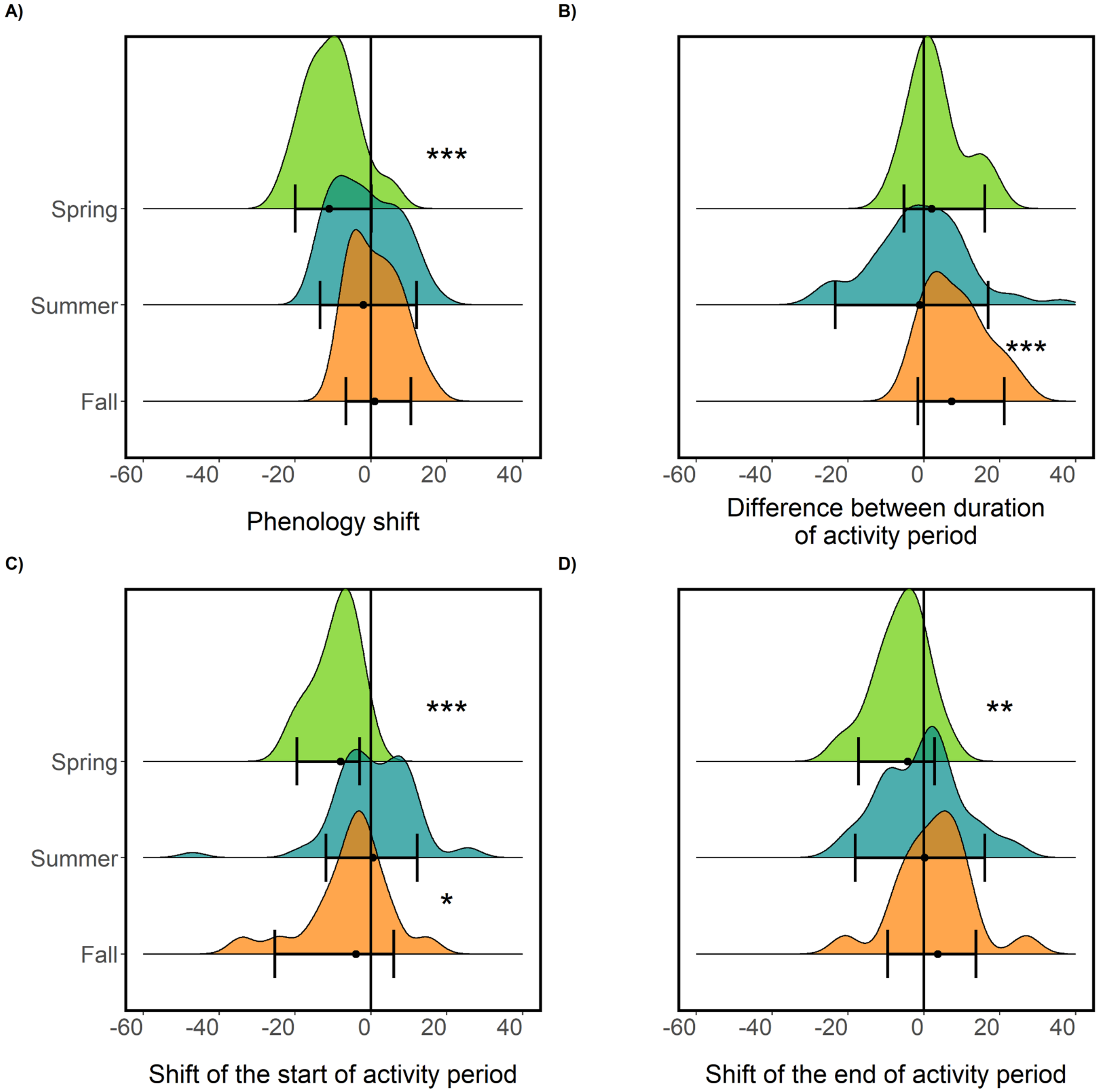

Fig. 2 Characterisation of phenology shifts in flight activity periods for moth species between historical and contemporary periods. **A**) Peak (midpoint) of activity period (phenology shift). **B**) Duration of the activity period. **C**) Start of the activity period. **D**) End of the activity period. The vertical bars represent the 5th and 95th percentiles, while the dots indicate the medians. Statistical differences from zero (one-sample *t*-test) are marked with an asterisk ("*")

Contrary to expectations based on long-term warming trends, the total heat accumulation in 1975 (Total CDD = 1523.7) was slightly higher than in 2019 (Total CDD = 1435.5). The mean daily degree-day accumulation was also marginally higher in 1975 (Mean ± SD: 4.17 ± 5.29) compared to 2019 (3.93 ± 4.94). A two-sample Kolmogorov-Smirnov test revealed no significant difference in the distribution of daily degree-days between the two years ($D = 0.04$, $p = 0.918$) (Supplementary Material 2).

Among the 96 moth species studied, we observed diverse response strategies: 35 species advanced their activity peaks, 23 delayed them, and 38 showed no significant change. Thermal niche preferences also shifted markedly. While the predominant response was a shift to cooler conditions (67 species), 11 species shifted to

Table 1 Predictors of species phenology shift. The table presents estimates, confidence intervals (CI), and *p*-values derived from the generalised linear model (GLM) with a Gaussian error structure. Significant predictors of phenological responses are highlighted. Note: analysis included 96 moth species (AIC = 673.09), with spring season as a reference level and statistical significance indicated by bold values ($p < 0.05$)

Predictors	Estimate	Std. Error	*P*-value
Intercept	-0.703	1.868	0.707
Temperature niche shift	-1.723	0.686	**0.012**
Season: summer†	-9.809	3.495	**0.005**
Season: autumn†	0.811	2.252	0.719
Temperature niche shift × Season: summer	1.732	1.168	0.138
Temperature niche shift × Season: autumn	2.327	0.759	**0.002**

significantly warmer conditions, and 18 maintained similar thermal preferences (Fig. 3). There was no overall correlation between phenological and thermal niche shifts across all pooled species ($r = 0.084$, $p = 0.418$). Instead, the association varied by season: shifts in peak activity were negatively associated with thermal niche shifts in spring species, positively associated in summer species, and independent in autumn species (Fig. 1D; Table 1), supporting the hypothesis of alternative response strategies.

Taxonomic affinity and life-history traits explained a substantial fraction of the variation in phenological responses. Moth species belonging to Geometridae generally advanced their peak activity, while other macro-moths showed delayed phenology, and Noctuidae maintained stable patterns (Fig. 4; Table 2, 3, Supplementary Material 1). Species with less variable wing colouration demonstrated stronger phenological advances than those with highly variable patterns. Species overwintering as pupae showed greater phenological advancement than those overwintering as eggs or larvae. The adult feeding strategy also emerged as crucial for phenological shifts ($\chi^2 = 7.45$, df = 1, $p = 0.006$), with non-feeding adults showing delayed phenology compared to feeding adults, which exhibited advanced activity patterns (Fig. 5). However, adult feeding behaviour did not significantly influence thermal niche shifts ($\chi^2 = 0.28$, df = 1, $p = 0.595$). Season of activity was strongly associated with phenological responses ($\chi^2 = 25.91$, df = 2, $p < 0.001$) but not with thermal niche shifts ($\chi^2 = 3.92$, df = 2, $p = 0.141$). These patterns are further detailed in Table 4.

Discussion

Our analysis of long-term moth activity patterns provides strong support for our hypotheses. First, we confirmed a strong season dependency in phenological responses: spring-active species consistently advanced their phenology, while autumn species exhibited complex responses, and summer species showed heterogeneous responses. Second, we provide evidence of alternative response strategies, with the direction of the association between shifts in peak activity and temperature exposure varying by season. Third, life-history traits—particularly overwintering stage, adult feeding strategy, and colour-pattern variation—emerged as important predictors of phenological shifts. A direct comparison of the study years revealed that the thermal accumulation profiles of 1975 and 2019 were statistically indistinguishable; in fact, 2019 was marginally cooler (Supplementary Material 2). The pronounced advancement of phenology in the absence of a corresponding thermal driver strongly refutes short-term plasticity as a primary explanation. This decoupling of the phenological response from the proximate conditions provides compelling evidence that the observed shifts reflect a genuine, long-term evolutionary response to climate change.

Complex phenological responses to climate change

Our study reveals complex, trait-mediated responses to climate change, challenging any assumption of uniform phenological shifts across taxa. While phenological advancement is a widely reported phenomenon, our results align with recent findings suggesting that such trends are not universal and that delays or stability are also common responses, depending on species-specific traits and regional climatic conditions (Hällfors et al. 2021; Colom et al. 2022). The strong association between phenological shifts and specific traits indicates that life-history strategies fundamentally constrain responses.

Species overwintering as pupae displayed a greater capacity for phenological advancement compared to species overwintering as eggs or larvae. This pattern likely reflects enhanced developmental readiness. Pupae are metabolically quiescent but are at a more advanced developmental stage, potentially allowing them to respond more rapidly to warming spring cues and complete development faster than species that must undergo both hatching and larval growth (Teder 2020). This convergence with other studies suggests that the overwintering stage is a robust predictor of a species' capacity to adjust its phenology (Hickinbotham et al. 2024).

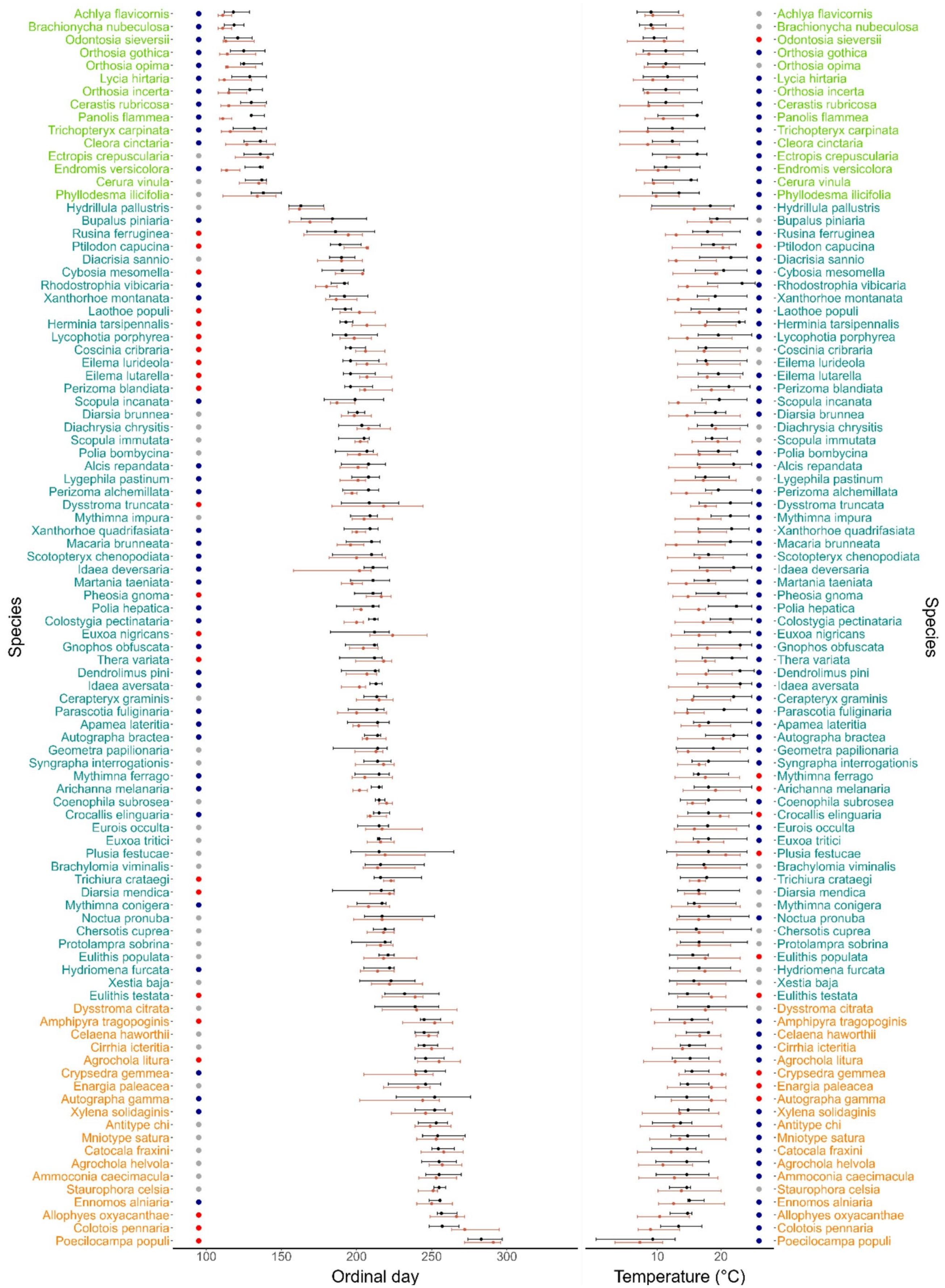
Achlya flavicornis
Brachionycha nubeculosa
Odontosia sieversii
Orthosia gothica
Orthosia opima
Lycia hirtaria
Orthosia incerta
Cerastis rubricosa
Panolis flammea
Trichopteryx carpinata
Cleora cinctaria
Ectropis crepuscularia
Endromis versicolora
Cerura vinula
Phyllodesma ilicifolia
Hydrillula pallustris
Bupalus piniaria
Rusina ferruginea
Ptilodon capucina
Diacrisia sannio
Cybosia mesomella
Rhodostrophia vibicaria
Xanthorhoe montanata
Laothoe populi
Herminia tarsipennalis
Lycophotia porphyrea
Coscinia cribraria
Eilema lurideola
Eilema lutarella
Perizoma blandiata
Scopula incanata
Diarsia brunnea
Diachrysia chrysitis
Scopula immutata
Polia bombycina
Alcis repandata
Lygephila pastinum
Perizoma alchemillata
Dysstroma truncata
Mythimna impura
Xanthorhoe quadrifasiata
Macaria brunneata
Scotopteryx chenopodiata
Idaea deversaria
Martania taeniata
Pheosia gnoma
Polia hepatica
Colostygia pectinataria
Euxoa nigricans
Gnophos obfuscata
Thera variata
Dendrolimus pini
Idaea aversata
Cerapteryx graminis
Parascotia fuliginaria
Apamea lateritia
Autographa bractea
Geometra papilionaria
Syngrapha interrogationis
Mythimna ferrago
Arichanna melanaria
Coenophila subrosea
Crocallis elinguaria
Eurois occulta
Euxoa tritici
Plusia festucae
Brachylomia viminalis
Trichiura crataegi
Diarsia mendica
Mythimna conigera
Noctua pronuba
Chersotis cuprea
Protolampra sobrina
Eulithis populata
Hydriomena furcata
Xestia baja
Eulithis testata
Dysstroma citrata
Amphipyra tragopoginis
Celaena haworthii
Cirrhia icteritia
Agrochola litura
Crypsedra gemmea
Enargia paleacea
Autographa gamma
Xylena solidaginis
Antitype chi
Mniotype satura
Catocala fraxini
Agrochola helvola
Ammoconia caecimacula
Staurophora celsia
Ennomos alniaria
Allophyes oxyacanthae
Colotois pennaria
Poecilocampa populi
Species
100
150
200
250
300
Ordinal day
10
20
Temperature (°C)
Species

Fig. 3 Summary of species-specific phenology and thermal niche shifts for the adult flight periods of 96 moth species between historical (1975) and contemporary (2019) periods in Gävle, central Sweden. Species are ordered by median flight day and colored by their season of peak activity: spring (green/chartreuse), summer (cyan/darkcyan), and autumn (orange/darkorange)
Left panel: Median flight day with horizontal lines representing 5th and 95th percentiles. Black markers and lines indicate 1975 values; orange markers and lines indicate 2019 values. Significance dots at x=95 indicate phenological shifts based on a 5-day threshold: blue dots denote species that significantly advanced their flight timing, red dots denote species that significantly delayed their flight timing, and grey dots indicate no substantial change
Right panel: Median flight temperature (°C) with horizontal lines representing 5th and 95th percentiles. Black markers and lines indicate 1975 values; coral markers and lines indicate 2019 values. Significance dots at x=26 indicate thermal niche shifts based on a 1.0 °C threshold: blue dots denote species that shifted to significantly cooler temperatures, red dots denote species that shifted to significantly warmer temperatures, and grey dots indicate no substantial thermal niche shift

Our finding that greater colour-pattern variation was associated with weaker phenological responses has not previously been reported in Lepidoptera. Morphological variability may reflect underlying physiological flexibility, enabling broader thermal tolerance and lessening the need to adjust seasonal activity patterns. This supports the general principle that intra-specific variation can buffer populations against environmental change (Forsman and Wennersten 2016).

The role of seasonal activity patterns and life history

Our findings reveal distinct seasonal patterns in phenological responses. For example, similar to findings in the Austrian Alps where phenological shifts vary systematically with elevation and season (Habel et al. 2024), our spring-active moths demonstrated consistent advancement. This is likely driven by selection for early emergence to exploit ephemeral resources (Thackeray et al. 2016). In contrast, autumn-active species exhibited more variable responses. This diversity may reflect complex trade-offs between thermal cues and other environmental signals, particularly photoperiod, which becomes a more dominant regulator of insect life cycles later in the season (Valtonen et al. 2011).

Limitations

Our study's primary limitation is its comparison of two discrete periods, which cannot capture the full dynamics

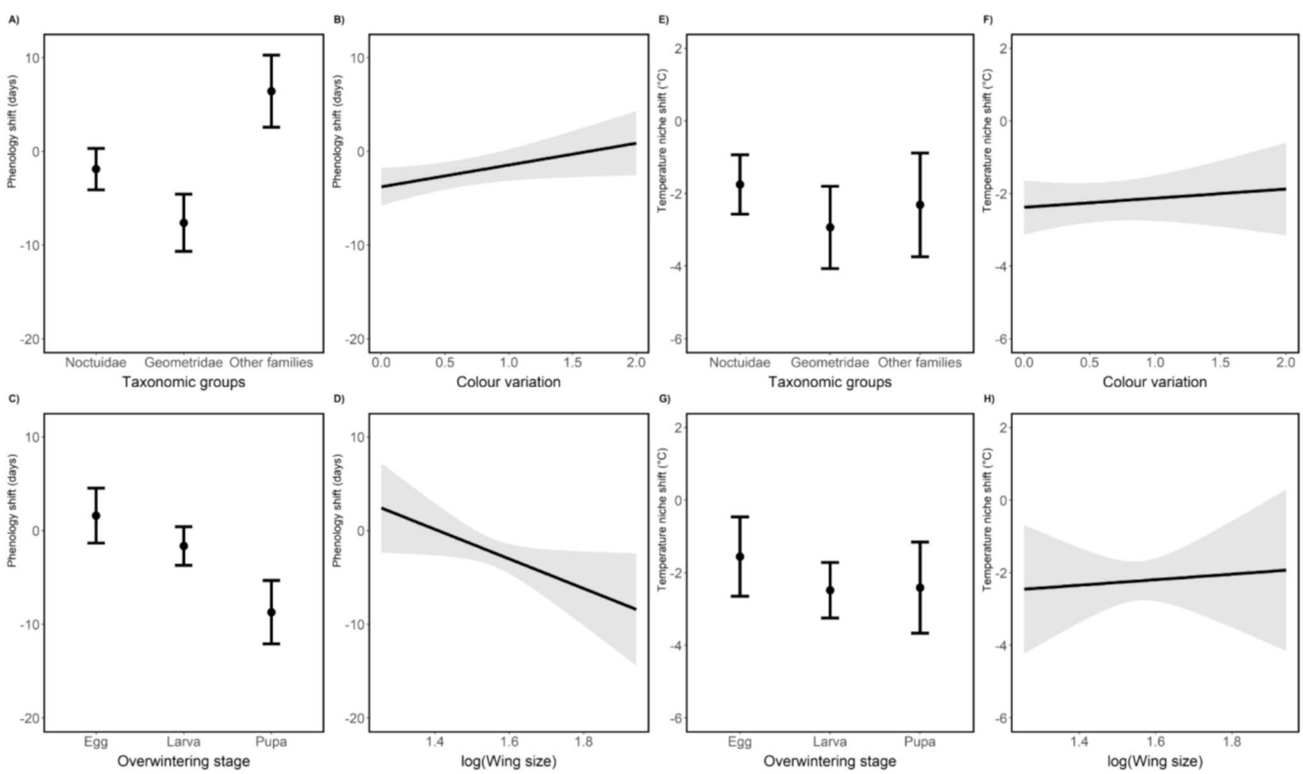

Fig. 4 Effect plots illustrating the associations of phenology and temperature niche shifts with taxonomic affinity and species traits in moths. Positive values for phenology shifts indicate later activity in the contemporary period, while negative values indicate earlier activity compared with the historical period. Effect plots are based on the model presented in Table 2. Shaded grey areas and error bars represent 95% confidence intervals

Table 2 Species characteristics associated with phenology (right) and temperature niche (left) shifts. Results are derived from an ANOVA table, highlighting significant relationships between species traits and their phenological or thermal niche responses. Note: χ^2 values from likelihood ratio tests; *df* = degrees of freedom; bold values indicate statistical significance at $p < 0.05$

Variables	Phenology shift			Temperature niche shift		
	χ^2	df	*P*-value	χ^2	df	*P*-value
Taxonomic group	28.93	2	**<0.001**	2.48	2	0.290
Colour variation	4.24	1	**0.039**	0.36	1	0.547
Diet category	0.45	1	0.500	0.43	1	0.512
Habitat preference	0.57	2	0.753	1.22	2	0.543
Wingspan (log)	4.31	1	**0.038**	0.07	1	0.787
European range	2.12	1	0.145	1.57	1	0.210
Overwintering	20.23	2	**<0.001**	2.00	2	0.369

Table 3 Species characteristics as predictors of phenology (right) and temperature niche (left) shifts. The table presents estimates, confidence intervals (CI), and *p*-values derived from a generalised linear model (GLM) with a Gaussian error structure. It highlights significant relationships between species traits and their responses to climate change. Note: analysis included 96 species, with substantial effects indicated by bold values ($p < 0.05$), using other moths, specialist diet, forest habitat, and egg stage as reference levels for the taxonomic group, diet specialisation, habitat preference, and overwintering stage, respectively (AIC = 673.078 and 482.916 for phenology and temperature shift models)

Predictors	Phenology shift			Temperature shift		
	Estimate	SE	*P*-value	Estimate	SE	*P*-value
Intercept	19.257	13.300	0.148	0.447	4.940	0.928
Geometridae[†]	-5.734	2.061	**0.005**	-1.182	0.766	0.123
Noctuidae[†]	8.318	2.211	**<0.001**	-0.559	0.821	0.496
Colour variation	2.325	1.129	**0.039**	0.253	0.419	0.547
Generalist diet[‡]	-1.413	2.097	0.500	-0.511	0.779	0.512
Generalist habitat[§]	-0.526	1.973	0.790	-0.808	0.733	0.270
Open habitat[§]	-1.928	2.681	0.472	-0.607	0.996	0.542
log(Wingspan)	-15.776	7.595	**0.038**	0.762	2.821	0.787
Geographic range	0.247	0.170	0.145	-0.079	0.063	0.210
Larva stage[¶]	-3.242	1.811	0.073	-0.926	0.673	0.169
Pupa stage[¶]	-10.311	2.317	**<0.001**	-0.857	0.860	0.320

of long-term trends and may be influenced by the specific climatic conditions of the sampled years (Didham et al. 2020). We have now analysed cumulative degree-days and temperature anomalies between 1975 and 2019. While 1975 showed marginally warmer conditions during early flight periods, the pronounced spring advancement patterns persisted, suggesting that our findings reflect genuine long-term responses rather than year-specific artefacts. Our use of a single trap location also limits broader inferences about spatial variability. While we standardised sampling effort, the mid-August gap in our time series may have truncated the flight periods of some late-summer species. Despite these limitations, it is unlikely that they would alter the fundamental associations we report between phenological shifts and species traits.

Ecological implications and future directions

Phenological shifts can cascade through ecological networks, altering species interactions (Memmott et al. 2007). Furthermore, historical changes in community composition may influence contemporary phenological patterns. Our previous work at this site documented

Table 4 Association of phenology and temperature niche shifts with adult diet. The table presents estimates, confidence intervals (CI), and *p*-values derived from a generalised linear model (GLM) with a Gaussian error structure, illustrating the impact of adult feeding behaviour on phenological and thermal niche responses. Note: models explained 24% and 4.6% of the variance in phenology and temperature shifts, respectively ($n = 96$ species), with significant effects indicated by bold values ($p < 0.05$), using non-feeding adults and spring as reference levels for adult feeding capability and seasonal activity (AIC = 670.933 and 475.460)

Predictors	Phenology shift			Temperature shift		
	Estimate	SE	*P*-value	Estimate	SE	*P*-value
Intercept	7.422	2.907	**0.012**	-1.507	1.050	0.155
Adult feeding[†]	-6.639	2.432	**0.008**	0.467	0.879	0.597
Summer[‡]	-13.086	2.719	**<0.001**	-1.199	0.982	0.225
Autumn[‡]	-2.959	2.031	0.149	-1.453	0.734	0.051

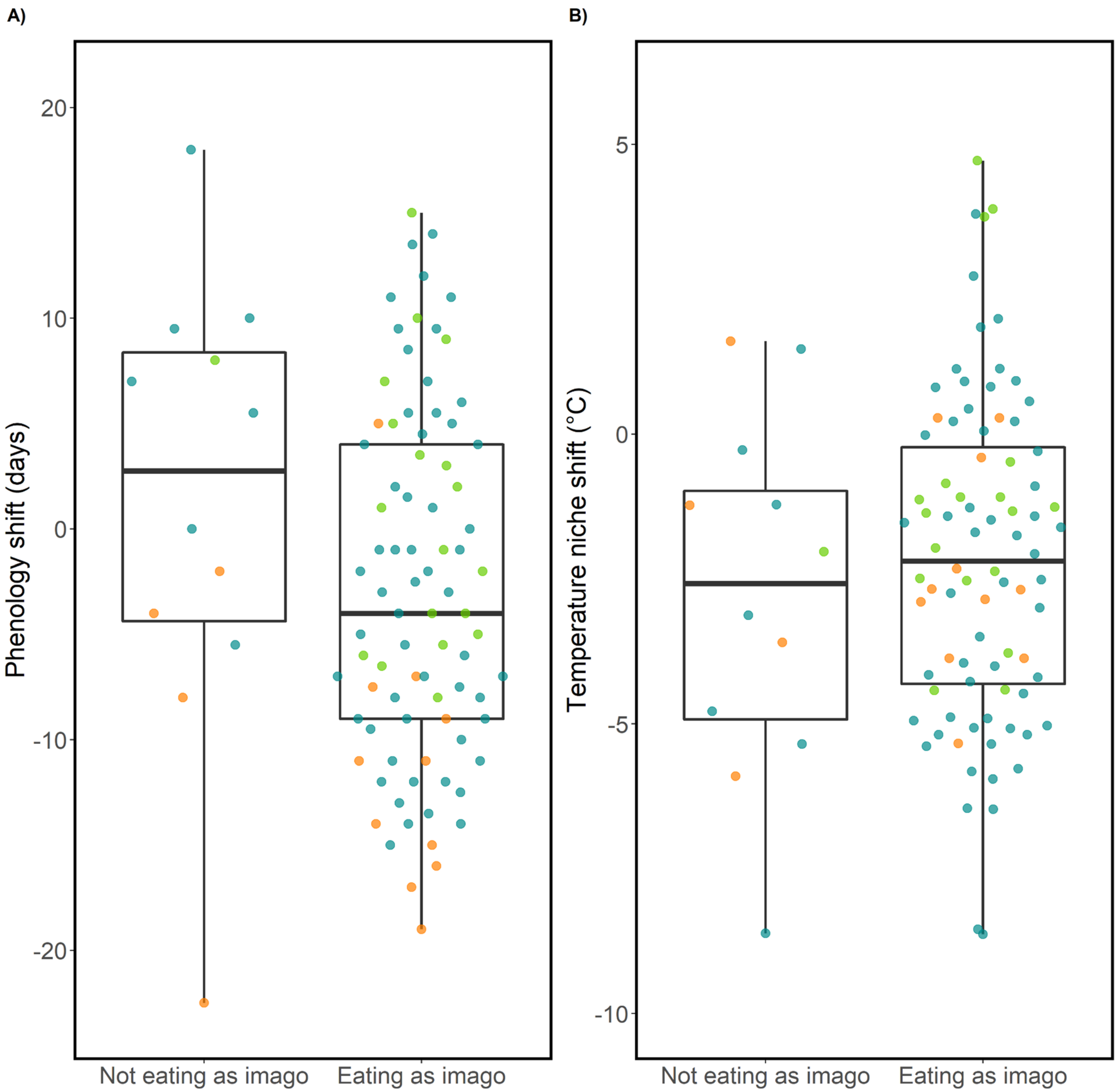

Fig. 5 Associations between phenology shifts (**A**) and temperature niche shifts (**B**) and adult feeding strategies. Each dot represents a species, and the colours indicate the season during the historical period: green (spring), blue (summer), and orange (autumn). Boxplots display the median, quartiles, and extreme values

significant species turnover between the two periods (Franzén et al. 2023). It is plausible that the extirpation of species unable to adapt their phenology has biased the remaining community towards species with greater plasticity, potentially inflating the magnitude of the average phenological shifts observed in this study. While collecting continuous daily data at multiple sites over many years is challenging, such datasets have proven invaluable for understanding large-scale ecological change (Macgregor et al. 2019). Emerging monitoring techniques, including automated camera traps and environmental DNA, promise to expand our capacity to track these changes, advancing our understanding of how life-history traits drive phenological shifts (Jain et al. 2024).

Conclusions

Moths respond to climate warming by shifting their phenology and temperature exposure in a season- and trait-dependent manner. Trait-based factors—including overwintering stage, adult feeding capacity, and colour pattern variation—emerged as key predictors of these shifts. By examining both phenological and temperature exposure changes, our study highlights the importance of a trait-based perspective for anticipating climate-driven impacts on moth communities and for improving targeted conservation strategies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-025-00697-1.

Acknowledgements The research was funded by the Swedish National Research Programme on Climate and Formas (grants to M.F. and A.F.; Dnr. 2018-02846 and Dnr. 2021-02142), Carl Tryggers Stiftelse för Vetenskaplig Forskning, Linköping, and Linnaeus University.

Author contributions M.F. and A.F. jointly conceived the research question and overall study design. G.S. collected historical data and maintained the trapping scheme in the mid-1970s and in 2019. Y.F. organised and standardised the dataset, performed statistical analyses in R, and produced the initial draft of the methods. M.F. and A.F. wrote the main manuscript text, and all authors contributed to revising and refining the manuscript. All authors read and approved the final version and accept responsibility for its content.

Funding Open access funding provided by Linköping University.

Data availability All datasets supporting this study are available upon request to the corresponding author.

Declarations

Ethics approval Ethical guidelines were adhered to throughout this study.

Competing interests The authors declare no competing interests.

References

Altermatt F (2010) Tell me what you eat and I will tell you when you fly: diet can predict phenological changes in response to climate change. Ecol Lett 13:1475–1484

Antão LH, Pöyry J, Leinonen R, Roslin T (2020) Contrasting latitudinal patterns in diversity and stability in a high-latitude species-rich moth community. Glob Ecol Biogeogr 29:896–907

Brooks M, Bolker B, Kristensen K, Maechler M (2023) Package 'glmmTMB'

Buckley LB, Kingsolver JG (2021) Evolution of thermal sensitivity in changing and variable climates. Annu Rev Ecol Evol Syst 52:563–586

Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH (2019) The mechanisms of phenology: the patterns and processes of phenological shifts. Ecol Monogr 89:e01337

Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. Nat Clim Change 8:224–228

Colom P, Ninyerola M, Pons X, Traveset A, Stefanescu C (2022) Phenological sensitivity and seasonal variability explain climate-driven trends in Mediterranean butterflies. Proceedings of the Royal Society B 289:20220251

Connoy JW, Leivesley JA, Brooks RJ, Litzgus JD, Rollinson N (2020) Body size of ectotherms constrains thermal requirements for reproductive activity in seasonal environments. Can J Zool 98:651–659

R Core Team (2024) R: a language and environment for statistical. R version 4.4.3, Vienna, Austria

Didham RK, Basset Y, Collins CM, Leather SR, Littlewood NA, Menz MH, Müller J, Packer L, Saunders ME, Schönrogge K (2020) Interpreting insect declines: seven challenges and a way forward. Insect Conserv Divers 13:103–114

Forrest J, Miller-Rushing AJ (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical transactions of the Royal Society of London. Ser B Biol Sci 365:3101–3112

Forsman A, Wennersten L (2016) Inter-individual variation promotes ecological success of populations and species: evidence from experimental and comparative studies. Ecography 39:630–648

Forsman A, Ahnesjö J, Caesar S, Karlsson M (2008) A model of ecological and evolutionary consequences of color polymorphism. Ecology 89:34–40

Forsman A, Polic D, Sunde J, Betzholtz P-E, Franzén M (2020) Variable colour patterns indicate multidimensional, intraspecific trait variation and ecological generalization in moths. Ecography 43:1–11

Fox J, Weisberg S, Price B, Adler D, Bates D, Baud-Bovy G, Bolker B (2019) car: companion to applied regression. R package version 3.0–2. Website: https://cran.r-project.org/web/packages/car/index.html [accessed 01 June 2019]

Franzén M, Francioli Y, Sjöberg G, Forsman A (2023) Positive shifts in species richness and abundance of moths over five decades coincide with community-wide phenotypic trait homogenisation. J Insect Conserv 27:323–333

Frei ER, Ghazoul J, Pluess AR (2014) Plastic responses to elevated temperature in low and high elevation populations of three grassland species. PLoS ONE 9:e98677

Grueber CE, Nakagawa S, Laws RJ, Jameson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711

Gutiérrez D, Wilson RJ (2021) Intra-and interspecific variation in the responses of insect phenology to climate. J Anim Ecol 90:248–259

Habel JC, Schmitt T, Gros P, Ulrich W (2024) Active around the year: butterflies and moths adapt their life cycles to a warming world. Glob Change Biol 30:e17103

Hällfors MH, Pöyry J, Heliölä J, Kohonen I, Kuussaari M, Leinonen R, Schmucki R, Sihvonen P, Saastamoinen M (2021) Combining range and phenology shifts offers a winning strategy for boreal Lepidoptera. Ecol Lett 24:1619–1632

Hickinbotham EJ, Pattison Z, Fox R, Rushton SP (2024) Drivers of moth phenology in England and Wales. J Insect Conserv 28:969–979

Hydén N (2007) Nationalnyckeln till sveriges flora och fauna. Fjärilar. Ädelspinnare - tofsspinnare: lepidoptera: Lasiocampidae - Lymantriidae. Artdatabanken, SLU, Uppsala

Jain A, Cunha F, Bunsen M, Pasi L, Viklund A, Larrivée M, Rolnick D (2024) A machine learning pipeline for automated insect monitoring. ArXiv Preprint arXiv:240613031

Karsholt O, Razowski J (1996) The Lepidoptera of Europe - a distributional checklist. Apollo books, Stenstrup

Kharouba HM, Paquette SR, Kerr JT, Vellend M (2014) Predicting the sensitivity of butterfly phenology to temperature over the past century. Glob Change Biol 20:504–514

Lüdecke D (2018) Ggeffects: tidy data frames of marginal effects from regression models. J Open Source Softw 3:772

Macgregor CJ, Williams JH, Bell JR, Thomas CD (2019) Moth biomass increases and decreases over 50 years in Britain. Nat Ecol Evol 3:1645–1649

Memmott J, Craze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant–pollinator interactions. Ecol Lett 10:710–717

Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. Philosophical transactions of the Royal Society of London. Ser B Biol Sci 365:3177–3186

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pörtner H-O, Roberts DC, Adams H, Adler C, Aldunce P, Ali E, Begum RA, Betts R, Kerr RB, Biesbroek R (2022) Climate change 2022: impacts, adaptation and vulnerability. IPCC Geneva, Switzerland:

Scranton K, Amarasekare P (2017) Predicting phenological shifts in a changing climate. Proc Natl Acad Sci 114:13212–13217

Skou P (1984) Nordens målare. Danmarks dyreliv. Bind 2. Apollo Books, Stenstrup

Skou P (1991) Nordens Ugler. Apollo Books, Stenstrup

SMHI (2024) Meteorologiska observationer. Retrieved from: https://www.smhi.se/data/meteorologi/ladda-ner-meteorologiska-observationer#param=airtemperatureInstant,stations=all,stationid=66110. Accessed 2024-03-17

Socolar JB, Epanchin PN, Beissinger SR, Tingley MW (2017) Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. Proc Natl Acad Sci 114:12976–12981

Teder T (2020) Phenological responses to climate warming in temperate moths and butterflies: species traits predict future changes in voltinism. Oikos 129:1051–1060

Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, Burthe S, Helaouet P, Johns DG, Jones ID, Leech DI (2016) Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245

Urban MC, Bocedi G, Hendry AP, Mihoub J-B, Pe'er G, Singer A, Bridle J, Crozier L, De Meester L, Godsoe W (2016) Improving the forecast for biodiversity under climate change. Science 353:aad8466

Valtonen A, Ayres MP, Roininen H, Pöyry J, Leinonen R (2011) Environmental controls on the phenology of moths: predicting plasticity and constraint under climate change. Oecologia 165:237–248

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol 75:1182–1189

Wickham H, Wickham MH (2007) The ggplot package. Google Scholar. http://ftp.uni-bayreuth.de/math/statlib/R/CRAN/doc/packages/ggplot.pdf

Zeuss D, Brandl R, Brändle M, Rahbek C, Brunzel S (2014) Global warming favours light-coloured insects in Europe. Nat Commun 5:3874

Zografou K, Swartz MT, Adamidis GC, Tilden VP, McKinney EN, Sewall BJ (2021) Species traits affect phenological responses to climate change in a butterfly community. Sci Rep 11:3283