

# Synergistic phenology and range shifts in boreal butterflies are controlled by species' overall response capacity

Running title: Synergistic phenology and range shifts

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## ABSTRACT

Species track climate warming through shifts in both phenology and geographic distributions, but the strength of association between these responses remains poorly understood. Although recent research points to a tendency of species to shift across either the temporal or spatial gradient, there is no comprehensive understanding of how generalizable these phenology and range shifts are and whether they are together mediated by species traits and could thus be predicted. We tested the hypothesis that coupling between phenology and range shifts emerges from the combined influence of species response capacity mediated by traits and phylogeny and environmental constraints.

Using opportunistic occurrence and systematic community-survey data for 70 Finnish butterfly species from 1999 to 2020, we derived probabilistic model predictions of the onset of adult flight time and northern range boundary. From model predictions we estimated species-specific phenology and northern range shifts and quantified how traits, phylogeny, and latitude contributed to variation in these responses.

Species generally advanced their adult flight periods and expanded their northern range boundaries northward. Across species, stronger phenological advances were associated with greater range expansion, indicating an overall synergistic relationship between temporal and spatial climate tracking. Environmental context generated a latitudinal trade-off: southern species showed stronger phenological advances whereas northern species exhibited stronger range shifts. Habitat breadth and thermal tolerance, primarily influenced range shifts and contributed to this trade-off. In contrast, traits associated with general response capacity, particularly mobility and flight-period length promoted both phenological and range responses simultaneously. Our results suggest that the relationship between phenology and range shifts is an emergent property arising from the balance between environmental constraints and intrinsic response capacity. Environmentally structured drivers tend to favour alternative climate-tracking strategies, whereas environmentally independent response-capacity traits promote simultaneous tracking across time and space.

Keywords: Geographical ranges, phenology, functional traits, climate warming, Bayesian analysis, butterflies

## 1 INTRODUCTION

Climate warming forces species to track changing environmental conditions through shifts in both seasonal timing (Roslin et al., 2021) and geographic distributions (Lenoir and Svenning, 2014; Chowdhury et al., 2026). Phenology advances and range shifts are therefore often viewed as alternative manifestations of the same underlying process: climate tracking (Buckley and Kingsolver, 2012b). Since both response mechanisms are ultimately driven by species' need to match the environmental niche of their life cycle events with suitable conditions, we can assume that phenology and range shifts are closely coupled (Hällfors et al., 2021; Chuine, 2010; Fredston et al., 2025). Highly responsive phenology shifts can alleviate the need to move in space (Socolar et al., 2017) and vice versa (Amano et al., 2014), as moving along with climate change can enable expressing phenology at similar times and conditions of the seasons as in the original occurrence area. In contrast, species ability to

advance phenology can indicate an analogous ability to range shifts to areas that become more suitable. Efficient phenology tracking could also support population growth and thus drive species range expansion (Willis et al., 2010; Chuine, 2010; Goded et al., 2024), leading to a coupling where one of the responses makes the other one more possible.

However, the few studies to date that have simultaneously estimated phenology and range shifts provide contrasting conclusions on coupling of the responses, finding that species tend to either respond in both ways (synergistic responses, i.e. coupling) (Radchuk et al., 2019; Goded et al., 2024; Sirois-Delisle et al., 2025) or one of them (complementary responses) (Hällfors et al., 2021), but there are also studies finding no connection between the two responses across large species pools (uncoupled responses) (Neate-Clegg et al., 2024). Consequently, these contrasting findings, although highlighting interesting potential connections between range and phenology shifts, point at a critical gap in our understanding of the mechanisms that drive the interaction between phenology and range shifts and their generalizability (Fredston et al., 2025). These contrasting results suggest that the key question is not whether phenology and range shifts are associated, but what determines the strength and direction of that association.

We propose that climate-driven phenological and range shifts emerge from the interaction between two broad processes: (1) response capacity, determined by species' physiological, life-history, behavioural, dispersal, and evolutionary characteristics; and (2) environmental opportunity and constraint, which determine the climatic gradients available for tracking and the extent to which abiotic conditions, resources, biotic interactions, and landscape structure permit those responses (Thurman et al., 2020; Fredston et al., 2025; Beissinger and Riddell, 2021; Chmura et al., 2018). Realized phenological and range shifts should therefore emerge from an interaction between capacity and context: high response capacity may produce only limited change where suitable temporal or spatial opportunities are unavailable, whereas favourable environmental opportunity may remain unused by species lacking the capacity to respond. Species response capacity through phenology or range shifts can be associated with species traits (see Cohen et al. (2018) for phenology and Angert et al. (2011); Sunde et al. (2023) for range shifts). If the same set of traits advances both responses, they could promote synergistic coupling between them. For butterflies (studied here), broad habitat use and dietary preferences (Buckley and Kingsolver, 2012b; Diamond et al., 2011; Altermatt, 2010), high mobility (Berg et al., 2010), high fertilisation (Angert et al., 2011; Pöyry et al., 2011), and low sensitivity to extreme temperatures (Kingsolver et al., 2011; Socolar et al., 2017) have previously been found to be positively connected to range shifts. However, only a few traits, predominantly traits related to overwintering strategies (Diamond et al., 2011; Hassall et al., 2007), such as overwintering of butterflies as pupae, have been found to predispose species to phenological adjustment (Hällfors et al., 2021). On the other hand, environmental constraints on species responses are reflected as spatially consistent differences in the pace of phenology and range shifts. Species communities of birds (Tonelli et al., 2024) and butterflies (Ittonen et al., 2022) have advanced the onset of their phenological cycles more rapidly at higher latitudes, whereas no similar differences have been found for range shifts (Rubenstein et al., 2023; Lawlor et al., 2024). These findings may reflect factors such as climate and photoperiod that impact species' abilities to shift their phenology. Environmental constraints along a latitudinal gradient could create either a synergistic or complementary association between response types. However, latitudinal differences in the pace of phenology and range shifts can as well be mediated by traits that vary between southern and northern species. For example, the breadth of habitat and temperature tolerances have been shown to increase to higher latitudes and allows us to expect an increasing ability of northern species to shift range (Diamond et al., 2011; Altermatt, 2010; Kingsolver et al., 2011; Socolar et al., 2017). We expect that resolving the role of traits, environment, and their interaction will essentially resolve also the underlying mechanism behind the interplay between phenology and range shifts.

In contrast to directional shifts, within-population variation and random interannual variation in mean phenological expression and range boundary could cause population-level resistance to a directional shift and short-term reversible responses to interannual environmental variability (Iler et al., 2017). Such variability could promote population persistence under fluctuating conditions and thus blur the measurable distinction between transient responses and long-term directional shifts: the higher the within-population and interannual variability, the more uncertain the estimate of the response (Iler et al., 2017). However, the uncertainty component has rarely been addressed or quantified in phenology and range shift studies (Chen et al., 2011; Hällfors et al., 2021). In practice, the low predictability of phenology and range shifts is also affected by the inherently high uncertainty in time series used for quantifying onset of adult flight time (Diamond et al., 2011) and range boundaries (MacLean and Beissinger, 2017; Beissinger and Riddell, 2021). Typically, sampling related factors, such as low sampling frequency, increase within-population variability in measured phenological timing and range boundaries (Beissinger and Riddell, 2021; Suggitt et al., 2023). This often leads researchers to restrict their analyses to a few relatively well-sampled species, leading to knowledge being generated mainly for the most common species, which additionally weakens predictability of the overall patterns across species pools.

Here, we narrow the knowledge gap regarding the key mechanisms of how species respond to climate warming, by assessing species-level phenology and range shifts while quantifying trait- and phylogeny-mediated contributions and spatial differences in the shifts. We study the temporal dynamics of adult flying time and range boundaries for 70 butterfly species in Finland over 22 years. The study species represent more than 2/3 of butterfly species occurring in Finland for which there are available

occurrence and trait data. Previous research has shown that boreal butterflies have shifted their ranges to higher latitudes (Sunde et al., 2023; Pöyry et al., 2009) and advanced their phenology (Roslin et al., 2021). Finland, like most of northern Europe, has warmed relatively fast in recent decades (Rantanen et al., 2022), and both responses are likely driven mainly by climate warming, as indicated by strong climatic associations with the responses (Luoto et al., 2006) (Roslin et al., 2021). However, trait-associations with responses have been found to be relatively weak (Hällfors et al., 2021). We hypothesise that, across the studied species, we should see an advance in phenology and an expansion of the northern range boundary as responses to climate warming (H1). We expect that the underlying mechanism for the type of coupling can be elucidated by quantifying trait- and phylogeny-associations, spatial differences in the shifts, and the magnitude of within-population variability (Fig. 1). In light of earlier research (e.g. (Kharouba et al., 2014; Hällfors et al., 2021)), we expect that shifts are controlled by different ecological mechanisms, which in turn can be associated with different combinations of traits (flight period with phenology and habitat use, dietary preferences, mobility, flight period, and sensitivity to extreme temperatures with range), and thus there is no combination of traits that would promote both response types (H2). Simultaneously, we expect that the pace of range shifts would be faster among southern species that may be constrained by climate and due to climate warming are able to expand their range faster than northern species, whereas we have no expectation for the latitudinal change in the pace of phenology shift (H3). Regarding uncertainty, we expect a larger magnitude of random variability in phenological timing compared to northern range boundaries due to the sensitivity of adult flight period to variable weather conditions (Iler et al., 2017) (H4). Finally, given no analogous trait-associations or latitudinal trends of phenology and range shifts and high levels of random variability in adult flight period, the paces of range and phenology shifts are uncoupled, instead of synergistic (phenology advances and northward shifts occur for the same species) or complementary (species tend to either advance phenology or range boundaries) (H5).

## 2 MATERIAL AND METHODS

### 2.1 Material

#### 2.1.1 Species data

We derived species occurrence data for 70 butterfly species from two complementary sources: systematically collected observations along survey transects and sporadically collected observations in point-wise locations. Survey transects occurred at higher densities in Southern than in Northern Finland (Fig. 2: panel A) and thus the analysis of species range dynamics benefits from supplementing the analysis with the presence-only data. Although point observations also occur in relatively high densities in Southern Finland (Fig. 2: panel A), they nevertheless cover northern Finland to a larger extent compared to the transect data, and thus add critical information about species northern range boundaries for our study. Whereas transect surveys inform provide presence-absence information, point observations only provide presence information. Therefore, we refer to the transect data as *presence-absence data* and point data as *presence-only data*. The study is constrained to 1999-2020, from which we have species, climate and vegetation data. For a list of study species and their prevalence in transect and point data, see Table S1 in the supporting information.

The systematic surveys were conducted in 101 one to three kilometer long line transects. Around 50 transects were surveyed annually. Active transects during each year were visited weekly during the flight period of the local butterfly community (May to August). Transects are typically focused on agricultural landscapes. The surveys are carried out by volunteers and the monitoring program is directed by the Finnish Environment Institute (Syke). For a complete description of the transect surveys, see Heliölä et al. (2022); Kuussaari et al. (2007).

The presence-only data originate from various sources that we accessed through the Finnish Biodiversity Information Facility ([laji.fi/en](https://laji.fi/en)) in April 2025. A large bulk of observations originate from the National Butterfly Monitoring Scheme (Saarinen et al., 2003). The point observations vary in terms of metadata completeness, and thus we removed observations that lack exact date information.

We extracted species traits that represent dietary (larval host) and habitat specificity, mobility, and flight period from Komonen et al. (2004), and the breadth of temperature tolerance (temperature breadth index) from Mäkinen et al. (2025b). The traits derived from Komonen et al. (2004) are based on a literature review and expert interviews. Importantly, these trait values have been defined based on Finnish populations of the butterfly species, which can differ from trait values based on other populations of the same species, such as for dietary specificity and flight period (Navarro-Cano et al., 2015; Van Dyck and Holveck, 2016). The temperature breadth index was measured as the standard deviation of the mean annual temperature conditions over the European ranges of the species based on Atlas distribution maps (Mäkinen et al., 2025b). The range of values and expected impact on phenology and range shifts of each trait variable are summarized in Table 1. As we did not have information on the overwintering strategy and voltinism (found important for phenology in Hällfors et al. (2021); Diamond et al. (2011); Hassall et al. (2007)), we were unable to base the phenology shifts on the mechanistically best supported traits.

We extracted species phylogenetic tree from (Wiemers et al., 2020) and (Wiemers et al., 2019) and computed phylogenetic distances with `cophenetic.phylo` function with `ape` R-package (Paradis and Schliep, 2019).

## 2.1.2 Environmental data

We characterized climatic conditions using temperature and precipitation data, with different parameters used for phenology and range analyses. We defined adult flight time at a daily resolution and geographical ranges at an annual resolution. Due to these differences, we linked phenology and range with climatic variables representing temperature and precipitation conditions at the relevant temporal resolution. For phenology, we explained species observations with daily temperature and precipitation records, whereas for ranges, we explained species observations with annual accumulation of thermal degree days over the growing season (sum of daily mean temperatures in days when mean temperature  $> 5^{\circ}\text{C}$ ; GDD5) and the annual precipitation sum. The temperature and precipitation variables were calculated based on interpolated weather maps at a daily temporal and 10 x 10 km spatial resolution from the Finnish Meteorological Institute (Aalto et al., 2016).

We also used vegetation surrounding the species observations to explain phenology and range related species densities, and chose specifically those land use types that have previously been found important for defining the spatio-temporal distribution of butterfly species (Luoto et al., 2006; Kuussaari et al., 2007). To characterize vegetation around the occurrence sites, we defined a 500-meter buffer around each observation. This buffer size reflects the average dispersal of butterflies (Nereu et al., 2024; Kasiske et al., 2023; Archaux et al., 2018). We defined vegetation variables as the proportional coverage of trees, shrubs, and grasslands within the buffer. The variables were calculated from the Global Plant Functional Types Dataset (v2.0.8) derived from the European Space Agency (Harper et al., 2023a), which has an annual temporal and a 300 meter spatial resolution.

## 2.2 Analyses

Onset of adult flight time and northern range boundary were defined comprehensively by fitting species distribution models (SDMs) based on a combination of systematically and opportunistically collected species records, creating probabilistic time series of species' onset of adult flight time over the season and distribution across latitudes. The uncertainty of annual prediction in the time-series reflects within-population variability in relation to the annual onset of adult flight time and the northern range boundary. Finally, we study annual change in onset of adult flight time and northern range boundary using a multi-species model where uncertainty of the annual change expresses the average deviation from the linear temporal trend, and thus reflects the random variability in population-specific annual average occurrences in relation to the temporal trend in phenology and northern range boundary.

We fitted spatio-temporally explicit statistical models for species occurrences in space (range) and time (phenology) and explained the occurrences with climatic and vegetation variables and spatio-temporal random effects. We applied model-based integration of the presence-absence and presence-only data to estimate not climatic and vegetation associations and spatio-temporal random effects (Fig. 2: panel B). Using the fitted models, we predicted, for each species and each study year, the flight time of adult butterflies and the geographical ranges across Finland (Fig. 2: panel C). We then summarized the information of the onset of adult flight time and northern range boundary with modal summary statistics (cf. Altermatt (2010)). Here, the advantage in comparison to Altermatt (2010) is that the modal statistics are computed over the entire estimated phenology of the adult flight time and geographical range and are accompanied by comprehensive uncertainty measures. Finally, we modeled the linear change in the onset of the flight period and northern range boundary jointly for all study species and utilized traits and phylogeny to test their mediating effect for explaining interspecific variation in the linear change over time. The analytical pipeline thus consisted of four steps, which are described in length in the following sections:

1. Species-specific distribution models (SDMs) are fitted separately for phenology and range.
2. Using fitted models, the species-specific phenology of the adult flight time and geographical range is predicted at an annual resolution.
3. Species-specific onset of adult flight time is extracted as the earliest 10% quantile of the annual total predicted abundance and the northern range boundary is extracted as the northern 90% quantile of the annual total predicted abundance.
4. Annual average change in the predicted onset and range boundary are estimated jointly across all species while including traits and phylogeny as mediators.

### 2.2.1 Species distribution modeling (step 1)

To estimate annual phenology and range dynamics for each butterfly species, we fitted species distribution models (SDMs) that integrated systematically collected presence-absence data from monitoring transects with opportunistically collected presence-only observations (Miller et al., 2019; Isaac et al., 2020). Combining these complementary data sources increases spatial and temporal coverage and improves inference on species distributions, particularly near range boundaries (Mäkinen et al., 2026, 2023).

Separate SDMs were developed for phenology and range dynamics and each species over 1999-2020 in Finland. Phenology and range models estimated the density of species individuals and the dependence of the species density on climatic and

vegetation variables together with latent spatio-temporal processes that accounted for residual variation in distribution patterns and observation processes. The phenology models quantified the density of species individuals at a daily temporal resolution and a spatial resolution of 1 km<sup>2</sup>. We interpret the variation in species density as a variation of adult flight activity. The range models quantified the density of species individuals at the annual temporal resolution and at 1 km<sup>2</sup> spatial resolution. Data integration was achieved by jointly modelling the two observation types while allowing them to share the same underlying ecological processes (Mäkinen et al., 2026). For phenology and range, we modelled species density with a generalised linear mixed effect model, in which presence-absence data were modelled with a Bernoulli observation model and presence-only data were modelled with a Poisson point process (Renner et al., 2015). Observation models were assigned a linear predictor of species density that shared parameters of climatic and vegetation cover variables and spatio-temporal random effect. Hence, both data types informed the same parameters and processes. For range, we included an additional spatio-temporal random effect that explained the variation in species density only in point data (*Latent sampling variable (J)* in Fig.2, panel B). Thus, the random effect was tailored to account for the variation in the sampling intensity in the point data. This random effect was left out of the predictions, so that the predictions reflect only the species distribution. For phenology, we did not include the additional random effect, since we assume that species phenology is less sensitive to spatial sampling bias.

We fitted the models using hierarchical Bayesian inference with INLA software through R (version 4.4.2; R Core Team (2021)) and the R-INLA package (version 24.12.11; Rue et al. (2009)). The species distribution models are explained with higher level of detail in the supporting information.

### 2.2.2 Species phenology and range predictions (step 2)

From the fitted models, we generated annual predictions describing the temporal distribution of adult flight time and the spatial range of each species across the study area (workflow illustrated in Figure 2). These predictions formed the basis for estimating annual onset of adult flight time, northern range boundaries, and associated uncertainty in subsequent analyses.

For phenology, we predicted species areal density for each day of the year across the whole study period. To capture spatial variability in the species phenology, we predicted species density in a coarse spatial grid with 11 prediction points (see a map of the prediction points in Fig. S1 in the supporting information). For the time series of each prediction point, we summarized the species densities over each year and then derived the day of the year when the sum of species densities exceeded the 10 % quantile of the annual sum. We used this day of the year for quantifying onset of adult flight time.

For range, we set a grid with a 1 km<sup>2</sup> resolution over the study area and predicted species areal density in each grid cell across the whole study period. We summarized the species densities over each year and then derived the latitude south of which 90 % of the species densities occurred. We use this latitude for quantifying the northern range boundary.

We derived posterior predictive distributions for the onset of a phenology and northern range boundary by sampling posterior samples (n=100) of the covariate and random effect estimates. With the posterior predictive samples, we calculated standard deviation for the annual onset of adult flight time and northern range boundary (Fig. 2: panel C).

### 2.2.3 Multispecies model for phenology and range shifts (steps 3 and 4)

We used the annual predictions from the SDMs to quantify species-specific rates of phenology and range change and to identify factors explaining variation among species. For each species, annual onset of adult flight time and northern range boundary were modelled as linear functions of time, yielding species-specific estimates of temporal shift. Prediction uncertainty from the SDMs was propagated into these analyses as a standard deviation of the annual onset of adult flight time and northern range boundary.

Species-level responses were estimated within a hierarchical multispecies framework in which the annual onset of adult flight time and northern range boundary were modeled with a linear mixed effect model. The estimate for species-level phenology and range shifts were modeled as latent variables that are correlated between species in relation to traits and phylogenetic distance. Therefore, we could ask whether species with similar ecological characteristics or evolutionary histories exhibited similar responses to climate warming. Traits represented habitat breadth, larval host specialization, mobility, flight-period length, and thermal tolerance. For phenology, we had predicted the onset in 11 locations, which covered the over 1000 km latitudinal gradient. We allowed the phenology shift vary between southern (hemi- and southern boreal) and northern (middle and northern boreal) boreal zones. The species-level intercepts (average onset of adult flight time and northern range boundary) were modelled also as mediated by traits and phylogeny and accounting for spatial variability between bioclimatic zones for phenology. In the model, phenology and range shifts were associated through the traits and phylogeny and through a correlation structure in relation to species-level process error. Correlated process error accounts for the fact that species may show high interannual variability in both responses.

The multispecies framework enabled estimation of species-level averages and shifts in relation to phenology and range, identification of trait- and phylogeny-mediated variation in phenology and range shifts, and quantification of covariance between the two responses. We further partitioned variation among traits, phylogeny, species-specific processes, and prediction uncertainty to assess their relative contributions to observed interspecific differences.

We fitted the models using hierarchical Bayesian inference with stan software (Stan Development Team, 2025b) accessed through R (version 4.4.2; R Core Team (2021)), using the rstan-package (Stan Development Team, 2025a). We took in a total of five chains each with 16000 posterior samples of which we discarded the first 2000 as burn-in and thinned the resulting samples with a factor of 10. This resulted in 7000 posterior samples. We confirmed the model convergence with a potential scale reduction factor and by checking effective sample sizes. The multi-species phenology-range model and variance partitioning are explained with higher level of detail in the supporting information.

### 3 RESULTS

We found that, on average, species advanced the onset of adult flight time (later referred to just as phenology; average response  $> 0$  with 0.0495% probability) and expanded their the northern range boundary (later referred to just as range shift; average response  $> 0$  with 97.0% probability) (Fig. 3: panel A). Overall, 41% of the species were uncertain in relation to phenology and range shifts (according to 95% credibility interval), whereas, 27% of the the species both advanced their phenology and shifted northward (Fig. 3: panel B).

The estimated trait associations showed that phenology shifts varied in relation to the length of the flight period, and mobility (Fig. 5: panel A). Species with a shorter flight period and high mobility advanced their phenology more readily compared to other species. In terms of range shift, species with broad habitat use, higher temperature breadth index, shorter flight period, and higher mobility shifted faster their northern range boundary northwards (Fig. 5: panel A).

The variance partitioning showed that the onset of adult flight time was mostly random: on average  $> 50\%$  of the variation originated from the prediction uncertainty of phenology, whereas the uncertainty of the species-level phenology shift (process uncertainty) was relatively low. The next most important sources of variation were those mediated by phylogeny ( $\sim 20\%$ ) and traits ( $\sim 8\%$ ) (Fig. 5: panel B). In contrast, the latitude of the northern range boundary varied primarily in relation to species-level shifts mediated by traits ( $\sim 25\%$ ) and phylogeny ( $\sim 30\%$ ). Prediction uncertainty of the northern range boundary and the uncertainty of the species-level range shift (process uncertainty) corresponded only to  $\sim 10\%$  of the total variation (Fig. 5: panel B).

To compare the levels of uncertainty in phenology and range shifts, we quantified the variability of the mean estimated shift between species (interspecific), and mean of the species specific uncertainty of the shift (uncertainty) (Fig. 4). This decomposition showed substantial heterogeneity between species in both phenology and range shifts: the variability of the mean estimated shift between species accounted for  $\sim 75\%$  of the total variation in phenology and range shifts, while the mean of the species specific uncertainty of the shift contributed 25% of the total variation.

When testing differences between southern and northern species in their phenology and range shifts (i.e., whether the shift depended on the average location of the species northern range boundary), we found interesting tradeoffs: Southern species advanced their phenology more while northern species tended to expand their northern range boundary further north (Fig. 6: panel A).

Finally, our results revealed a significantly synergistic coupling pattern, with stronger phenology advances being connected with stronger northwards shifts of the northern range boundary (Fig. 6: panel B). The synergy between these shifts remained consistent when looking southern and northern species as separate groups although southern species more often advanced their phenology compared to shifting their ranges while northern species tended to do the opposite (Fig. 6: panel C).

In addition to interspecific differences, we inspected how the average phenology varied intraspecifically between the simplified southern (hemi- and southern boreal zones) and northern (middle- and northern boreal zones) bioclimatic zones. Although we found that for most species, phenology onset occurred later in the northern bioclimatic zones (Fig. S2 in the supporting information), the direction and magnitude of phenology shift did not differ between bioclimatic zones for any of the species.

### 4 DISCUSSION

Climate warming creates a spatial-versus-temporal tracking trade-off, but species with high response capacity overcome this trade-off and shift in both dimensions simultaneously.

We found that boreal butterflies have advanced the onset of adult flight time and expanded their northern range boundary, indicating that temporal and spatial climate tracking are generally coupled (Fig. 6). This supports the synergistic-response scenario (H5.2) in contrast to shifts being complementary (species going either for phenology or range shift) or uncoupled (no association between the shifts) and suggests that species differ primarily in overall responsiveness to climate warming rather than in their choice between phenology and spatial tracking. Such synergy between phenology and range shifts has previously been found for birds (Radchuk et al., 2019), while complementary shifts were more common for butterflies and moths (Hällfors et al., 2021; Goded et al., 2024). This would indicate that pressure and ability to respond to environmental change are both clustered within the species pool and support the dichotomy of winners and losers when facing environmental

change. Considering our finding that species were equally heterogeneous in relation to phenology and range shifts (equally strong interspecific variation in mean shifts compared to the species-level uncertainty of the shifts), we conclude that phenology and range shifts were equally strong in comparison to random year-to-year variation and uncertainty (Fig. 4 and 5). Hence, we interpret that there was **equally strong** selection to both shifts among species. This conclusion slightly contrasts with the conclusions of Neate-Clegg et al. (2024), which found that North American birds shift their phenology more compared to shifts in their latitudinal and altitudinal ranges.

Almost 30% of the species both advanced their phenology and expanded their range boundary northward (coupled and synergistic responses). This is a larger proportion compared to Hällfors et al. (2021), who found this type of combined response for only 15% of boreal butterflies and moths. Almost half of the species advanced their phenology, which is consistent with previous findings (Roy and Sparks (2001); Diamond et al. (2011)). The average phenology advance of ~1 day per decade was less than what has been found for butterflies in Britain (~5 days per decade in Diamond et al. (2011)). The contrast between the estimates of phenology shift for butterflies in Finland and Britain may be due to a longer time frame (more than 30 years in Diamond et al. (2011)) and differences in the abiotic and photoperiodic constraints between the temperate and boreal bioclimatic zones (Mills et al., 2017). Regarding range shifts, we found that every third species expanded their northern range boundary, which is slightly fewer compared to earlier studies on partly the same species (Pöyry et al., 2009; Parmesan et al., 1999). The average rate of range boundary shift that we found, 25 km per decade, is also weaker compared to the almost 60 km per decade shift revealed by Pöyry et al. (2009). Although the average phenology and range shifts were slower than expected based on previous studies, the shifts showed clear associations with traits and consistent spatial differences.

#### 4.1 Trait and phylogenetic associations

Species with broad habitat use, broad thermal tolerances, short flight periods, and high mobility shifted their ranges more strongly. These results are in accordance with our expectations and previous findings (Pöyry et al., 2009; Hällfors et al., 2024; Sunde et al., 2023; Buckley and Kingsolver, 2012b; Altermatt, 2010) and implies that well-dispersing species with affinities to several different habitat types and temperature conditions allow climatic tracking through range shifts. The short flight period and high mobility also promoted advances in phenology. These traits likely represent a general response capacity that enables species to track climate change along spatial and temporal dimensions and creates synergy between phenology and range shifts. Although there is no theoretical or empirical support for the short flight period in itself to directly promote phenology or range shifts, or high mobility to support phenology shifts, these traits may obscure the effects of unobserved traits, such as voltinism and the over wintering strategy (Diamond et al., 2011; Zografou et al., 2021). In addition, a short flight period can be associated with a relatively high temperature breadth index (Diamond et al., 2011), and therefore it may capture a part of the mechanistic association between the temperature breadth index and the range shift. Previously, Hamon et al. (2025); Larsen et al. (2022) found that short flight periods were correlated with late phenology and that late appearing butterflies had better abilities to use advancing suitable environmental conditions and appear earlier in the season. They also found that relatively early emerging species needed to cope with early-season variation in weather conditions and photoperiodic constraints, potentially restricting phenology advancement. In this study, we did not include the photoperiod as an explanatory variable, but investigating its effects would be important, especially to understand the potential restrictions in the advancement of the phenology of early-season species (Mushegian et al., 2021; Lindestad et al., 2019).

In general, we found that traits were strong predictors of range shifts, whereas phenology shifts were relatively weakly mediated by traits. Phylogeny was a relatively strong predictor of both phenology and range shifts. This indicates that response capacity is phylogenetically conserved. Hence, we include the phylogenetic signal as one of the mechanisms that maintain synergy between phenology and range shifts.

Our finding of high importance of traits for range shifts contrasts with previous studies (Beissinger and Riddell, 2021; MacLean and Beissinger, 2017; Hällfors et al., 2021), which found that traits are relatively poor predictors of range shifts. We expect that our methodological choices increased the mediating impact of traits on range shifts. Compared to Hällfors et al. (2021), we partially used the same data, but used them in a more comprehensive manner by modelling species distributions, accounting for different survey types of presence-absence and presence-only data and expanding the number of butterfly species in the analysis.

#### 4.2 Spatial differences

We found that the pace of the phenology shift increased south, while the pace of range shift increased north creating a tendency toward complementary responses. This latitudinal tradeoff between phenology and range shift is likely due to the latitudinally varying abiotic environment. Previous studies have shown that high interannual variation in snow melt and strict photoperiod at high latitudes can limit the ability of species to advance the onset of adult flight time, as found by (Lindestad et al., 2019) and supporting our finding of slower advance of the onset of adult flight time at higher latitudes. In relation to range shifts, seasonality and extreme conditions are the main selective forces at the leading range boundaries, and increasing interannual variability towards higher latitudes may limit range expansions of thermally specialised species compared to thermal generalists

(Bontrager et al., 2021; Buckley and Kingsolver, 2012a). Therefore, species with a broader thermal niche and thus a higher temperature breadth index have a better ability to expand their geographical range (Hällfors et al., 2024), and broader niches tend to be positively correlated with latitude, also known as Rapoport's rule (Stevens, 1989; Deutsch et al., 2008). This is supported by our result showing faster range shifts for species with high temperature breadth index.

Despite the evident latitudinal gradient of phenology and range shifts, factors related to response capacity, such as traits and phylogeny, that are not related to latitude (as much discussed in Buckley and Kingsolver (2012b)) were strong enough to override the latitudinal effect and create a synergy between phenology and range shifts. This conclusion was supported by the finding that phenology and range shifts were also synergistic **within** the southern and northern species groups.

### 4.3 Random variability

The onset of adult flight time was, in contrast to the northern range boundary, more dominated by prediction uncertainty than by the directional shift or interannual variation of the mean value (=process uncertainty in Fig. 5). The uncertainty of phenology predictions reflects strong within-population variability. We expect that an important factor beyond the difference between the onset of adult flight time and the northern range boundary is that the onset of adult flight time is sensitive to short-term temperature cues that vary from year to year (Hamon et al., 2025; Larsen et al., 2022; Gerlich et al., 2025), while the northern range boundary is a product of population level processes throughout the year. We account for this difference by defining the phenology at a daily resolution and the northern range boundary at an annual resolution. We expect that weather conditions and the emergence of flying adults become more uncertain in a daily resolution compared to an annual resolution, and hence we found the high level of prediction uncertainty for the onset of adult flight time. However, the high uncertainty of the prediction did not inflate the uncertainty of the estimates for the species-level phenology shifts.

### 4.4 Integration of different observational data

We applied a novel modelling framework to study joint phenology and range shifts. First, we combined systematically and opportunistically collected species data for fitting species distribution models. Second, we used species distribution models for deriving probabilistic predictions of phenology and range time-series. Third, we fitted a multi-species joint model for the time-series to estimate the species-level pace of phenology and range shift and assess the mediating effects of traits and phylogeny. Such innovations have been called for as applications for integrated species distribution models (Isaac et al., 2020) and to study in parallel the trait mechanisms governing phenology and range shifts (Beissinger and Riddell, 2021; Fredston et al., 2025). Although we find consistent but slightly more conservative estimates for the magnitude of both phenology and range shifts compared to previous studies, this may likely be an effect of a statistically robust and comprehensive method that accounts for data and model uncertainties. However, methodological comparison and validation for accurately predicting time-series with integrated species distribution models are still required. For example, the risk of confounding an increasing sampling effort with a shift in range boundary would require more investigation. We expect that if having mixed parallel changes in sampling effort and population densities, we would have found more uniform and stronger phenology and range shifts. In general, we expect that this study will precede and set the stage for efforts to link data sets and response mechanisms in analytically comprehensive ways.

In summary, we found that in relation to phenology and range shifts species are split into two categories: responsive and non-responsive. Species response capacity was explained primarily by phylogeny, whereas traits could explain only the pace of range shift. Despite a strong indication for phenology and range shifts reflecting species overall response capacity, climate warming creates a spatial-versus-temporal tracking trade-off: southern species advanced phenology more strongly while northern species showed stronger range expansion. This demonstrates that the same intrinsic capacity produces different realized responses in different environmental or biogeographic contexts. To our knowledge, this is the first study to show such latitudinally structured phenology and range shifts. Importantly, we show that studying phenology and range shifts jointly can improve our understanding of how species respond to climate warming, and thus help develop predictions on species' adaptive capacity under climate change. Shifts in phenology and range seem to be connected and evaluating them together has the potential to uncover new insights into the drivers of biodiversity change.

## DATA AVAILABILITY STATEMENT

Data and code are shared with the reviewers as a repository that will be published in Zenodo after the manuscript has been accepted. The raw data for climate, vegetation, species occurrences and species traits are stored in public repositories and can be accessed through them. The annual predictions for the onset of the phenological cycles and northern range boundaries along with the standardized trait and phylogenetic distances for running the multispecies joint model are stored in the repository accompanying the manuscript.

Climate data for daily mean temperature and daily precipitation sum in 10km\*10km were derived from the Finnish Meteorological Institute (Institute, 2016). Data are publicly available through the Finnish Meteorological Institute and described

in Aalto et al. (2016).

Vegetation data were derived from the European Space Agency (ESA) Land Cover Climate Change Initiative: Global Plant Functional Types (PFT) Dataset, v2.0.8 (Harper et al., 2023b). The data are publicly available through the data repository of ESA.

Species transect surveys are part of the European Butterfly Monitoring Schemes (EBMS). The data are not directly available as the data users need to commit to the user policies of the EBMS network. However, the data are accessible as part of a wider European butterfly transect dataset through EBMS after formally completing a license form (<https://butterfly-monitoring.net/ebms-dataaccess>)

Species point occurrences were downloaded through the Finnish Biodiversity Info Facility. The specific download is identified and reproducible following <http://tun.fi/HBF.104415>. The data sources are Lajitietokeskus/FinBIF - Notebook, general observations, Iisalmi Natural History Museum Collections, Porvoo Museum / Natural History, Collections of University of Turku, Data sources of the Parks & Wildlife Finland, Collections of the Kuopio Natural History Museum, Collections of the Finnish Museum of Natural History Luomus, Data sources of the Finnish Environment Institute Syke (Syke), National Butterfly Recording Scheme in Finland (NAFI). The specific sources can be accessed through the Finnish Biodiversity Information Facility/FinBIF (<http://tun.fi/HR.175>, <http://tun.fi/HR.203>, <http://tun.fi/HR.209>, <http://tun.fi/HR.447>, <http://tun.fi/HR.527>, <http://tun.fi/HR.528>, <http://tun.fi/HR.1747>, <http://tun.fi/HR.2029>, <http://tun.fi/HR.2269>, <http://tun.fi/HR.2832>, <http://tun.fi/HR.3431>, <http://tun.fi/HR.3553>, <http://tun.fi/HR.3931>, <http://tun.fi/HR.4131>, <http://tun.fi/HR.4191>, <http://tun.fi/HR.4251>, <http://tun.fi/HR.4471>, <http://tun.fi/HR.4511>, <http://tun.fi/HR.4612>, <http://tun.fi/HR.4752>, <http://tun.fi/HR.5018>, <http://tun.fi/HR.5042>, <http://tun.fi/HR.5095>, <http://tun.fi/HR.5115>, <http://tun.fi/HR.5235>, <http://tun.fi/HR.5236>, <http://tun.fi/HR.5256>, and <http://tun.fi/HR.5257>. The data were accessed 2025-04-28.

Bioclimatic zones were derived from the data for forest vegetation zones through the Finnish Environment Institute <https://www.syke.fi/en/environmental-data/downloadable-spatial-datasets>, (Finnish Environment Institute (Syke), 2026).

Species trait data (host use, habitat breadth, flight period and mobility) were derived from the appendix of Komonen et al. (2004).

Species temperature breadth index was derived from the data repository (Mäkinen et al., 2025a) that accompanies to Mäkinen et al. (2025b).

Species phylogenetic distances were derived from the phylogenetic tree in Wiemers et al. (2019) that accompanies to Wiemers et al. (2020).

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## TABLES

**Table 1.** Summary of traits and their expected impacts on the responses.

| Trait                                                    | Values                                                                                                             | Expected impact                                                                                                                                                                                                                                                                                                          |
|----------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Host use                                                 | monophagous (single plant species), oligophagous (single plant genus), and polyphagous (at least one plant family) | Species with strict host-plant requirements shift their ranges and phenology only if the host plants also track climate change across space or seasonal time, making them more sensitive to mismatches and limiting their ability to exploit new areas on the geographical or seasonal axes (Navarro-Cano et al., 2015). |
| Habitat breadth                                          | 1 (single habitat types), 2 (two habitat types), 3 (three to four habitat types)                                   | Habitat specialists can only expand or shift their ranges if climate-driven changes coincide with the availability of their specific habitat types, making them less flexible vis-a-vis range shifts compared to generalists (Oliver et al., 2009).                                                                      |
| Flight period                                            | Continuous value ranging 8.1-114.4 (days)                                                                          | Species with longer flight periods can adjust emergence to warming temperatures more easily, facilitating phenology shifts and potentially increasing the number of generations during one season (Zografou et al., 2021). Thus, longer flight period corresponds associates with higher flexibility.                    |
| Mobility                                                 | Index 0 (sedentary) - 10 (very mobile)                                                                             | More mobile species can track shifting climate zones faster and colonize new suitable areas, enabling quicker range expansions and reducing the risk of local extinction (Evans et al., 2020).                                                                                                                           |
| Breadth of thermal tolerance (Temperature breadth index) | Continuous value ranging 1.74-4.12 (°C)                                                                            | Species with wide thermal tolerance (high temperature breadth index) can maintain performance across a wider range of climatic conditions, allowing them to persist during warming and occupy newly suitable climates (Hällfors et al., 2024)                                                                            |

**Table 2.** Summary of hypothesis and evaluating them with parameter estimates.

|    | Hypothesis explanation                                                                                                    | Parameter test                                                                |
|----|---------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------|
| H1 | Species have advanced their onset of adult flight time and expanded their northern range boundary                         | $\mu < 0$ for phenology and $> 0$ for range                                   |
| H2 | Advancing onset of adult flight time and expanding northern range boundary are associated with different trait categories | Comparison of $\theta$ estimates among trait categories                       |
| H3 | Northern range boundary expands faster for southern compared to northern species                                          | Comparison of $\theta$ estimates between southern and northern species        |
| H4 | High magnitude of random variability in both shifts                                                                       | Variance partitioning of shifts, prediction uncertainty and model uncertainty |
| H5 | Shifts are uncoupled (scenario 5.1 in Fig. 1)                                                                             | Correlation between $\theta$ of phenology and range shifts                    |

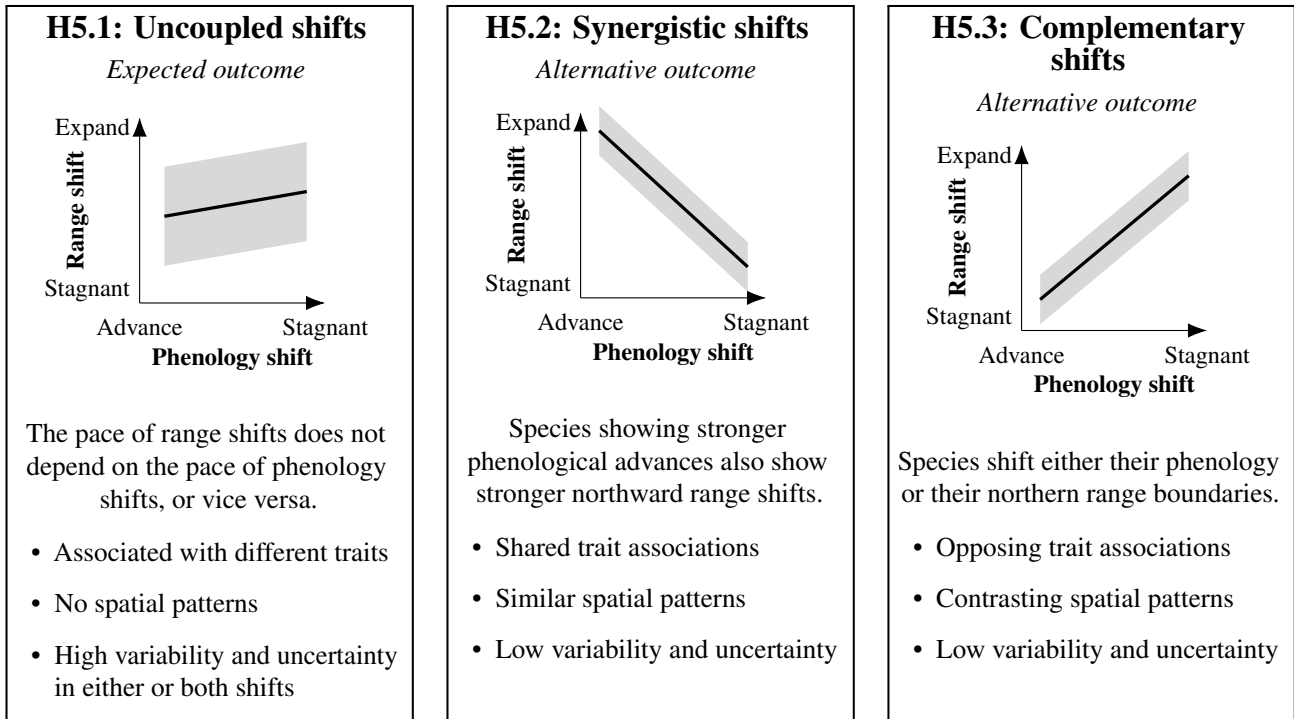


**Figure 1.** Conceptual framework linking the mechanisms underlying phenology and range shifts to the expected coupling between the two responses. In hypothetical graphs, black line denotes the mean shift and gray area the associated uncertainty. We hypothesise that phenology and range shifts are associated with different combinations of species traits (H2), show different spatial patterns (H3), and differ in the magnitude of random variability (H4). Together, these mechanisms lead us to predict that the paces of phenology and range shifts are uncoupled (H5.1). Synergistic shifts, in which species showing stronger phenological advances also show stronger northward range shifts (H5.2), and complementary shifts, in which species predominantly shift either phenology or range (H5.3), represent alternative coupling patterns.

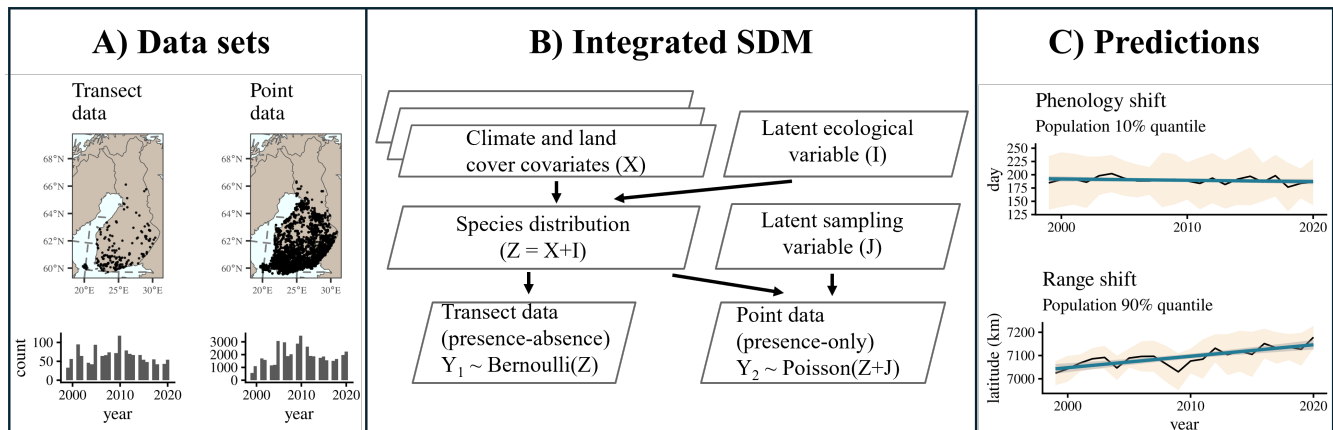


**Figure 2.** Summary of the modeling workflow. Panel A shows the spatial and temporal distribution of systematically and opportunistically collected data for an example species, *Thymelicus lineola*. Panel B lays out the concept of model-based data integration, where the inference of an SDM is based on shared parameters between presence-absence and presence-only data types. Panel C shows the model-based timeseries of the onset of adult flight time and the northern range boundary with the prediction mean (black line), prediction standard deviation (yellow shaded area), linear change in the mean (blue line), and the associated uncertainty (grey shading).

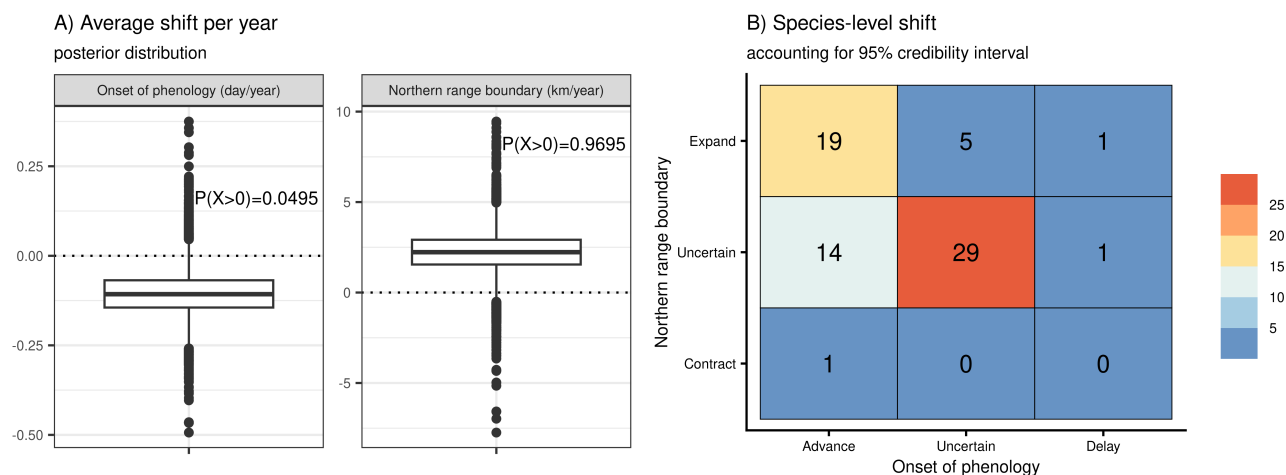


**Figure 3.** Panel A shows the population mean of the annual shift in phenology and northern range boundary through boxplots of the full posterior distributions. Panel B shows the combined responses in number of species. The x-axis separates the species with respect to phenology shifts and the y-axis separates the species with respect to range shifts.

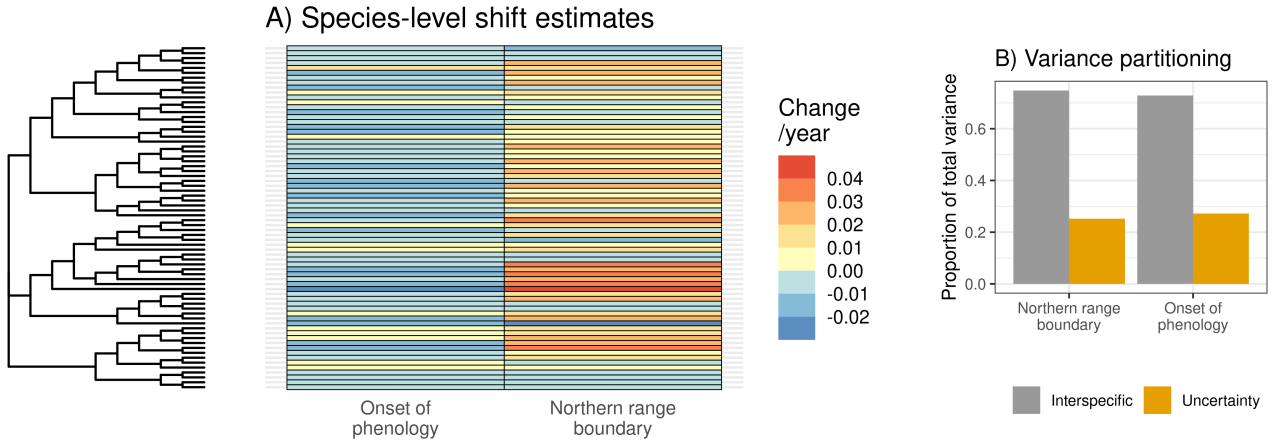


**Figure 4.** Panel A shows the species-level mean shifts in relation to phylogeny. Values are on standardized scales to make their comparison easier. In panel B, bars denote the proportions of total variance in the species-level shift estimates that are due to variability of the mean estimated shift between species (interspecific) and mean of the species specific uncertainty of the shift (uncertainty).

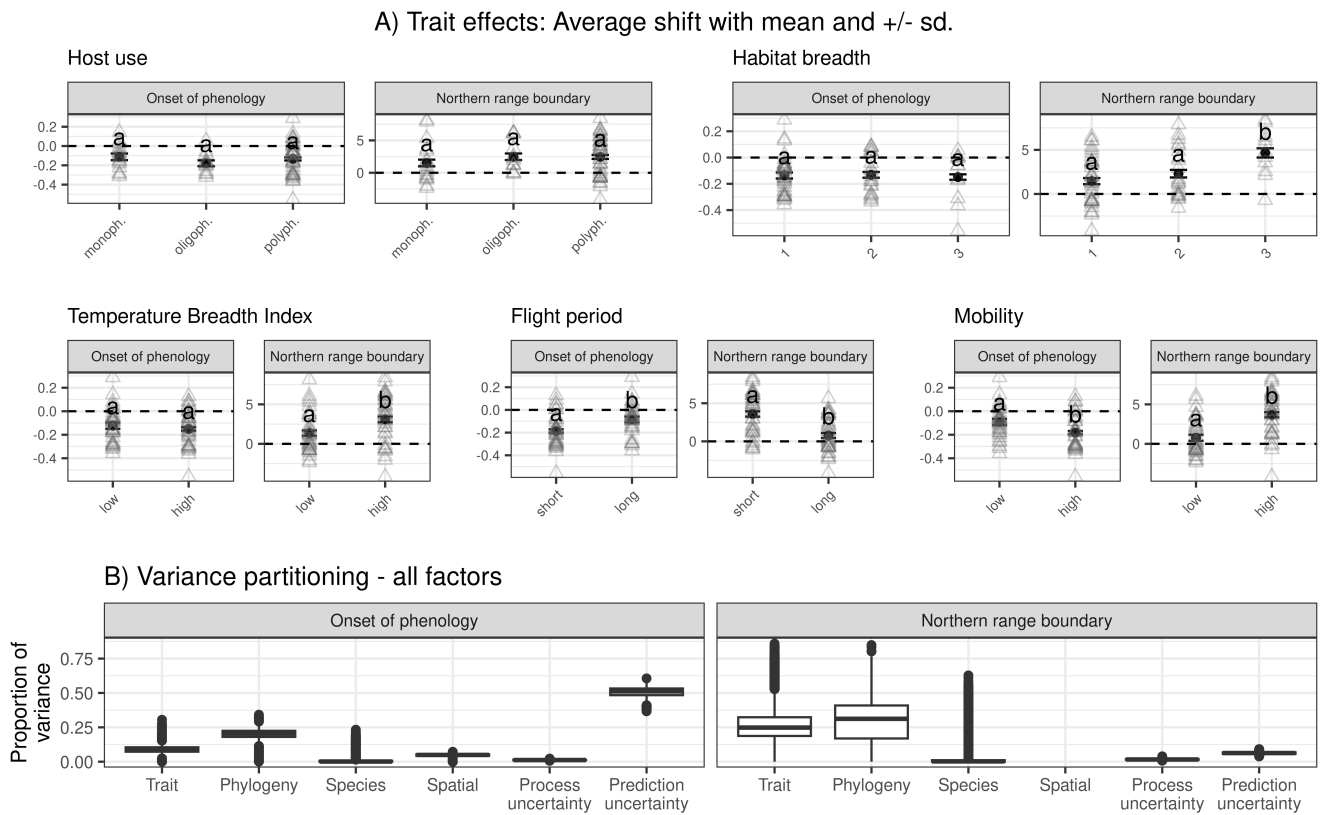


**Figure 5.** In panel A, each plot shows the species level shifts with respect to phenology and range. Grey triangles show the posterior means of the species level shifts, black dots show the posterior means for species of the different trait categories and error bars show the standard deviation of the mean of the posterior samples. For visualization we simplified the continuous trait variables (temperature breadth index, length of the flight period, and mobility) by discretizing species to binary groups based on that whether species are above or below the median trait value. We used the median value as the threshold. Panel B shows the variance partitioning for the onset of the adult flight time and northern range boundary. Note that there was no spatial term included in the model for range shift.

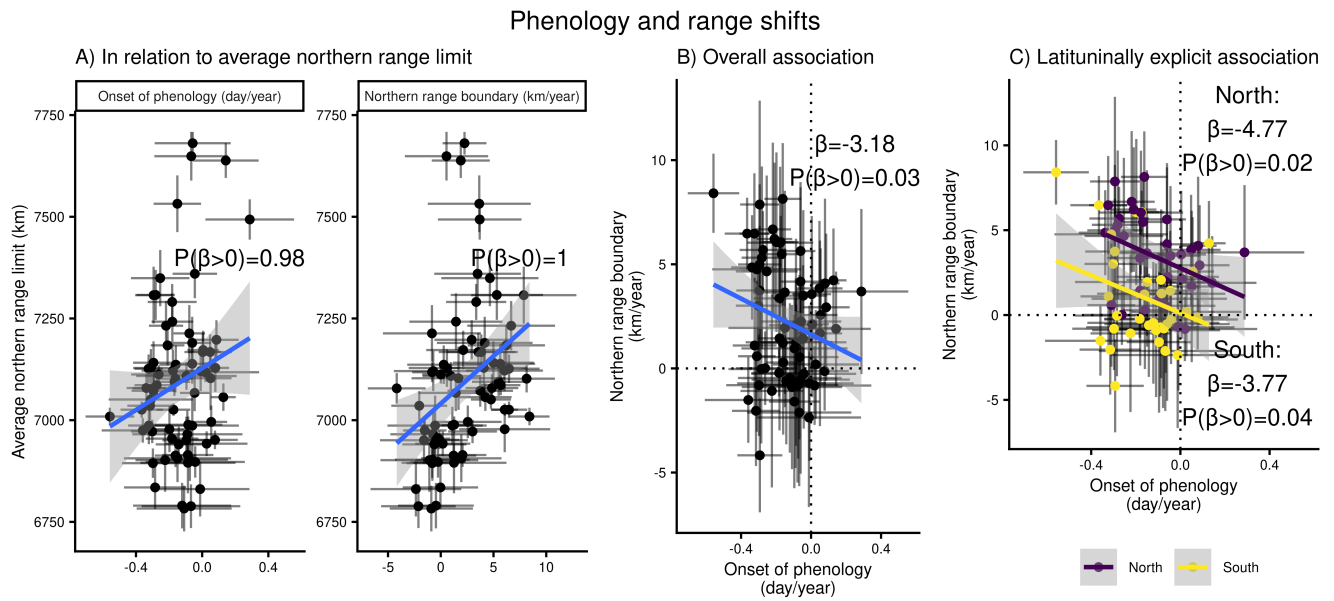


**Figure 6.** Panel A shows the association between the species-level phenology and range shifts (x-axis) and the average latitude of the species northern range boundary (y-axis). Points denote mean estimates, and error bars show the 95 % credibility intervals. The blue lines denote the linear association between the mean values while the gray area denotes the 95 % credibility interval of the linear association. Panel B shows the association between the species-level phenology and range shifts. Points denote means shifts, and error bars show the 95 % credibility intervals. The blue line denote the linear association between the mean values while the grey area denotes the 95 % credibility interval of the linear association. Panel C shows the respective association separately for northern and southern species. In each panel  $\beta$  denotes the linear association between the variables on the x- and y-axes, with probability computed over the posterior samples of the variables.

1 Supporting information for "Synergistic phenology  
2 and range shifts in boreal butterflies reflect species'  
3 overall response capacity"

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14 September 24, 2026

# 1 Species list

Table 1: Species, number occurrence records in presence-only (PO) and presence-absence (PA) data sets, number of absence records in PA data set, estimate for phenology and range shifts (positive, negative or uncertain) and position of average northern range boundary (southern or northern).

| Species                          | PO    | PA Occ. | PA Abs. | Phenology | Range     | Range Avg. |
|----------------------------------|-------|---------|---------|-----------|-----------|------------|
| <i>Agriades optilete</i>         | 6217  | 1192    | 16163   | Negative  | Positive  | North      |
| <i>Anthocharis car-damines</i>   | 18824 | 3355    | 14000   | Uncertain | Uncertain | North      |
| <i>Apatura iris</i>              | 979   | 108     | 17247   | Uncertain | Uncertain | South      |
| <i>Aphantopus hyperantus</i>     | 69052 | 6275    | 11080   | Negative  | Positive  | South      |
| <i>Aporia crataegi</i>           | 11849 | 1382    | 15973   | Negative  | Negative  | South      |
| <i>Araschnia levana</i>          | 12069 | 2469    | 14886   | Uncertain | Uncertain | North      |
| <i>Argynnis laodice</i>          | 137   | 17      | 17338   | Uncertain | Uncertain | South      |
| <i>Argynnis paphia</i>           | 11440 | 1842    | 15513   | Negative  | Uncertain | South      |
| <i>Aricia artaxerxes</i>         | 3682  | 1562    | 15793   | Negative  | Positive  | South      |
| <i>Aricia nicias</i>             | 347   | 17      | 17338   | Negative  | Positive  | North      |
| <i>Boloria aquilonaris</i>       | 1472  | 82      | 17273   | Negative  | Positive  | North      |
| <i>Boloria eunomia</i>           | 1701  | 57      | 17298   | Negative  | Uncertain | North      |
| <i>Boloria euphrosyne</i>        | 11648 | 2159    | 15196   | Uncertain | Uncertain | North      |
| <i>Boloria freija</i>            | 1317  | 3       | 17352   | Uncertain | Positive  | North      |
| <i>Boloria frigga</i>            | 867   | 14      | 17341   | Uncertain | Uncertain | North      |
| <i>Boloria selene</i>            | 23696 | 4520    | 12835   | Negative  | Positive  | North      |
| <i>Boloria titania</i>           | 367   | 13      | 17342   | Negative  | Uncertain | North      |
| <i>Brenthis ino</i>              | 31820 | 5521    | 11834   | Negative  | Positive  | North      |
| <i>Callophrys rubi</i>           | 28297 | 4219    | 13136   | Uncertain | Positive  | North      |
| <i>Carterocephalus palaemon</i>  | 557   | 90      | 17265   | Uncertain | Uncertain | North      |
| <i>Carterocephalus silvicola</i> | 7908  | 2045    | 15310   | Uncertain | Uncertain | South      |
| <i>Celastrina argiolus</i>       | 9670  | 2054    | 15301   | Uncertain | Uncertain | North      |
| <i>Coenonympha glycerion</i>     | 11510 | 2517    | 14838   | Negative  | Uncertain | South      |
| <i>Coenonympha pamphilus</i>     | 3299  | 645     | 16710   | Uncertain | Positive  | North      |
| <i>Coenonympha tullia</i>        | 974   | 31      | 17324   | Negative  | Uncertain | North      |
| <i>Colas palaeno</i>             | 7536  | 650     | 16705   | Negative  | Positive  | North      |
| <i>Cyaniris semiargus</i>        | 12509 | 3366    | 13989   | Negative  | Positive  | North      |
| <i>Erebia embla</i>              | 641   | 24      | 17331   | Positive  | Uncertain | North      |
| <i>Erebia ligea</i>              | 20723 | 2905    | 14450   | Negative  | Positive  | North      |
| <i>Euphydryas aurinia</i>        | 486   | 67      | 17288   | Uncertain | Uncertain | North      |
| <i>Euphydryas maturna</i>        | 3722  | 536     | 16819   | Negative  | Uncertain | South      |

| Species                         | PO     | PA Occ. | PA Abs. | Phenology | Range     | Range Avg. |
|---------------------------------|--------|---------|---------|-----------|-----------|------------|
| <i>Fabriciana adippe</i>        | 13903  | 3319    | 14036   | Negative  | Uncertain | South      |
| <i>Fabriciana niobe</i>         | 626    | 132     | 17223   | Negative  | Uncertain | South      |
| <i>Favonius quercus</i>         | 569    | 82      | 17273   | Uncertain | Uncertain | South      |
| <i>Glaucopsyche alexis</i>      | 1196   | 180     | 17175   | Uncertain | Uncertain | South      |
| <i>Hipparchia semele</i>        | 646    | 13      | 17342   | Uncertain | Uncertain | South      |
| <i>Issoria lathonia</i>         | 2354   | 374     | 16981   | Negative  | Uncertain | South      |
| <i>Lasiommata maera</i>         | 13245  | 2568    | 14787   | Uncertain | Uncertain | South      |
| <i>Lasiommata petropolitana</i> | 3638   | 743     | 16612   | Uncertain | Positive  | North      |
| <i>Leptidea sinapis</i>         | 13761  | 3285    | 14070   | Positive  | Positive  | South      |
| <i>Limenitis populi</i>         | 3029   | 321     | 17034   | Negative  | Positive  | South      |
| <i>Lopinga achine</i>           | 256    | 7       | 17348   | Uncertain | Uncertain | North      |
| <i>Lycaena helle</i>            | 640    | 10      | 17345   | Negative  | Uncertain | North      |
| <i>Lycaena hippothoe</i>        | 4647   | 1548    | 15807   | Negative  | Uncertain | South      |
| <i>Lycaena phlaeas</i>          | 8570   | 2314    | 15041   | Uncertain | Uncertain | South      |
| <i>Lycaena virgaureae</i>       | 22714  | 4584    | 12771   | Negative  | Positive  | North      |
| <i>Maniola jurtina</i>          | 951    | 99      | 17256   | Uncertain | Uncertain | South      |
| <i>Melitaea athalia</i>         | 8737   | 1909    | 15446   | Negative  | Positive  | South      |
| <i>Melitaea cinxia</i>          | 110    | 9       | 17346   | Uncertain | Uncertain | South      |
| <i>Nymphalis antiopa</i>        | 19164  | 2776    | 14579   | Negative  | Uncertain | North      |
| <i>Ochlodes sylvanus</i>        | 24474  | 4699    | 12656   | Negative  | Positive  | South      |
| <i>Oeneis jutta</i>             | 1265   | 7       | 17348   | Uncertain | Uncertain | North      |
| <i>Papilio machaon</i>          | 5592   | 584     | 16771   | Uncertain | Uncertain | North      |
| <i>Pararge aegeria</i>          | 1498   | 393     | 16962   | Uncertain | Uncertain | South      |
| <i>Parnassius apollo</i>        | 850    | 2       | 17353   | Uncertain | Uncertain | South      |
| <i>Parnassius mnemosyne</i>     | 2005   | 210     | 17145   | Negative  | Uncertain | South      |
| <i>Pieris napi</i>              | 103132 | 13324   | 4031    | Uncertain | Uncertain | North      |
| <i>Plebejus argus</i>           | 9805   | 1870    | 15485   | Negative  | Positive  | North      |
| <i>Plebejus idas</i>            | 7535   | 1517    | 15838   | Negative  | Positive  | North      |
| <i>Polyommatus amandus</i>      | 18124  | 4220    | 13135   | Negative  | Positive  | South      |
| <i>Polyommatus icarus</i>       | 10277  | 2762    | 14593   | Negative  | Positive  | North      |
| <i>Pyrgus alveus</i>            | 643    | 103     | 17252   | Negative  | Uncertain | South      |
| <i>Pyrgus centaureae</i>        | 394    | 2       | 17353   | Uncertain | Uncertain | North      |
| <i>Pyrgus malvae</i>            | 3254   | 721     | 16634   | Uncertain | Uncertain | South      |
| <i>Satyrrium pruni</i>          | 768    | 272     | 17083   | Uncertain | Uncertain | South      |
| <i>Satyrrium w-album</i>        | 385    | 17      | 17338   | Uncertain | Uncertain | South      |
| <i>Scolitantides orion</i>      | 769    | 15      | 17340   | Uncertain | Uncertain | South      |
| <i>Speyeria aglaja</i>          | 15199  | 3576    | 13779   | Uncertain | Positive  | North      |
| <i>Thecla betulae</i>           | 1504   | 357     | 16998   | Uncertain | Uncertain | South      |
| <i>Thymelicus lineola</i>       | 45856  | 5791    | 11564   | Negative  | Positive  | South      |

## 2 Species distribution modeling

For both phenology and range, we applied SDMs to explain species-environment associations and predict adult flight time and geographical ranges. Commonly, SDMs associate species occurrence records with environmental variables and assume spatial or spatio-temporal variation in the underlying species distribution (4). We utilised model-based data integration (later referred to as data integration) for systematically (presence-absence) and opportunistically (presence-only) collected species observations. The basic idea of data integration is that discrepant data types and data collection methods are considered through appropriate model types and terms while still estimating spatio-temporal dynamics of species distributions and species-environment associations with both data types (9; 7). Previous research has shown that such data integration can improve the general predictive accuracy of SDMs (11), and especially the predictions of species range boundaries (12).

For both phenology and range, we defined observation models for the presence-absence (1) and presence-only (2) data:

$$p(y(s, t)_{PA}) \sim \text{Bernoulli}(\pi(s, t)_{PA}), \quad (1)$$

where  $y(s)_{PA}$  is the species presence-absence status (1/0) in a location (s) and time point (t), and  $\pi(s)_{PA}$  is the probability of species presence.

$$p(y(s, t)_{PO}) \sim \text{Poisson}(\lambda(s, t)_{PO}), \quad (2)$$

where  $y(s)_{PO}$  is the species presence record in a location (s) and time point (t), and  $\lambda(s)_{PO}$  is the species areal density. We then integrated the presence-absence and presence-only data by summing the likelihoods of the observation models following common procedures for data integration in SDMs (9; 12),

$$p(y(s, t)_{PA}, y(s, t)_{PO}) = p(y(s, t)_{PA}) p(y(s, t)_{PO}). \quad (3)$$

We calculated the likelihood of the presence-absence data over the spatio-temporally explicit survey transects. In contrast to the conventional presence-absence model, we modeled presence-only data as an inhomogeneous Poisson point process, where the locations and the total number of species presences depend on a spatially varying species areal density ( $\lambda(s)_{PO}$ ) (15). Due to the lack of absence information for the presence-only data, we approximated the likelihood over the spatio-temporal extent by sampling background points (also known as quadrature points), which we treated as absence observations (15). Until this point, the SDMs for phenology and range shifts were treated analogously, but because they differ in terms of the spatio-temporal resolution and linear predictors for the presence probability and areal density, we used different background point schemes for them.

*Phenology SDM*

We defined the SDMs for phenology at a daily resolution over the study period to capture the interannual change in adult flight time. We also accounted for latitudinal variation in phenology by conditioning phenology by bioclimatic zones. The study area was divided into three major bioclimatic zones, the southern, middle, and northern boreal (Ahti et al.) (by combining the relatively small hemiboreal zone with the southern boreal zone, as done in (2)). Although we modeled the phenology of the adult flight time at a relatively coarse spatial resolution, we included environmental variables (climate and land use type) at the resolution of the exact spatial locations of the observations.

We assigned linear predictors for the presence probability of the presence-absence data and the areal density of the presence-only data. The linear predictor associates environmental covariates and spatio-temporal random effects with species observations. To scale the presence probability to linear space, we transformed it with a synergistic log-log link function:

$$\log(-\log(1 - \pi(s, d, t)_{PA})) = f(s, d, t)_{PA} = \alpha_{PA} + \beta \mathbf{X}(s, d, t) + g(d, t) + h(s, t), \quad (4)$$

where  $\pi(s, d, t)_{PA}$  is a species presence probability at location (s), on day of year (d) in year (t),  $\alpha_{PA}$  is an intercept specific to the data set,  $\beta$  is a vector of linear weights associated with the first and second order polynomial effects of environmental variables in the vector  $\mathbf{X}(s, d, t)$ , and  $g(d, t)$  is a temporal random effect. This random effect varies between day of the year and years and captures the average temporal species density (= adult flight time) across both data types and the interannual variation in the average species density. Finally,  $h(s, t)$  is a random effect which varies between the bioclimatic zones and years and captures the species average areal density in bioclimatic zones and the interannual variation in the areal density. We scaled the areal density for the presence-only data with a log link function:

$$\log(\lambda(s, d, t)_{PO}) = f(s, d, t)_{PO} = \alpha_{PO} + \beta \mathbf{X}(s, d, t) + g(d, t) + h(s, t) + \log(w), \quad (5)$$

where  $\lambda(s, d, t)_{PO}$  is the species areal density at location (s), on day of year (d) in year (t),  $\alpha_{PO}$  is a data set specific intercept, and  $\log(w)$  is log-transformed weight which corresponds to the area related to a presence observation (=0) or background point (=area of a Voronoi tessellation). The rest of the model terms are the same as in the linear predictor for the presence-absence data.

As sampling background points across the entirety of Finland at a daily resolution over 22 years would inflate the total number of background points, we simplified the sampling scheme for background points. We divided Finland into a systematic grid of 120 x 120 km resulting as 11 cells and extracted the center points of each cell in the resulting grid (Fig. S1: panel A). Next, we divided each year into 73 five-day bins. We sampled five-day bins across the study period at each center point of the spatial grid which resulted in 17666 background points.

#### Range SDM

We defined the SDM for species geographical range at a 1 x 1 km spatial resolution and an annual temporal resolution to capture annual range dynamics. Similarly to

phenology, we included the environmental variables in the exact spatial locations where observations were made.

The scaling between the probability of presence and the density of areals and the linear predictors was done as for phenology, but the linear predictors differed in terms of spatial and temporal resolution and model terms.

$$1 - \log(\log(\pi(s, t)_{PA})) = f(s, t)_{PA} = \alpha_{PA} + \beta \mathbf{X}(s, t) + i(s, t), \quad (6)$$

where  $\pi(s, d, t)_{PA}$  is a species presence probability at location (s), in year (t),  $\alpha_{PA}$  is an intercept specific to the data set,  $\beta$  is a vector of linear weights associated with the first and second order polynomial effects of environmental variables in the vector  $\mathbf{X}(s, t)$ , and  $i(s, t)$  is a spatio-temporal random effect.

$$\log(\lambda(s, t)_{PO}) = f(s, t)_{PO} = \alpha_{PO} + \beta \mathbf{X}(s, t) + \tau i(s, t) + j(s, t), \quad (7)$$

where  $\lambda(s, d, t)_{PO}$  is the species areal density at location (s), on day of year (d) in year (t), and  $\alpha_{PO}$  is an intercept specific to the data set.  $\beta$ ,  $\mathbf{X}(s, t)$  and  $i(s, t)$  are the same as in the linear predictor for the presence-absence data, and  $\tau$  is a parameter which scales the magnitude of variance between presence-absence and presence-only data. Finally,  $j(s, t)$  is a spatio-temporal random effect which aims to capture the spatio-temporally varying survey effort of the opportunistically collected presence-only data.

We applied Voronoi tessellation over the study area to sample spatial background points, (following (18)) and approximate the spatial component of the spatio-temporal random effect. We divided the study area into 1295 tessellation cells, each representing a background point (Fig. S1: panel B). While we had 22 years with each year having an analogous spatial tessellation, we finished with 28490 background points (see Fig. S2 in the supporting information), which is in line with the recommended magnitude of background points (15; 22). We used the same tessellation and background point locations for each year.

### Model fitting

The parameter sharing was enabled by link functions that scale different measures of a species population, namely the presence probability and the areal density, to the same linear space. The combination of complementary log-log and log link functions have been applied previously (e.g., (5; 17)). We used separate intercepts since the presence-absence data reflect species' relative presence probability while presence-only data reflect species' relative areal density. Neither of the data sets have been collected with a protocol that would allow estimating the detection probability and assign shared intercepts for the different data types via data integration. In our study, the separate intercepts reflect the difference between the unknown average detection probabilities between the data types. In effect, the shared parameters link the species' presence probability ( $\pi(s)_{PA}$ ) at the grid cell-level (1 km<sup>2</sup>) to the areal density of the point process ( $\lambda(s)_{PO}$ ).

We defined all temporal ( $g(d, t)$ ) and spatio-temporal ( $h(s, t)$ ,  $i(s, t)$ ,  $j(s, t)$ ) random effects as Gaussian processes. We applied Stochastic Partial Differential Equations

(SPDE) for approximating and computing the random effects (8; 10). The spatial component of the random effects  $i(s,t)$  and  $j(s,t)$  was approximated by coarsening its spatial resolution to 1295 tessellations (Fig. S1: panel B). For spatio-temporal random effects ( $i(s,t)$ ,  $j(s,t)$ ) we defined the full covariance as a separable spatio-temporal structure (3). The covariance is a Kronecker product of spatial and temporal covariance matrices. Spatial covariance is defined with a Matérn ( $\alpha=3/2$ )-type covariance function. Due to the large spatial and long temporal extent, we simplified the model by assuming temporal independence, and thus the covariance between years was fixed to zero. We set penalized complexity priors for the range and variance parameters of the spatial covariance function (19). The Matérn ( $\alpha=3/2$ ) covariance function is commonly applied in spatial statistics to capture spatially smooth variation (e.g., (17)). Priors were set to increase variation at short distances (probability 0.01 that the range parameter has a value corresponding to less than 20 km) and to constrain the magnitude of variance (with probability 0.01 that the standard deviation is over 1) following recommendations by (6; 13). Model intercepts, effects of environmental variables, and the scaling parameter ( $\tau$ ) were assigned Gaussian distributed priors with a mean of zero and variance of ten.

We followed the same procedure when defining the temporal ( $g(d,t)$ ) and spatio-temporal ( $h(s,t)$ ) random effects. For  $g(d,t)$ , we defined the temporal covariance in relation to the day of the year. Similarly, for applying spatio-temporal random effects, we used SPDE to approximate the temporal random effect and defined the covariance structure as a Kronecker product of two temporal covariance matrices (in relation to (1) the day of the year and (2) year). The random effect in relation to the day of the year was approximated by coarsening its temporal resolution to five-day bins. The temporal covariance with respect to the day of the year was defined with a Matérn ( $\alpha=3/2$ )-type covariance function and the temporal covariance with respect to the year was defined with a first-order autoregressive covariance (AR1) function (3). For the Matérn-covariance, we set priors to increase variation in longer temporal spans than 10 days (probability 0.1 that the range parameter has a value corresponding to less than 10 days) and to constrain the magnitude of variance (with probability 0.01 that the standard deviation is over 1). For AR1-covariance we set a vague prior to increase the magnitude of interannual variance (with probability 0.9 that the standard deviation is over 0). The spatio-temporal random effect ( $h(s,t)$ ) was defined similarly to the temporal random effect ( $g(d,t)$ ) with the difference that we replaced covariance in relation to the day of the year with covariance in relation to the bioclimatic zone. We defined the covariance for bioclimatic zone with a Matérn ( $\alpha=3/2$ )-type covariance function and the temporal covariance with respect to the year with a first-order autoregressive covariance (AR1) function (3). For the Matérn-covariance, we set priors to decrease variation between bioclimatic zones (probability 0.1 that the range parameter has a value corresponding to less than 10 bioclimatic zones, effectively pushing probability towards high covariance between bioclimatic zones) and to constrain the magnitude of variance (with probability 0.01 that the standard deviation is over 1).

### 3 Multispecies model for phenology and range shifts

In the final steps, we used the model based predictions of the onset of adult flight time and northern range boundary as inputs in a multispecies trait model. In these two multispecies models, we estimated the species-specific average change in phenology onset and range boundary, while accounting for trait- and phenology-mediated interspecific covariance in the models. We modeled trait-mediated covariance using a product kernel comprising squared-exponential covariance functions for continuous traits (species temperature breadth index, flight period, mobility) and exponential mismatch kernels for categorical traits (host use and habitat use breadth). On the log-covariance scale, the squared continuous trait distances and weighted Hamming distances contributed additively. Consequently, differences in either continuous or categorical traits reduced covariance multiplicatively. We also accounted for the potential difference in the average onset of phenology between southern and northern Finland. We simplified this by combining hemi- and southern boreal zones and middle and northern boreal zones into southern and northern zones.

#### *Phenology*

For the onset of adult flight time, we used the predicted phenology for 11 prediction locations. We explained the variation in the onset with a linear model:

$$y_{s,t,i} \sim N(\theta_{1,i} + \eta_{1,i} * BC_s + (\theta_{2,i} + \eta_{2,i} * BC_s) * X_t, \sigma_i^2 + \omega_{i,t}^2), \quad (8)$$

where  $y_{s,t,i}$  is the onset of the adult flight time of species  $i$ , in year  $t$  and in location  $s$ ,  $\theta_{1,i}$  is the intercept capturing the average day of phenology onset,  $\eta_{1,i}$  is the change in the intercept between the southern and northern (middle and northern) bioclimatic zones,  $BC_s$  is the bioclimatic zone,  $\theta_{2,i}$  is the average change of the onset per year,  $\eta_{2,i}$  is the difference between bioclimatic zones in the average of the onset per year,  $X_t$  is the scaled year (start from zero),  $\sigma_i$  is the standard deviation of the linear predictor for species  $i$ , and  $\omega_{i,t}$  is the standard deviation of the posterior prediction of species  $i$  in year  $t$  of the phenology SDM.

We modeled the effect of species traits on  $\theta : s$  by defining a joint distribution for the intercept and the rate of change across our study species:

$$\begin{bmatrix} \theta_1 \\ \theta_2 \end{bmatrix} \sim N\left(\begin{bmatrix} \mu_1 \\ \mu_2 \end{bmatrix}, \begin{bmatrix} \rho_{1,1}, \rho_{1,2} \\ \rho_{2,1}, \rho_{2,2} \end{bmatrix} \otimes \Sigma_{I*I}\right), \quad (9)$$

where  $\mu$  parameters are the population means across all species,  $\rho$ :s are variance/-covariance of the population means, and  $\Sigma$  is the covariance matrix for interspecific covariances. Interspecific covariance is defined as a function of species trait values. We set squared exponential covariance functions for continuous traits (flight period and temperature breadth index), and Hamming distance (weighted covariance if trait values differ between species) for categorical traits (larval dietary preference and habitat breadth). The final covariance was defined as:

$$\sigma_{i,j} = \begin{cases} \nu_1 \exp\left(-\frac{1}{2}\left(\frac{d_1^2}{l_1^2} + \frac{d_2^2}{l_2^2} + \frac{d_3^2}{l_3^2}\right) - \psi_1 d_4 - \psi_2 d_5\right) + \nu_2 \exp\left(-\frac{1}{2} \frac{d_6^2}{l_4^2}\right) & \text{if } i \neq j, \\ \nu_1 + \nu_2 + \nu_3, & \text{if } i = j. \end{cases} \quad (10)$$

where  $\sigma_{i,j}$  is the covariance between two species,  $\nu : s$  are parameters for the magnitude of variance related to the traits ( $\nu_1$ ), phylogeny ( $\nu_2$ ) and random interspecific variation ( $\nu_3$ ). The  $d$  parameters capture interspecific differences in length of the flight period ( $d_1$ ), mobility index ( $d_2$ ), temperature breadth index ( $d_3$ ), larval dietary preference (0 or 1) ( $d_4$ ), and habitat breadth (0 or 1)  $d_5$ . Finally,  $d_6$  is the distance between two species in a phylogenetic tree. The  $l$  parameters are the range of the covariance related to flight period ( $l_1$ ), mobility index ( $l_2$ ), temperature breadth index ( $l_3$ ), and phylogenetic distance ( $l_4$ ). The  $\psi$  parameters are weights associated with larval dietary preference ( $\psi_1$ ) and habitat breadth ( $\psi_2$ ). We standardized the continuous traits (flight period and temperature breadth index) to allow comparing the range parameter estimates between the traits.

The joint distribution for  $\eta$ :s is exactly like for  $\theta$ :s. However, for  $\eta : s$  we did not model trait effects, but instead modeled the non-trait-related magnitude of variance:

$$\sigma_{i,j} = \begin{cases} 0, & \text{if } i \neq j, \\ \nu_3, & \text{if } i = j. \end{cases} \quad (11)$$

## Range

The model for the northern range boundary was analogous to the model for phenology, with the exception that we did not include spatial variation in the northern range boundary within a year. We explained the variation in the northern range boundary with a linear model:

$$y_{t,i} \sim N(\theta_{1,i} + \theta_{2,i} * X_t, \sigma_i^2 + \omega_{i,t}^2), \quad (12)$$

where  $y_{t,i}$  is the northern range boundary of species  $i$ , in year  $t$ ,  $\theta_{1,i}$  is the intercept capturing the average latitude of the northern range boundary,  $\theta_{2,i}$  is the average change of the northern range boundary per year,  $X_t$  is the scaled year (start from zero),  $\sigma_i$  is the standard deviation of linear predictor of species  $i$ , and  $\omega_{i,t}$  is the standard deviation of the posterior prediction of species  $i$  in year  $t$  of the range SDM.

We modelled the effect of species traits on  $\theta : s$  by defining a joint distribution for the intercept and the rate of change across our study species. This followed the approach for the phenology model. Interspecific covariance was defined as a function of species trait values. We set squared exponential covariance functions for the continuous traits (mobility score and temperature breadth index) and Hamming distance (weighted covariance if trait values differ between species) for the categorical traits (larval dietary preference and habitat breadth). The covariance was defined as in Eq. 10 for the covariance in phenology shifts.

The linear predictors for phenology (Eq. 8) and range (Eq. 12) were related through the species-specific variance ( $\sigma^2$ ). We applied the same formula as for  $\theta : s$  so that

$$\begin{bmatrix} \sigma_{phen.} \\ \sigma_{range} \end{bmatrix} \sim N\left(\begin{bmatrix} \kappa_{phen.} \\ \kappa_{range} \end{bmatrix}, \begin{bmatrix} \zeta_{phen.}, \zeta_{phen.,range} \\ \zeta_{range,phen.}, \zeta_{phen.} \end{bmatrix}\right), \quad (13)$$

where  $\kappa$  parameters are average  $\sigma : s$  over the population and  $\zeta : s$  are variance and covariance of the phenology and range specific  $\sigma : s$ .

We standardised the continuous traits (mobility score and temperature breadth index) so that we could compare the range parameter estimates between the traits.

### *Model fitting*

We fitted the models with stan software (21) accessed through R (version 4.4.2; (14)), using the rstan-package (20). We took in a total of five chains each with 16000 posterior samples of which we discarded the first 2000 as burn-in and thinned the resulting samples with a factor of 10. This resulted in 7000 posterior samples. We confirmed the model convergence with a potential scale reduction factor and by checking effective sample sizes.

As prior distributions for parameters, we assigned Normal distributions (mean zero, and standard deviation two) for the population means of the intercept and year-effect ( $\mu_1$  and  $\mu_2$ ). We further assigned a Normal distribution (mean zero, and standard deviation one) constrained to  $\geq 0$  to covariance range parameters of the categorical traits ( $\psi : s$ ) and magnitude of variance ( $\nu_1$  and  $\nu_2$ ). We treated unstructured interspecific variation ( $\nu_3$ ) as a nugget term and assigned it a tighter prior distribution (Normal distribution with mean zero, standard deviation 0.05 and constrained to  $\geq 0$ ). Finally, we assigned a Normal distribution (mean zero, and standard deviation two) constrained to  $\geq 0$  for the covariance range parameters of the continuous traits ( $l : s$ ). The species-specific random variation ( $\sigma$ ) was sampled from a joint distribution for the standard deviation of phenology and range (Eq. 13). We assigned priors for the log-transformed version of the joint distribution: a Normal distribution (mean -0.2 and variance 0.5) for  $\kappa$  parameters and a Student-t distribution (degrees of freedom three, mean zero and standard deviation 0.5) for  $\zeta : s$ . Standard deviations were transformed exponentially after sampling from the joint distribution.

The parameters of interest are  $\theta : s$  that correspond to species-level estimates of the mean shift,  $\sigma : s$  that correspond to uncertainty of the phenology and range predictions and  $\omega : s$  that correspond to uncertainty of the predicted onset of phenology onset and northern range boundary. The  $\sigma$  can be translated as the uncertainty of when individuals express their phenology and how far individuals traverse north and thus represents the variability within the species population. In contrast,  $\omega$  can be translated as the uncertainty of how early, **on average**, individuals occur during the season or how far, **on average**, individuals traverse north compared to the expected shift. Together,  $\sigma$  and  $\omega$  represent the total variability. We conducted hypothesis testing with parameter estimates (Table 2).

### *Variance partitioning*

We computed variance partitioning for each model component: trait-mediated, phylogeny-mediated, random interspecific variation, spatial (for phylogeny only), process uncer-

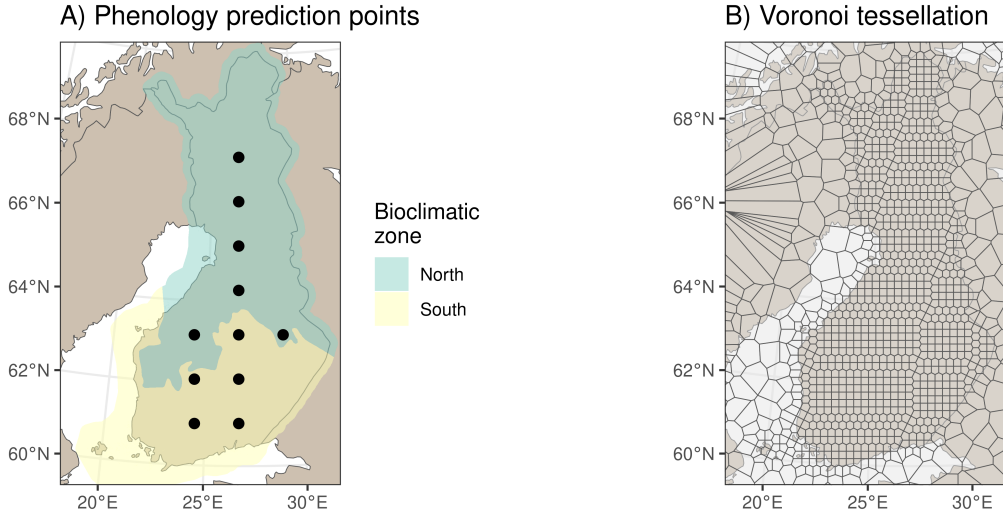


Figure 1: Panel A shows the Voronoi tessellation used for approximating the spatial random effect in the species distribution model for northern range boundary. Panel B shows the locations of prediction points of the phenology time-series and the spatial location of bioclimatic zones.

tainty, and prediction uncertainty and used each posterior sample to derive a probabilistic distribution of the measures. We derived a prediction for each species and study year using each model component in turn, and computed the variance of the predictions. Variation mediated by traits, phylogeny, random interspecific, and spatial variation were computed accounting for only the variance and covariance of the respective model component and ignoring all other components. Thus, we could predict the phenology onset and range boundary solely with the respective model component. Finally, we calculated the proportional differences between the variance of the predictions of each model component (16).

#### *Quantifying spatial differences in phenology and range shift*

To quantify the spatial differences in species phenology and range shifts, we split the species into southern and northern categories. We did this using the estimated mean of the species northern range boundary from the range shift model ( $\theta_{1,i}$  in Eq. 12). The southern and northern categories were defined in relation to the median value of the mean northern range boundaries.

## 4 Additional figures

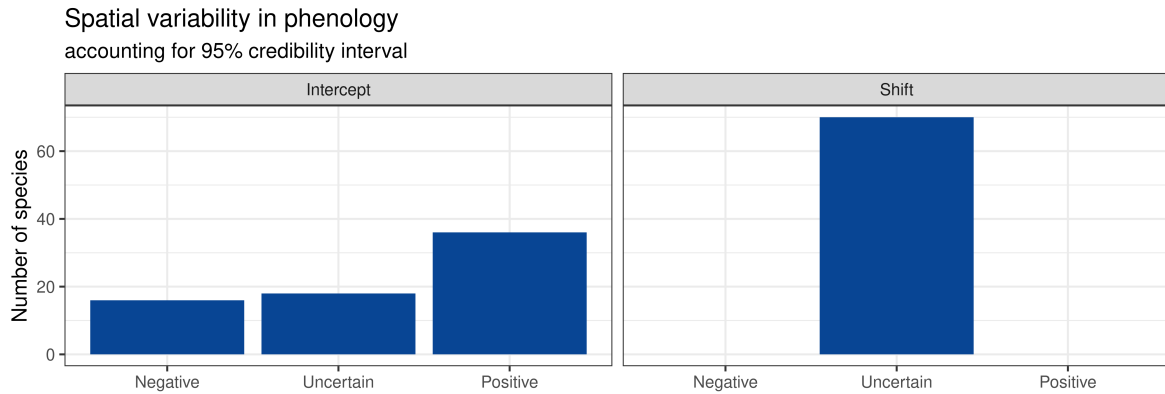


Figure 2: Bars denote the number of species in relation to the estimated change in intercept and shift of phenology between southern and northern halves of the study period. Negative denotes earlier start and advancement of the onset of the phenology cycle whereas positive denotes the opposite.

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