

Combining range and phenology shifts offers a winning strategy for boreal Lepidoptera

Maria Hällfors¹, Juha Pöyry², Janne Heliölä³, Ilmari Kohonen¹, Mikko Kuussaari³, Reima Leinonen⁴, Reto Schmucki⁵, Pasi Sihvonen¹, and Marjo Saastamoinen¹

¹University of Helsinki

²Finnish Environment Institute (Syke)

³Finnish Environment Institute

⁴Kainuu Centre for Economic Development, Transport and the Environment

⁵UK Centre for Ecology & Hydrology

January 8, 2021

Abstract

Species can adapt to climate change by adjusting in situ or by dispersing to new areas, and these strategies may complement or enhance each other. Here, we investigate temporal shifts in phenology and spatial shifts in northern range boundaries for 289 Lepidoptera species by using long-term data sampled over two decades. While 40% of the species neither advanced phenology nor moved northward, nearly half (47%) -used one of the two strategies. The strongest positive population trends was observed for the minority of species (13%) that both advanced flight phenology and shifted their northern range boundaries northward. We show that, for Boreal Lepidoptera, a combination of phenology and range shifts is the most viable strategy under a changing climate. Effectively, this may divide species into winners and losers based on their propensity to capitalize on this combination, with potentially large consequences on future community composition.

Introduction

Biodiversity is threatened by a multitude of anthropogenic factors, including ongoing climate change (IPCC 2014; Díaz *et al.* 2019). Under environmental change, species have two avenues for escaping decline and consequent extinction: adapting in situ through plastic or evolutionary responses, or moving to areas where conditions are more favorable (Davis *et al.* 2005). Phenology and range shifts are the most conspicuous responses of species to rapid environmental change, and they have been referred to as the fingerprints of climate change (Parmesan & Yohe 2003; Root *et al.* 2003). The spatial distribution of a species and the temporal manifestation of life-history events reflect its realized niche (Socolar *et al.* 2017). As shifts in distribution and phenology represent the mechanisms through which a spatial or temporal change in the utilization of the niche can be observed (Amano *et al.* 2014), they are expected to offer fitness benefits as means of adaptation under climate change. Species can adapt to climatic change by advancing their early-season phenology in accordance with warmer temperatures (Parmesan & Yohe 2003). Such shifts in phenology have often been shown to be related with positive population trends and increased demographic stability (Cleland *et al.* 2007; Møller *et al.* 2008; Saino *et al.* 2011; Franks *et al.* 2018). Range shifting towards cooler areas is the other main strategy for species to adapt to warmer climatic conditions, both under contemporary and past climate changes (Parmesan *et al.* 1999; Davis & Shaw 2001; Donoghue 2008; Spence & Tingley 2020). Species that are able to shift their geographic distribution to track climate change and thus remain within their climatic niches are less likely to suffer population declines and local extinctions (Cooper *et al.* 2011; Devictor *et al.* 2012; Urban 2015).

The most straightforward expectation is that species would use either range or phenology shift to respond to changing climatic conditions (Hypothesis 1; Fig. 1a). Mobile species would not have as strong a need to advance their phenology as they can track suitable conditions in space. Less mobile species, however, will experience stronger selection pressure to adapt in situ and adjust their phenology in order to maintain suitable thermal conditions during critical life-history events (Amano *et al.* 2014; Socolar *et al.* 2017). Indications for such complementary thermal niche tracking via space or time have been found for both plants and birds (Amano *et al.* 2014; Socolar *et al.* 2017). Nevertheless, these strategies are not necessarily mutually exclusive and can provide enhancing benefits that together buffer species against climate warming and increased variation in extreme events. In such a case, species would benefit from using *both range and phenology shift* (Hypothesis 2; Fig. 1a). The ability to adapt in one dimension of niche utilization is likely to be correlated with high responsiveness to variability in others, not least through positive feedback loops that increase population persistence (Willis *et al.* 2010). Phenological timing is perhaps the most important aspect of life-history that affects species distributions (Chaine 2010), as it defines where and how successfully individuals of a population can proliferate. Hypothesis 2 is thus based on the assumption that adaptive in situ responses in phenology increase the fitness of individuals, leading to higher survival rates and more offspring (Cleland *et al.* 2007). Evidence suggests that stable or positive population trends, that is, no change or increase in abundance, are a prerequisite for species to expand their ranges (Mair *et al.* 2014) as emigration is higher from larger populations (Pärn *et al.* 2012; Glorvigen *et al.* 2013). Also, the probability of successful establishment increases with the summed contribution of individuals from neighboring source populations (Hanski *et al.* 1995; Hanski & Ovaskainen 2003).

In this study, we assess how 289 species of Lepidoptera in Finland have responded to nearly 30 years of climate change. Lepidoptera have been shown to be responsive to climate change, as exemplified by the observed range shifts towards higher latitudes (Parmesan *et al.* 1999; Pöyry *et al.* 2009; Chen *et al.* 2011) and altitudes (Konvicka *et al.* 2003; Wilson *et al.* 2005), as well as phenology shifts (e.g., advance in the date of first appearance [Roy & Sparks 2000; Stefanescu *et al.* 2003; Diamond *et al.* 2011] and increased voltinism [Altermatt 2010; Pöyry *et al.* 2011]). Previous studies have shown that the distribution of butterflies in Finland is mainly determined by climatic factors (Luoto *et al.* 2006) and that the phenology of moths tends to be controlled by temperature (Valtonen *et al.* 2014). During the last few decades, the mean temperature in Finland has risen by 0.2-0.4 °C/decade (Mikkonen *et al.* 2014; Fig. S1), with springs starting earlier and the timing of phenological events being advanced for many species (Helama *et al.* 2020; Hällfors *et al.* 2020). Therefore, we expect Lepidoptera to respond to changing climatic conditions by either shifting their ranges or adjusting their phenology in situ, or both. However, it is unclear how these different strategies influence species' population trends. Here we ask whether Lepidoptera have advanced their mean flight period (=adaptive phenology shift) or shifted their northern range boundary (NRB) northwards (=adaptive range shift). Using these response estimates, we test two main hypotheses: do the same species tend to 1) *either* advance their mean flight period *or* shift their NRB northwards, or 2) *both* advance their mean flight period *and* shift their NRBS northwards (Fig. 1b). To gain understanding on the potential causes and effects of the response combinations, we further relate the responses to life-history traits and population trends (Fig. 1).

Methods

Measures for phenology and range shifts

The start of the growing season in Europe, including Finland, has advanced over the past decades (Menzel & Fabian 1999; Helama *et al.* 2020), and suitable conditions for seasonally recurring life-history events now often occur earlier than before. To investigate the strategy of adjusting phenology in situ, we focus on the phenological timing of adult flight period, with the assumption of advanced flight period mirroring an adaptive response.

The area of Finland extends over a ca. 1100 km latitudinal gradient across boreal and subarctic climates and is topographically relatively homogenous. The climatic isoclines roughly follow latitudes (Ahti *et al.* 1968), but they are currently shifting northwards due to climate change (Jylhä *et al.* 2010). Species range shifts as a response to climate change should thus be observable in Finland through colonization of new suitable

areas north of their previous distribution (cf. Pöyry *et al.* 2009). To study the strategy of colonizing new suitable areas, we focus on measuring shifts in the northern range boundary (NRB).

Data

Systematic data for phenological analyses and population trends

To analyze phenological change in adult flight periods of Lepidoptera, we use c. 20 years of systematically collected data from butterfly transects and moth traps. For butterflies, we combined data from two butterfly surveys conducted in agricultural landscapes in Finland during 1999-2017 (Fig. 2): 1) volunteer transects with varying length and sampling frequency, and 2) professional transects with standardized length and sampling frequency. For moths, we use data that have been collected in the Finnish national moth monitoring scheme (Nocturna) during 1993-2017 (Leinonen *et al.* 2016, 2017).

The raw data and how they were refined to fit the purposes of phenological analyses and population trend estimation in this study are described more in depth in Text S1. For example, to ensure enough phenological resolution, we removed all sampling events in the moth data with a sampling interval longer than ten days. All the observation dates for butterflies and moths were converted into Julian dates (day of year), to represent the timing of adult flight. To ensure sufficient data for each analyzed species per year, we included only species with observations from at least ten years during the 19- (butterflies) and 25- (moths) year study periods and with at least 30 observations from each of the included years. This procedure left us with a total of 289 species. As a consequence of this conservative inclusion of data, our set of study species does not contain rare species. Lastly, to exclude the effect of potentially differing phenological timing in recently colonized areas, we also excluded records of species from sites located further north of the estimated NRB for T_1 (see section below and Text S2). The final data for phenological analyses and population trend estimations consisted of 725 106 and 355 970 abundance observations of the 289 species, respectively.

Observational data for shift in the northern range boundary (NRB)

To analyze shift in the NRB, we used observational data on the 289 species that were selected for the study through defining data for the phenological analyses (see above; and Text S1). 2 474 498 observations on the 289 study species available through the Insect database and National Butterfly Monitoring Scheme (Saarinen *et al.* 2003) were sourced from the Finnish Biodiversity Information Facility (FinBIF) in December 2019 (Text S2).

To measure shift in NRB over time, we compared NRB between two five-year periods: 1992-1996 (hereafter T_1) and 2013-2017 (hereafter called T_2). The total number of presence cells for T_2 was, however, substantially higher than for T_1 due to overall increased sampling effort over time. To avoid effects caused by differences in overall observation intensity, we randomly subsampled the observations in T_2 across species to equal the number of observations in T_1 . The temporal span of the distributional data in relation to the systematic data used to estimate phenological shift is depicted in Fig. S1.

Data on life history traits

We used data on four key life history traits to potentially explain shifts in phenology and NRB, and in population trends. The trait variables used included: body size (continuous variable), overwintering stage (factor with four levels: Adult, Larvae, Pupa, Egg), specificity of larval host plant use (factor with two levels: Generalist, Specialist), and voltinism (factor with two levels: Univoltine, Multivoltine). These traits were chosen as they were linked to variation in responses to climate and environmental change in previous empirical studies on Lepidoptera (Pöyry *et al.* 2009, 2017; Betzholtz *et al.* 2013; WallisDeVries 2014), and because information on these traits is available for both moths and butterflies. See Fig. S3 for further details and data sources.

Analyses

Shift in phenology

We analyzed phenological shift with the following linear mixed effects model:

$$Y_i = a + X_i b + \frac{Zu + \varepsilon_i}{\sqrt{w_i}}$$

Where Y is the day of year that species i was observed, a is the intercept (average day of year for observing species i), X is the year when the observation occurred (continuous, centered variable), b is the effect of Year on day of year (Y), Z is a design matrix for the site-level random effects u , and e are the residuals weighted by the abundance of species i on the observation day. The model was fitted separately for each species, and resulted in a slope coefficient describing the mean annual shift in adult flight timing over the study period.

Shift in NRB

To estimate shifts in NRB, we calculated the average latitude of the ten northernmost grid cells and the prevalence (proportion of occupied 10x10 km cells for each species out of all cells with observations of any of the species) in both in T_1 and T_2 (following Thomas & Lennon 1999). We calculated shifts in NRB (kilometers) by subtracting the NRB in T_2 from that in T_1 , and similarly the change in prevalence by subtracting the prevalence in T_2 from that in T_1 . The statistical significance of an average shift in NRB across all species can be estimated by modeling the change in kilometers between the periods as a function of change in prevalence. This approach was first presented by Thomas and Lennon (1999) and has been used in similar analyses (e.g. Brommer 2004; Pöyry *et al.* 2009; Mason *et al.* 2015). If the intercept is positive and significantly different from zero, the inference is that the species group has, overall, shifted their NRBs more towards the north than expected purely from their change in prevalence. We used this approach to obtain a linear effect estimate of shift in km as a function of change in prevalence (Fig. S4a). We extracted the residuals of the model, per species, to obtain a corrected measure of NRB shifts. This estimate thus describes the residual shift in NRB that is not explained by the linear effect of prevalence across the studied species. These residuals correlate strongly with the raw shift in kilometers (Fig. S4b), but are a more conservative metric as the linear effect of prevalence change across species has been removed. To ensure that the results and conclusions were not biased by underlying differences in sampling patterns between the two periods, we conducted the same analysis with systematically collected data to confirm that the observational data does not overestimate the direction of shift in NRB (Text S3).

Population trends

We calculated the population trends from their collated annual abundance indices. This was done separately for butterflies and moths.

For the butterflies, at each site, annual indices were computed from the weekly counts, following the method described in Dennis *et al.* (2013, 2016) and implemented in the `rbms` R package (Schmucki *et al.* 2020). Missing week counts were derived from a Poisson generalized linear model (GLM) that included the regional flight curve as an offset (Schmucki *et al.* 2016). Collated annual abundance indices were then estimated with a weighted Poisson regression, accounting for site, transect length and using the proportion of the flight curve monitored as weight. Thereby, sites with many missing counts during the flight period had lower weight than well monitored sites. For each species, we calculated the long-term trends with a linear model that we fitted on the \log_{10} transformed collated annual indices, starting with the year the species was first recorded until the last within the 1999-2017 period.

For the moth species, population trends were estimated using the TRIM software (Pannekoek & Van Strien 2005), as implemented in the `rtrim` R package (Boogart *et al.* 2020). TRIM uses Poisson regression to estimate annual abundance indices, while accounting for missing observations, site differences, overdispersion and temporal autocorrelation. As a long-term trend estimate, TRIM calculates a regression through the annual indices, and this linear trend slope (on the log scale; the “additive” slope in TRIM) was used as a measure of population trend for the moth species over 1993-2016. Four species appeared in the dataset after 1993, with the first year of occurrence marking the start of the timeframe for trend calculation.

Conversion of species responses into categories

The slope coefficients from the phenology models and the estimates of NRB shift in kilometers formed our main results and are hereafter jointly referred to as the *responses* (as in climate change response). To enable a comparison of directionality in responses, we converted the continuous results into categories (Table 1). For the sake of visualization in Fig. 3, and in order to calculate the percentage of species with population trends in different directions, population trends were also assigned into similar categories: a significantly positive trend was assigned into the “Positive” group; an insignificant trend with any sign into the “Stable” group; and a significantly negative trend into the “Negative” group.

Phylogenetic Generalized Linear Models

To test the effect of traits on the responses and population trend, the responses on each other, as well as the effect of responses on population trends, we applied Phylogenetic Generalized Least Squares (PGLS; Freckleton *et al.* 2002; also called Phylogenetic Generalized Linear Models; Symonds & Blomberg 2014) through the *pgls* function as implemented in the *caper* R-package (Orme 2018). The PGLS method is an extension to generalized least squares where the phylogenetic relationships of species are incorporated into the modeling framework via estimation of covariance in multispecies data. Related species cannot be considered independent from each other in neither their life history traits (Freckleton *et al.* 2002; Ives & Zhu 2006) nor in their responses to environmental change (Davies *et al.* 2013; Fei *et al.* 2017). Thus, any model residuals of closely related species would often be more similar than by chance, which requires modification to the estimated slopes and intercepts of the models (Revell 2010; Symonds & Blomberg 2014). To allow controlling for phylogenetic dependence, we constructed a phylogenetic tree for the 289 species based on the hypothesis derived by Pöyry *et al.* (2017) for Nordic Macrolepidoptera (available in the associated data: (<https://github.com/MariaHallfors/LepidopteraShift>)). We measured the phylogenetic signal in our data which confirmed that controlling for phylogenetic relatedness in subsequent analyses was needed to account for phylogenetic non-independence of the species. For more details and description of multicollinearity checks and scaling of variables, see Text S4.

Models for hypothesis testing

To test the degree to which Lepidoptera use range shifts and/or phenology shifts as a response to climate change, the effect of the responses and their combinations on population trends, and the role that life-history traits may play for identifying species able to capitalize on the responses, we use the PGLS-models described above. For the purpose of statistical analyses, these categorical variables were converted into dummy variables, and the trait *body size* was square-root transformed.

First, to measure average response across species, we conducted intercept-only PGLS-models on both continuous responses and the population trend. For this purpose, we used the unscaled versions of the variables to allow inference directly on the measured scale (days, kilometers). The model is defined as:

$$Y = a + \varepsilon$$

where Y stands for the continuous dependent variable, a is the intercept (average response), and e are the residuals with covariance matrix C , which is optimized based on the phylogeny.

Second, to test our main hypotheses (Fig. 1), we fitted five separate models. Hypothesis 1 suggests that either phenology advance or a northwards shift of NRB would be mirrored in positive population trends (Fig. 1). Thus, we tested the effect of direction of shifts in a) phenology and b) NRB on population trend. Hypothesis 2 postulates that an advance in phenology would increase the probability that species can shift their NRB northwards. Thus, we tested the effect of c) the direction of shift in phenology on shift in NRB. To test the effect of different combinations of the responses on population trends, and which hypothesis provides a more viable strategy for species (as opposed to which strategy is the more common), we tested the effect of the d) combined responses and e) hypothesis-wise responses on population trend.

Finally, to test the effect of life-history traits on the responses and population trend, we fitted three PGLS-models, one on each continuous and scaled response and population trend as response variables, with all four

life-history traits as explanatory variables. We also applied PGLS-models to test for a potential difference in the responses and population trends of the major taxonomic groups (moths and butterflies).

Models a)-e), and models on the effect of traits and taxonomic groups are structured as follows:

$$Y = a + Xb + \varepsilon$$

where Y stands for the continuous dependent variable, a is the intercept (average response), X is a $289 \times k$ -1 dimensional design matrix indicating the independent factorial variables, b are the effects of the independent variables, and ε are the residuals with covariance matrix C , which is optimized based on phylogenetic signal (Symonds & Blomberg 2014).

The assumptions of the models were verified by visually observing plots of the residuals against each response and explanatory variable validation, and the distribution (histogram) and QQ plots of the residuals. All patterns indicated normally distributed residuals with no signs of heteroscedasticity nor extreme outliers. All data management and analyses were conducted in R studio (R version 3.5.3; R Core Team 2019).

Results

We found, on average, no systematic shift in any direction across the species responses (Fig. 3). Among the 289 species studied, 45.3% of species expanded their NRB towards the north and 27% of species advanced their phenology (Fig. 3). By contrast, 40.8% of species contracted their NRB towards the south and 35.6% delayed their phenology. This lack of a systematic directional shift was evidenced by the fact that the estimates of the intercept-only PGLS -models were not significantly different from zero. We also found no difference in the estimates between the two main taxonomic groups, butterflies and moths (Table S2).

Almost half of the species (46.7%) responded according to hypothesis 1, i.e. they either shifted their NRB northwards or their phenology earlier, but not both. A minority of the studied species (12.8%) responded according to hypothesis 2, i.e. they shifted both their NRB northwards and phenology earlier. Finally, 40.5% of the species showed no adaptive response, i.e. they neither shifted their NRB northwards nor phenology earlier (hypothesis 0). Instead, the NRBs remained stable or shifted southwards and their phenology remained stable or delayed.

More than half of the studied species (61.5%) showed positive or stable population trends, but on average there was no systematic trend for neither positive nor negative population trends across the studied species (Fig. 3). Nevertheless, population trends differed between species that responded differently in NRB and phenology shifts. Species that advanced their phenology showed more positive (although insignificant) population trends over the study period than those that delayed or did not change their phenology (Table 2 - model a). Species that shifted their NRBs further north (>20 km) showed significantly stronger positive population trends compared to other species (Table 2 - model b; Fig. 4a). In addition, species that advanced their phenology tended to move their NRB more towards the north, but this effect was not significant (Table 2 - model c). The positive effect of a northwards shift in NRB on population trends in model b) was also mirrored in model d) which indicates that both combined responses including a northwards shift, no matter how the species reacted phenology-wise, showed stronger positive population trends (Table 2 - model d). This effect was stronger for species that also advanced their phenology. Thus, species able to utilize a combined response as postulated by Hypothesis 2 (both northwards shift of NRB and advance in phenology) showed significantly stronger population trends (Table 2 - model e; Fig. 4b). An ability to utilize either of the responses (as postulated by Hypothesis 1) showed, on average, lower but also positive population trend, but this effect was not significant. The species that were not able to utilize either of the presumed adaptive responses (Hypothesis 0) showed the lowest, and on average negative population trends (Table 2 - model e; Fig. 4b).

None of the four life-history traits tested showed a significant connection with population trends. *Overwintering stage* was the only trait that had an effect on shift in phenology and on NRB (Fig. S6; Table S3).

Species overwintering as adults were more likely to advance their phenology while species that overwinter as pupae tended to retreat their NRB towards the south. However, due to imbalance in the number of species representing different host plant-use categories, we had combined species feeding on lichen and fungi into the specialist group (8 species; 2.7% of studied species: see *Methods*). In an additional PGLS analysis treating lichen and fungi feeders as a separate group, the eight species that feed on lichen and fungi showed a significant shift in their NRB further north ($t= 1.97$; $p<0.05$) and also had more positive population trends ($t= 3.93$; $p<0.001$; Fig. S7).

Discussion

Our analysis reveals that Lepidoptera in Finland most often use only one of the commonly assumed adaptive responses to climate change, as 47% of the studied species responded by either shifting their NRB northwards or by advancing their phenology. However, nearly as a large a proportion (41%) were unable to utilize either of the two strategies. Importantly, this un-responsiveness coincided with more negative population trends. In contrast, the 13% of species that responded by both shifting their NRB northwards and advancing their phenology showed, on average, the strongest positive population trends. This minority of species, able to capitalize on both responses, advanced their flight period by 3.8 days/decade and shifted their NRBs 124.5 kilometers further north between T_1 and T_2 , on average. Although this study cannot provide evidence for *de facto* on underlying processes giving rise to the observed patterns, the results point to pervasive fitness benefits of combining in situ adjustments with range shifts.

We found only few trait effects on the responses and population trends (cf. Pöyry *et al.* 2009; Angert *et al.* 2011; Coulthard *et al.* 2019), which raises concerns related to the potential to identify species vulnerable based on their life history. However, we found that adult overwintering species tended to advance their phenology and species overwintering as pupae were less likely to shift their ranges further north, with some even contracting their range southwards. Earlier studies have hypothesized that species overwintering as adults are among the species mostly benefiting from increased spring temperatures, whereas species overwintering as pupae are likely to increase the number of generations produced per year (Virtanen & Neuvonen 1999; Teder 2020). The lack of effect of voltinism was surprising in light of the general trend towards an overall increase in voltinism in European Lepidoptera (Altermatt 2010; Pöyry *et al.* 2011), which would assumedly affect both species phenology and range shifts. However, the effect of added generations may not offer actual benefits to all species, rather “tricking” some species into another generation too late in the season, which could cause a so-called lost-generation effect (cf. Pöyry *et al.* 2011).

Responding by advancing phenology was, overall, relatively rarely observed among the studied species, as a striking 73% of the species did not shift their phenology, or even delayed it. This result is surprising and in contrast to several reports that are based on similar data and show strong advances in Lepidoptera phenology (e.g., Roy & Sparks 2000; Stefanescu *et al.* 2003; Diamond *et al.* 2011). However, most of the previous studies have been conducted in temperate regions, and regional differences in abiotic conditions and rates of climate change may induce different responses (Renner & Zohner 2018). Several other species groups in Finland have, however, been reported to advance their phenology (e.g., Helama *et al.* 2020 for plants; Lehtikoinen *et al.* 2019 for birds). It is possible that other environmental factors prevailing in northern latitudes, such as light conditions (Arietta *et al.* 2020; Hodgson *et al.* 2011) or variation in weather conditions in the early season, limit the possibility for advanced phenology of Lepidoptera. These findings are also in line with those by Fric *et al.* (2020) who observed less advancement and even delays in early flight periods of butterflies towards higher latitudes.

Although there was a positive connection between phenological response and population trends, the effect was not statistically significant. Radchuk *et al.* (2019) found that even though phenological advance is often stated as an adaptive strategy under climate change, this may not be the rule for all species, nor is phenological advance always enough to provide fitness benefits under ongoing rapid environmental change. Climate change also introduces more variable weather conditions (Rummukainen 2012; Vasseur *et al.* 2014), whereby environmental cues may become less reliable and advanced phenology may not offer the expected fitness benefits, but even cause declines in readily responding species. Additionally, declining populations

may not only be less able to disperse and colonize new areas (fewer individuals that emigrate) but also have a lower potential for adjusting in situ, because of loss of genetic variability (Anderson 2016). Large declines in insect populations have recently been reported, and although these trends vary greatly between regions and taxa (Crossley *et al.* 2020; van Klink *et al.* 2020; Pilotto *et al.* 2020), our results also point to comprehensive population declines among Finnish Lepidoptera as 38.5% of the studied species showed negative population trends.

In contrast to advanced phenology alone, northwards shifts in NRB was associated with significantly stronger population trends. Our results also show that the studied species are more often capitalizing on range shifts than phenology shifts. This is in line with previous studies that documented strong range shifts among Lepidoptera (Parmesan *et al.* 1999; Kharouba *et al.* 2009; Pöyry *et al.* 2009; Mason *et al.* 2015) and points to range shifts perhaps being a more readily available response for many species of Lepidoptera. Simultaneously, however, only less than half (45%) of the species studied here, had shifted their NRBs northwards. Habitat availability plays a crucial role when species are moving as a response to climate change (Platts *et al.* 2019), and other abiotic factors than rising temperatures are likely to affect the ability of species to shift their ranges (Spence & Tingley 2020). In Finland, decrease in the area and quality of suitable habitats is known to have substantial negative effects on butterflies (Kuussaari *et al.* 2007; Ekroos *et al.* 2010; Pöyry *et al.* 2018). This highlights the importance of considering species dispersal in land-use planning as it is one of the main pathways through which species can adapt to ongoing changes. Halting habitat decline and fostering the persistence and even reconstruction of large and connected habitat areas can help sustain large enough populations that can both colonize new area and harbor sufficient genetic and phenotypic variation to respond, in situ, to global changes. Policies like the European Union's Biodiversity Strategy for 2030 that aims at protecting at least 30% of terrestrial and aquatic areas (European Commission 2020) could enable more species to combine the two viable strategies for maintaining within their thermal niche.

Our study highlights that combining advanced phenology and a northwards range shift provides the best potential for population viability. Among boreal Lepidoptera, however, only a small proportion of species are currently able to use both responses to form a winning strategy. Together with the large proportion of species that were not able to utilize either of the adaptive responses, this indicates that moths and butterflies in Finland are presently on a track towards becoming either winners or losers, and that this division is likely strongly affected by habitat availability and species' abilities to make use of newly available habitat and adjust appropriately within their ranges.

Acknowledgements

We are grateful to all the volunteers who carried out the systematic sampling of butterflies and moths. We thank Tanja Lindholm and Bess Hardwick for assistance in data management and compilation of trait information. We acknowledge Manuel Frias for advice on visual elements and Mirikka Jones and Jukka Sirén for statistical advice. We thank the Finnish Ministry of the Environment for financial support for the moth monitoring scheme.

References:

- Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* , 5, 169–211.
- Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences* , 277, 1281–1287.
- Amano, T., Freckleton, R.P., Queenborough, S.A., Doxford, S.W., Smithers, R.J., Sparks, T.H., *et al.* (2014). Links between plant species' spatial and temporal responses to a warming climate. *Proc. R. Soc. B.* , 281, 20133017.
- Anderson, J.T. (2016). Plant fitness in a rapidly changing world. *New Phytol* , 210, 81–87.
- Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011). Do species'

traits predict recent shifts at expanding range edges? *Ecology Letters* , 14, 677–689.

Arietta, A.Z.A., Freidenburg, L.K., Urban, M.C., Rodrigues, S.B., Rubinstein, A. & Skelly, D.K. (n.d.). Phenological delay despite warming in wood frog *Rana sylvatica* reproductive timing: a 20-year study. *Ecography* , n/a.

Betzholtz, P.-E., Pettersson, L.B., Ryrholm, N. & Franzén, M. (2013). With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society B: Biological Sciences* , 280, 20122305.

Boogart, J., Van Strien, A. & Pannekoek, J. (2020). rtrim: Trends and Indices for Monitoring Data. R package version 2.1.1.

Brommer, J.E. (2004). The range margins of northern birds shift polewards. *Annales Zoologici Fennici* , 41, 391–397.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* , 333, 1024–1026.

Chuine, I. (2010). Why does phenology drive species distribution? *Phil. Trans. R. Soc. B* , 365, 3149–3160.

Cleland, E., Chuine, I., Menzel, A., Mooney, H. & Schwartz, M. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* , 22, 357–365.

Cooper, N., Freckleton, R.P. & Jetz, W. (2011). Phylogenetic conservatism of environmental niches in mammals. *Proceedings of the Royal Society B: Biological Sciences* , 278, 2384–2391.

Coulthard, E., Norrey, J., Shortall, C. & Harris, W.E. (2019). Ecological traits predict population changes in moths. *Biological Conservation* , 233, 213–219.

Crossley, M.S., Meier, A.R., Baldwin, E.M., Berry, L.L., Crenshaw, L.C., Hartman, G.L., *et al.* (2020). No net insect abundance and diversity declines across US Long Term Ecological Research sites. *Nature Ecology & Evolution* , 4, 1368–1376.

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., *et al.* (2013). Phylogenetic conservatism in plant phenology. *Journal of Ecology* , 101, 1520–1530.

Davis, M.B. & Shaw, R.G. (2001). Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science* , 292, 673–679.

Davis, M.B., Shaw, R.G. & Etterson, J.R. (2005). Evolutionary Responses to Changing Climate. *Ecology* , 86, 1704–1714.

Dennis, E.B., Freeman, S.N., Brereton, T. & Roy, D.B. (2013). Indexing butterfly abundance whilst accounting for missing counts and variability in seasonal pattern. *Methods in Ecology and Evolution* , 4, 637–645.

Dennis, E.B., Morgan, B.J.T., Freeman, S.N., Brereton, T.M. & Roy, D.B. (2016). A generalized abundance index for seasonal invertebrates. *Biometrics* , 72, 1305–1314.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., *et al.* (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* , 2, 121–124.

Diamond, S.E., Frame, A.M., Martin, R.A. & Buckley, L.B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology* , 92, 1005–1012.

Díaz, S., Settele, J., Brondízio, E., Ngo, H.T., Guèze, M., Agard, J., *et al.* (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 44.

Donoghue, M.J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences* , 105, 11549–11555.

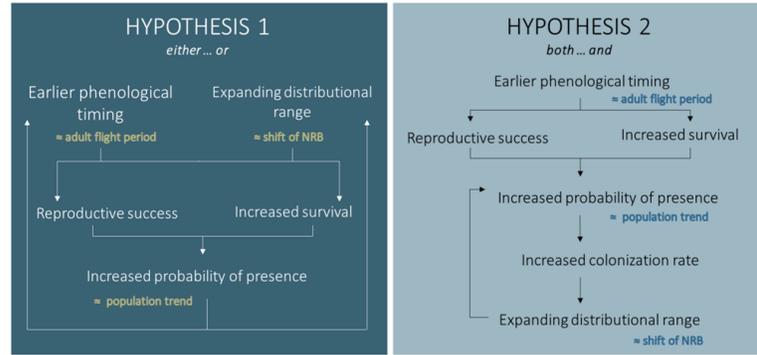
- Ekroos, J., Heliölä, J. & Kuussaari, M. (2010). Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. *Journal of Applied Ecology* , 47, 459–467.
- European Commission. (2020). *COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS EU Biodiversity Strategy for 2030 Bringing nature back into our lives COM/2020/380 final* .
- Fei, S., Desprez, J.M., Potter, K.M., Jo, I., Knott, J.A. & Oswalt, C.M. (2017). Divergence of species responses to climate change. *Science Advances* , 3, e1603055.
- Franks, S.E., Pearce-Higgins, J.W., Atkinson, S., Bell, J.R., Botham, M.S., Brereton, T.M., *et al.* (2018). The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. *Glob Change Biol* , 24, 957–971.
- Freckleton, R.P., Harvey, P.H., Pagel, M. & Losos, A.E.J.B. (2002). Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. *The American Naturalist* , 160, 712–726.
- Fric, Z.F., Rindoš, M. & Konvička, M. (2020). Phenology responses of temperate butterflies to latitude depend on ecological traits. *Ecology Letters* , 23, 172–180.
- Glorvigen, P., Gundersen, G., Andreassen, H.P. & Ims, R.A. (2013). The role of colonization in the dynamics of patchy populations of a cyclic vole species. *Oecologia* , 173, 161–167.
- Hällfors, M.H., Antão, L.H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T., *et al.* (2020). Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *PNAS* , 117, 18557–18565.
- Hanski, I. & Ovaskainen, O. (2003). Metapopulation theory for fragmented landscapes. *Theoretical Population Biology* , 64, 119–127.
- Hanski, I., Pöyry, J., Pakkala, T. & Kuussaari, M. (1995). Multiple equilibria in metapopulation dynamics. *Nature* , 377, 618–621.
- Helama, S., Tolvanen, A., Karhu, J., Poikolainen, J. & Kubin, E. (2020). Finnish National Phenological Network 1997–2017: from observations to trend detection. *Int J Biometeorol* , 64, 1783–1793.
- Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crone, E.E. (2011). Predicting insect phenology across space and time. *Global Change Biology* , 17, 1289–1300.
- IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]*. IPCC, Geneva, Switzerland,.
- Ives, A.R. & Zhu, J. (2006). Statistics For Correlated Data: Phylogenies, Space, And Time. *Ecological Applications* , 16, 20–32.
- Jylhä, K., Tuomenvirta, H., Ruosteenoja, K., Niemi-Hugaerts, H., Keisu, K. & Karhu, J.A. (2010). Observed and Projected Future Shifts of Climatic Zones in Europe and Their Use to Visualize Climate Change Information. *Wea. Climate Soc.* , 2, 148–167.
- Kharouba, H.M., Algar, A.C. & Kerr, J.T. (2009). Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. *Ecology* , 90, 2213–2222.
- Klink, R. van, Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* , 368, 417–420.
- Konvička, M., Maradova, M., Benes, J., Fric, Z. & Kepka, P. (2003). Uphill Shifts in Distribution of Butterflies in the Czech Republic: Effects of Changing Climate Detected on a Regional Scale. *Global Ecology and Biogeography* , 12, 403–410.

- Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen, K. (2007). Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *J Insect Conserv* , 11, 351–366.
- Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T.L., Dunn, E.H., *et al.* (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators* , 101, 985–991.
- Leinonen, R., Pöyry, J., Söderman, G. & Tuominen-Roto, L. (2016). *Suomen yöperhosseuranta (Nocturna) 1993–2012* . Suomen ympäristökeskus.
- Leinonen, R., Pöyry, J., Söderman, G. & Tuominen-Roto, L. (2017). Suomen yöperhosyhteisöt muutoksessa – valtakunnallisen yöperhosseurannan keskeisiä tuloksia 1993–2012. *Baptia*, 42, 74– 92. *Baptia* , 42, 74–92.
- Luoto, M., Heikkinen, R.K., Pöyry, J. & Saarinen, K. (2006). Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography* , 33, 1764–1778.
- Mair, L., Hill, J.K., Fox, R., Botham, M., Brereton, T. & Thomas, C.D. (2014). Abundance changes and habitat availability drive species’ responses to climate change. *Nature Climate Change* , 4, 127–131.
- Mason, S.C., Palmer, G., Fox, R., Gillings, S., Hill, J.K., Thomas, C.D., *et al.* (2015). Geographical range margins of many taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society* , 115, 586–597.
- Menzel, A. & Fabian, P. (1999). Growing season extended in Europe. *Nature* , 397, 659–659.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., *et al.* (2006). European phenological response to climate change matches the warming pattern. *Global Change Biol* , 12, 1969–1976.
- Mikkonen, S., Laine, M., Mäkelä, H.M., Gregow, H., Tuomenvirta, H., Lahtinen, M., *et al.* (2014). Trends in the average temperature in Finland, 1847–2013. *Stochastic Environmental Research and Risk Assessment* , 29, 1521–1529.
- Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *PNAS* , 105, 16195–16200.
- Orme, D. (2020). The caper package: comparative analysis of phylogenetics and evolution in R, 36.
- Pannekoek, J. & Van Strien, A. (2005). *TRIM 3 Manual (Trends & Indices for Monitoring data)* . Statistics Netherlands, JM Voorburg, The Netherlands.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., *et al.* (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* , 399, 579–583.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* , 421, 37–42.
- Pärn, H., Ringsby, T.H., Jensen, H. & Sæther, B.-E. (2012). Spatial heterogeneity in the effects of climate and density-dependence on dispersal in a house sparrow metapopulation. *Proceedings of the Royal Society B: Biological Sciences* , 279, 144–152.
- Pilotto, F., Kühn, I., Adrian, R., Alber, R., Alignier, A., Andrews, C., *et al.* (2020). Meta-analysis of multi-decadal biodiversity trends in Europe. *Nature Communications* , 11, 3486.
- Platts, P.J., Mason, S.C., Palmer, G., Hill, J.K., Oliver, T.H., Powney, G.D., *et al.* (2019). Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Scientific Reports* , 9, 15039.
- Pöyry, J., Carvalheiro, L.G., Heikkinen, R.K., Kühn, I., Kuussaari, M., Schweiger, O., *et al.* (2017). The effects of soil eutrophication propagate to higher trophic levels: Effects of soil eutrophication on herbivores. *Global Ecol. Biogeogr.* , 26, 18–30.

- Pöyry, J., Leinonen, R., Söderman, G., Nieminen, M., Heikkinen, R.K. & Carter, T.R. (2011). Climate-induced increase of moth multivoltinism in boreal regions. *Global Ecology and Biogeography* , 20, 289–298.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology* , 15, 732–743.
- Pöyry, J., Heikkinen, R. K., Heliölä, J., Kuussaari, M., & Saarinen, K. (2018). Scaling distributional patterns of butterflies across multiple scales: Impact of range history and habitat type. *Diversity and Distributions*, 24 , 1453-1463.
- R Core Team. (2019). *R: A Language and Environment for Statistical Computing* . R Foundation for Statistical Computing, Vienna, Austria.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., *et al.* (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nat Commun* , 10, 3109.
- Renner, S.S. & Zohner, C.M. (2018). Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates. *Annual Review of Ecology, Evolution, and Systematics* , 49, 165–182.
- Revell, L.J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* , 1, 319–329.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* , 421, 57–60.
- Roy, D.B. & Sparks, T.H. (2000). Phenology of British butterflies and climate change. *Global Change Biology* , 6, 407–416.
- Rummukainen, M. (2012). Changes in climate and weather extremes in the 21st century. *WIREs Climate Change* , 3, 115–129.
- Saarinen, K., Lahti, T. & Marttila, O. (2003). Population trends of Finnish butterflies (Lepidoptera: Hesperioidea, Papilionoidea) in 1991–2000. *Biodiversity and Conservation* , 12, 2147–2159.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., *et al.* (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences* , 278, 835–842.
- Schmucki, R., Harrower, C.A. & Dennis, E.B. (2020). rbms: Computing generalised abundance indices for butterfly monitoring count data. R package version 1.0.0.
- Schmucki, R., Pe’er, G., Roy, D.B., Stefanescu, C., Swaay, C.A.M.V., Oliver, T.H., *et al.* (2016). A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *Journal of Applied Ecology* , 53, 501–510.
- Socolar, J.B., Epanchin, P.N., Beissinger, S.R. & Tingley, M.W. (2017). Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proc Natl Acad Sci USA* , 114, 12976–12981.
- Spence, A.R. & Tingley, M.W. (2020). The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography* , 43, 1571–1590.
- Stefanescu, C., Peñuelas, J. & Filella, I. (2003). Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology* , 9, 1494–1506.
- Symonds, M.R.E. & Blomberg, S.P. (2014). A Primer on Phylogenetic Generalised Least Squares. In: *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice* (ed. Garamszegi, L.Z.). Springer, Berlin, Heidelberg, pp. 105–130.

- Teder, T. (2020). Phenological responses to climate warming in temperate moths and butterflies: species traits predict future changes in voltinism. *Oikos* , 129, 1051–1060.
- Thomas, C.D. & Lennon, J.J. (1999). Birds extend their ranges northwards. *Nature* , 399, 213–213.
- Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science* , 348, 571–573.
- Valtonen, A., Leinonen, R., Pöyry, J., Roininen, H., Tuomela, J. & Ayres, M.P. (2014). Is climate warming more consequential towards poles? The phenology of Lepidoptera in Finland. *Glob Change Biol* , 20, 16–27.
- Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G., McCann, K.S., *et al.* (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences* , 281, 20132612.
- Virtanen, T. & Neuvonen, S. (1999). Climate change and macrolepidopteran biodiversity in Finland. *Chemosphere - Global Change Science* , 1, 439–448.
- WallisDeVries, M.F. (2014). Linking species assemblages to environmental change: Moving beyond the specialist-generalist dichotomy. *Basic and Applied Ecology* , 15, 279–287.
- Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B. & Davis, C.C. (2010). Favorable Climate Change Response Explains Non-Native Species' Success in Thoreau's Woods. *PLOS ONE* , 5, e8878.
- Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* , 8, 1138–1146.

(a) Processes giving rise to patterns predicted by hypotheses 1 and 2



(b) Patterns in data predicted by hypotheses 1 and 2

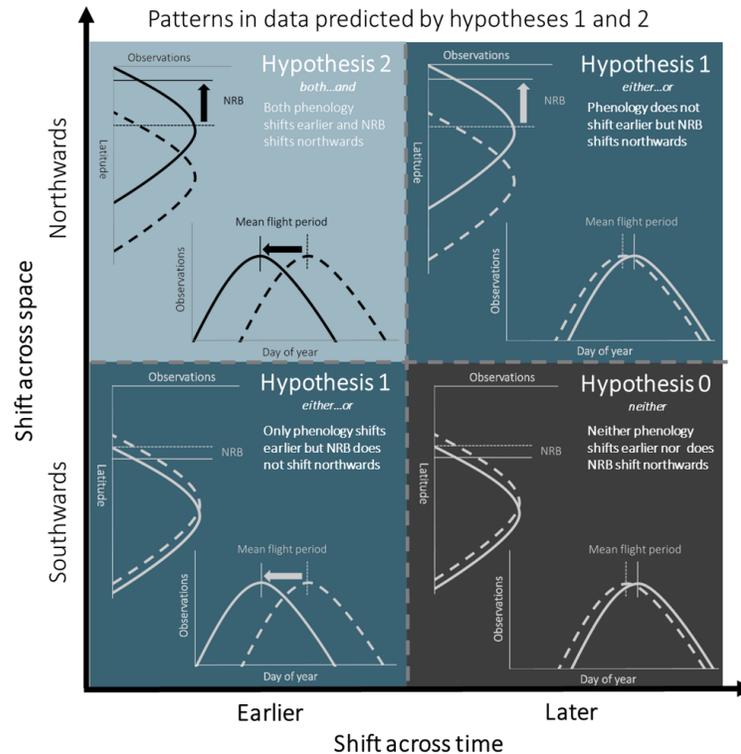


Figure 1. Chart describing processes and predictions of the hypotheses. Panel (a) describes the underlying processes that may give rise to the patterns predicted by the outlined hypotheses. Underpinning hypothesis 1 (*either phenology or range shift*) is the assumption that species differ fundamentally in their abilities to adjust either in situ or via dispersal. As both strategies are likely to be adaptive, being able to use either will lead to an increased probability of presence, which should be reflected in positive population trends. Positive feedback loops through larger population size further enhance the ability of both mechanisms to act. Underpinning hypothesis 2 (*both phenology and range shift*), on the other hand, is the assumption that adaptive in situ responses in phenology increases the fitness of the individuals, leading to higher rates of survival and/or more offspring. This in turn increases the probability of presence (stronger population trends) and thus higher colonization rates which leads to the species being able to expand into habitats becoming suitable as climate changes (=shift in the northern range boundary (NRB)). In this study, the hypothesized

underlying processes are investigated through proxies for range shift, phenology shift, and probability of presences as depicted by derived estimates in yellow versus blue font in the process charts: shift in NRB as a measure of species range shift; change in adult flight period as a proxy for phenology shift; and population trends as a proxy for probability of presence across the distribution. Panel (b) describes the expected patterns in the data, i.e. the combinations of responses, as regards NRB and phenology shift estimates, that would support hypotheses 1 (*either* advanced phenology *or* northwards shifting NRB), 2 (*both* advanced phenology *and* northwards shifting NRB), and 0 (*neither* advanced phenology *nor* northwards shifting NRB). Although these proxies do not allow us to infer evidence for the underlying processes, they can inform us of the patterns across a wide sample of species. By combining them with information on population trends, we can infer how successful the strategies are on their own and in combination for species experiencing climate change, and what may be the consequences if species cannot utilize either of the highlighted strategies.

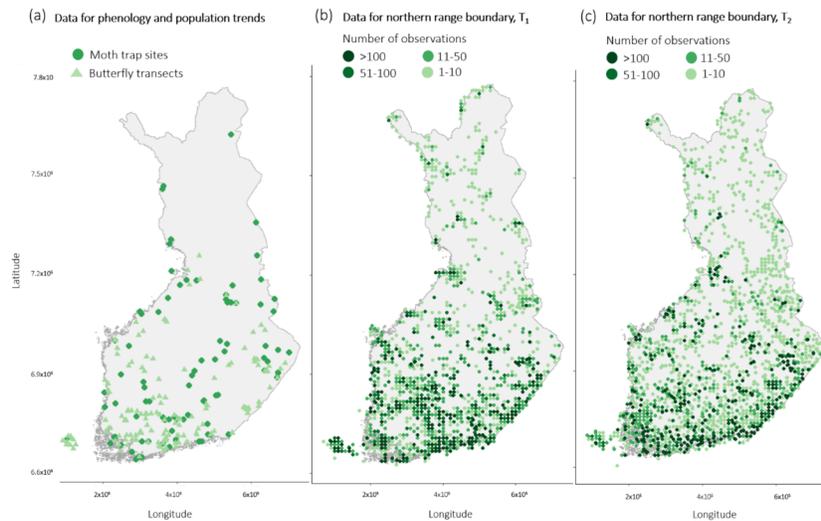


Figure 2. Spatial distribution of data. Panel (a) shows the location of butterfly transect ($n=158$) and moth traps ($n=93$) where phenological data on the 289 species used in this study had been collected during 1999-2017 and 1993-2017 for the butterflies and moths, respectively. Panel (b) and (c) show the locations with observational data for T_1 and T_2 , respectively, with samples size per coordinate depicted by different shades of green, on the 289 species used for calculating shifts in the northern range boundary. Longitude and latitude in the ETRS89 coordinate system. Also see Fig. S1 for the temporal span of the data sets used in this study.

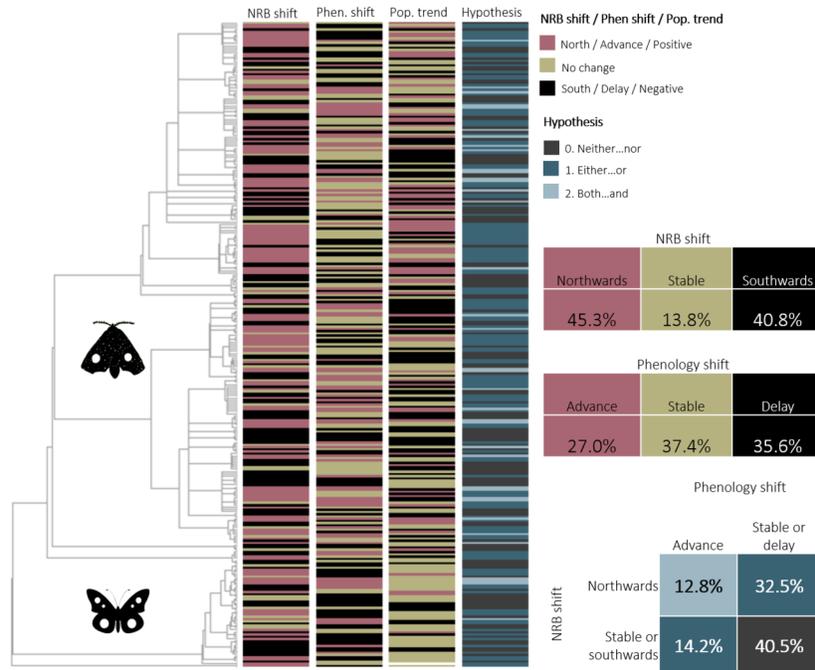


Figure 3. Direction of shift in NRB, phenology shift, population trend, and hypothesis-related response per species, organized by their phylogeny. There was no systematic community-wide direction in any of the three responses (phenology shift: mean= 0.02 ± 0.02 days/year; $t=0.63$; $p=0.53$; range shift (residual km): mean= -28 ± 39.3 km; $t=-0.71$; $p=0.48$; population trend: mean= -0.005 ± 0.01 ; $t=-0.32$; $p=0.75$). We also found no difference in the estimates between the two main taxonomic groups, butterflies and moths (Table S2). 46.7% (32.5+14.2) of the studied species either shifted their NRB northwards or phenology earlier (hypothesis 2), 40.5% neither shifted their NRB northwards nor phenology earlier (hypothesis 0), and 12.8% of the studied species shifted both their NRB northwards and phenology earlier (hypothesis 1). Moth icon by Carpe Diem and butterfly icon by tulpahn, both from the Noun Project <https://thenounproject.com/>.

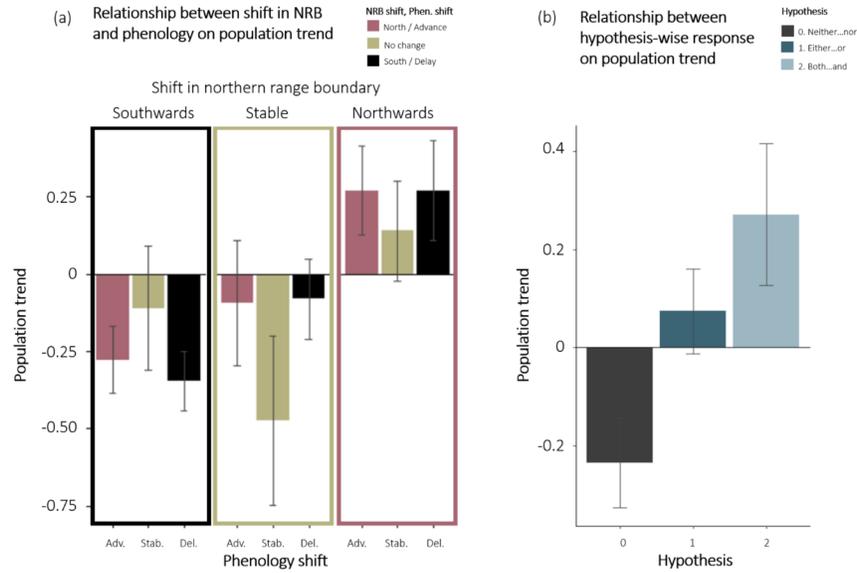


Figure 4. Relationship between responses and population trends. Panel (a) shows the mean population trend (\pm SEM) for species with different combinations of responses in phenology and NRB. The pgsI model b) indicated that a range shift had a significant positive effect on the population trend (Est.= 0.37; $t=2.15$; $p<0.05$). Panel (b) shows the mean population trend (\pm SEM) for species with different hypothesis-wise responses (dark grey= hypothesis 0 - the species neither shift NRB nor phenology; dark blue= hypothesis 1 - the species shifts either NRB or phenology; light blue= hypothesis 2 - the species shifts both NRB and phenology). Species that responded according to Hypothesis 2 showed the strongest population trends (Est.= 0.55; $t=3.08$; $p<0.01$).

Table 1. Conversion of phenology and NRB estimates into categorical response groups. a) The slope coefficients from the phenological analyses and NRB shift estimates were used to convert continuous responses into categorical response groups. b) To enable tests of our hypotheses, we further combined these phenology and NRB response groups into 1) a four-level category describing combined response groups (RG) and 2) a three-level category describing hypothesis-wise responses (Hypotheses 0, 1, or 2), both corresponding to the potential combined responses shown in Fig. 1b.

a) Criteria for placement into response groups		a) Criteria for placement into response groups
Response		Response groups
Phenology	significantly negative slope coefficient	Advancing
	insignificant slope coefficient with any sign	Stable
	significantly positive slope coefficient	Delaying
NRB	shift of 20 or more kilometers	Northwards
	shift between -20 and 20 kilometers	Stable
	shift of -20 kilometers or less	Southwards

b) combined and hypothesis-wise response groups		b) combined and hypothesis-wise response groups	b) combined and hypothesis-wise response groups
NRB	Phenology	<i>RG A+N / Hypothesis 2:</i>	Phenology
	Advance + Northwards	<i>RG SD+N / Hypothesis 0:</i>	Stable + Northwards
	<i>RG A+SS / Hypothesis 1</i>	<i>RG SD+SS / Hypothesis 1</i>	Stable + Southwards

b) combined and hypothesis-wise response groups	b) combined and hypothesis-wise response groups	b) combined and hypothesis-wise response groups
	<i>Advancing + Stable</i>	<i>Stable + Stable</i>
	<i>Advancing + Southwards</i>	<i>Stable + Southwards</i>

Table 2. Model statistics of PGLS-models a)-e). To test our main hypotheses (see Fig. 1) we fitted five separate models. We tested the effect of direction of shifts in a) phenology and b) NRB (Table 1a) on population trend (continuous). We tested the effect of c) categorical shift in phenology (Table 1a) on shift in NRB (continuous). To test the effect of different combinations of the responses on population trends, and which hypothesis provides a more viable strategy for species (as opposed to which strategy is the more common), we tested the effect of the d) combined response groups (Fig. 1b; RGs in Table 1b) and e) hypothesis-wise responses (Fig. 1b; Hypotheses in Table 1b) on population trend (continuous).

	a) Phenology shift effect on population trend	a) Phenology shift effect on NRB
	Estimate	SE
Stable (Intercept)	-0.1431	0.32
Advance	0.161	0.1433
Delay	0.0246	0.1347
	b) NRB shift effect on population trend	b) NRB shift effect on NRB
	Estimate	SE
Stable (Intercept)	-0.2335	0.2923
North	0.3729	0.1731
South	-0.0158	0.1736
	c) Phenology shift effect on shift in NRB	c) Phenology shift effect on NRB
	Estimate	SE
Stable (Intercept)	-0.217	0.2904
Advance	0.1263	0.1448
Delay	-0.0201	0.136
	d) Combined effect on population trend	d) Combined effect on NRB
	Estimate	SE
Delay or Stable + Southwards or Stable (Intercept)	-0.2494	0.2968
Advance + Northwards	0.5479	0.179
Advance + Southwards or Stable	0.0407	0.1726
Delay or stable + Northwards	0.3228	0.1359
	e) Hypothesis-wise effect on population trend	e) Hypothesis-wise effect on NRB
	Estimate	SE
Hypothesis 0 (Intercept)	-0.248	0.319
Hypothesis 1	0.228	0.122
Hypothesis 2	0.552	0.179