

# The impact of climate change on species in Finland

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Climatic conditions constitute the very defining dimensions of abiotic conditions for biodiversity. Now these fundamental settings are changing at rapid pace, and this transformation is not only something looming around the corner, but the change is already here. In this summary I want to emphasize the responses through which species can adjust to a change in climate and I will describe some signatures of the effect of climate change on the fauna and flora in Finland.

Globally we have seen an increase in mean annual temperature of 1.3 °C since the pre-industrial baseline (berkeleyearth.org/data; Rohde and Hausfather 2020). In Finland, however, a 2-fold temperature increase, 2.6 °C, over the same time has occurred. By the end of the 21st century, we can expect an increase of more than 5 °C in Finland, i.e., in case we are globally able to halt the increase in emissions by 2050 and thereafter reduce them (SSP2-4.5; IPCC 2021). If we continue on our current path, however, and do not curtail greenhouse gas emissions (SSP3-7.0; IPCC 2021) Finns can expect to see a 6.8 °C degree increase by the end of the century. If we start cutting down emissions immediately and succeed in reaching net zero emissions globally by around 2080 (SSP1-2.6; IPCC 2021) Finland would not warm by more than a total of 3.5 °C. A total increase ranging between 3–7 °C will, in any case, constitute a tremendous change for Finnish nature considering that the difference in mean annual temperature between Helsinki in the very south of the country and Sodankylä in mid-Lapland is on average 6 °C (Normal period 1991–2020; Finnish Meteorological Institute). What will a change of

such magnitude imply for the species that make up our living environment? And should not this change be visible already, if we've already seen a 2.6 °C increase? The answer to the first question can be approached through the answer to the second. By quantifying and documenting the changes that we can see to date, we can, if not predict, at least approximate what nature might be up against during the coming decades. And nature is already changing, that is for certain.

In my research, I aim to understand how species are coping with climate change – which species are managing or even thriving under the new conditions, and which are suffering and might thus need focused conservation attention. One way of approaching this massive and burning question is by consider the alternatives that species have when confronted with environmental change. Over time, species have adjusted to specific environmental conditions under which they thrive and reproduce. Thus, if environmental conditions of a species should change, it must either (i) adjust in place to the new conditions through evolutionarily or plastic responses, or (ii) shift in space, i.e. disperse to areas where its require-

ments are better fulfilled. The speed of current climate change may outpace the ability of populations to respond through either pathway which means individuals will fail to replace themselves with offspring, populations will shrink and eventually the species will go extinct. In my research I have found examples of species fitting into each one of the above-mentioned categories: species that move, species that adjust, species that can do a bit of both, and species that are not responding. Let us begin with an example from the latter category, of a species that is possibly already heading towards the decline and extinction.

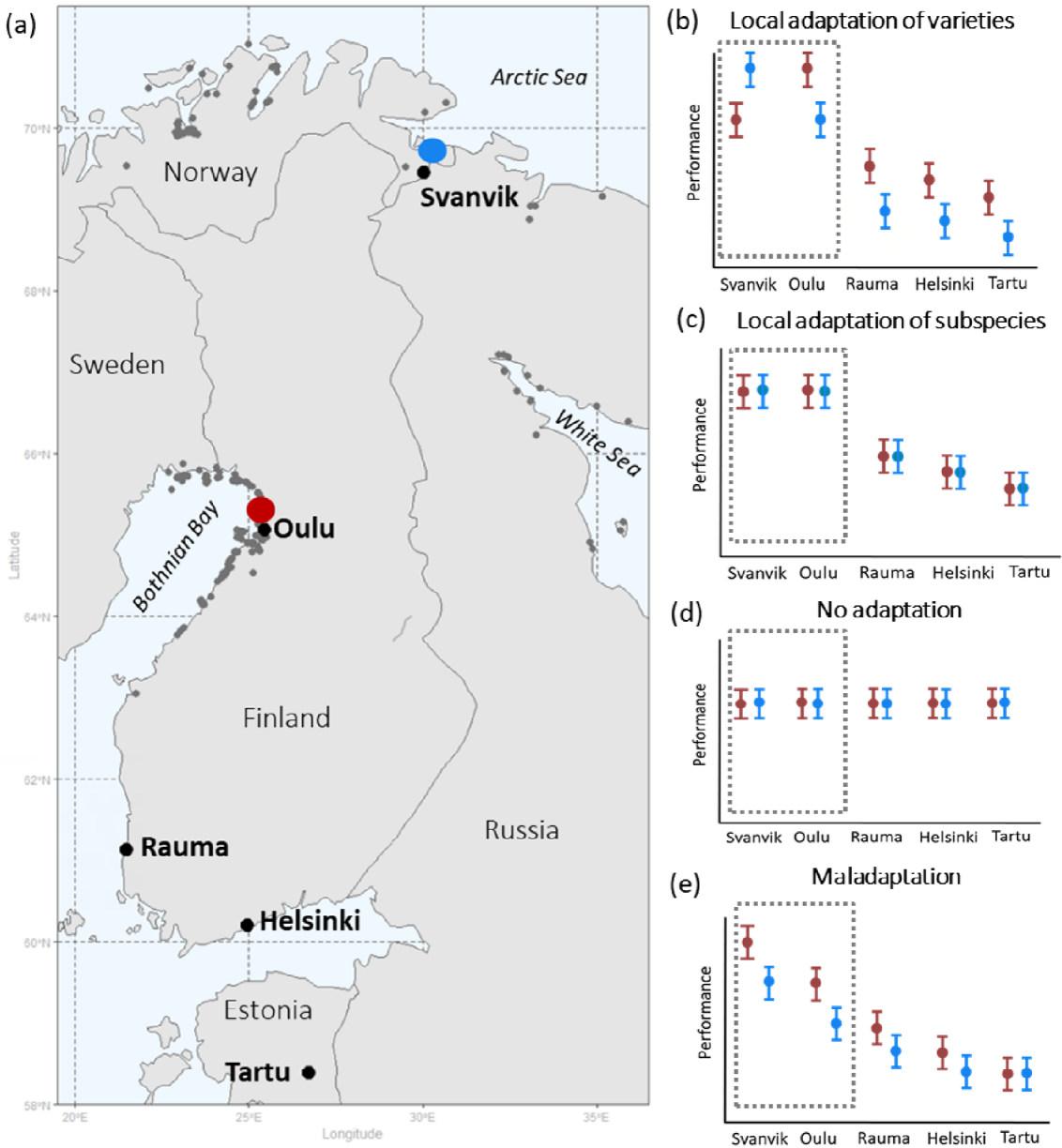
The Siberian primrose (*Primula nutans* subsp. *finmarchica*) is a perennial plant that grows on seashore meadows. The variety *jokelae* (henceforth the southern variety) grows in Finland and Sweden by the Bothnian Bay and in Russia by the White Sea. The variety *finmarchica* (henceforth the northern variety) occurs on the shore of the Arctic Sea in Norway and Russia (Fig. 1). We collected seeds from populations of both varieties and planted them in five botanic gardens: in their home environments in Svanvik, northern Norway, and in Oulu, northern Finland, as well as in Rauma and Helsinki further south in Finland and in Tartu, Estonia (Fig. 1; Hällfors et al. 2020a). We wanted to find out how strongly adapted the two varieties are to the local climatic conditions and how a warmer climate might affect them. We took measures on survival, size, and flowering over the next three years and expected that both varieties would thrive best within the range of the species (Oulu and Svanvik), potentially even showing higher fitness in their specific home locations if they are strongly locally adapted, and worse further towards the south.

Our results showed that both varieties, indeed, fared poorer in the southern gardens compared to Oulu and Svanvik, indicating that a warmer climate may be unfavorable for the species if it is incapable of adjusting or relocating. We were surprised, however, by our finding that the southern populations were more successful in northern Norway than in Oulu – even more successful than the northern variety there, in its home environment. When we compared our results to weather data from the study years and to historic average climate conditions, our findings started to make more sense. It turned out, that the experi-

enced temperature conditions in Svanvik resembled the historic average temperatures in Oulu, while the experienced temperatures in Oulu resembled the historic average temperatures in the out-of-range gardens in Rauma, Helsinki, and Tartu. Within our experiment the northern variety did not experience conditions corresponding to historical temperature in its home site in any of the experimental sites, since even the coldest site, Svanvik, deviated from the historic mean annual temperature. This suggests that the climatic optima of both varieties have moved, at least partly, outside their current range and that the conditions that we aimed to mimic through our experimental design had in practice already shifted further north, which we did not consider initially when forming our hypotheses.

Based on our findings, we conclude that the Siberian primrose is already suffering from adaptational lag (McGraw et al. 2015) due to climate change, and that further warming may increase this maladaptation, especially for the northern variety. If it cannot adjust or move, the effects of global warming may contribute to the demise of this species. Dispersal is likely not a viable option, since suitable habitat lies hundreds of kilometers away with no effective dispersal corridors in between. One way to help species like this to survive current and future challenges would be to relocate them, by human hand, further north. In other words, species could be conserved though what is known as assisted migration (Hällfors et al. 2014). To investigate the potential for this species to adjust in place, we are currently conducting experiments utilizing quantitative genetics approaches to estimate the evolvability of the Siberian primrose. To increase the likelihood of adjustment, it would be important to ensure that species have sufficiently large high-quality habitats to preserve populations at a viable level. This would safeguard enough genetic variation within the populations, that is, different individuals that have a higher probability to possess characteristics that are suitable in the new conditions.

Let us next turn our focus towards the two adaptive alternatives and some studies identifying species able to capitalize on them. As a reminder, to avoid population decline and extinction when faced with environmental change like climate change, species can (i) adjust in place



**Figure 1.** Geographical distribution of seed sampling sites and experimental gardens (a), and hypotheses of plant performance in experimental gardens (b–e) in the translocation trial on Siberian primrose (Hällfors et al. 2020a).

(a) shows the geographical distribution of seed sampling sites and experimental gardens with occurrences of *Primula nutans* ssp. *finmarchica* marked by dark grey points: Var. *finmarchica* occurs by the Arctic Sea in N-Norway and var. *jokelae* by the Bothnian bay in Finland and Sweden and the White Sea in Russia. Red, seed sampling sites of the southern variety (var. *jokelae*) in Finland; Blue, seed sampling sites of the northern variety (var. *finmarchica*) in Norway.

(b–e) show hypothesized overall performance of the tested varieties in all experimental gardens following opposing underlying scenarios of (b) local relative adaptation (sensu Brady et al. 2019) at the varietal and subspecies level, (c) relative adaptation of the subspecies to its current environment vs. areas outside it, (d) tolerance (through plasticity) towards all tested conditions (including those not currently present within the occurrence area of the subspecies), and (e) relative maladaptation caused by climate change (see text for hypotheses). Dashed area demarks within-range gardens, i.e., the reciprocal part of the experiment. Red, southern variety; blue, northern variety. Figure and caption reproduced from the original publication (Hällfors et al. 2020a) which is distributed under the Creative Commons Attribution-Non Commercial License 4.0 (CC BY-NC).

or (ii) shift in space. Let us start with thinking about how a species can adjust in place as temperatures increase. One such way could be, e.g., to simply develop a higher physiological temperature tolerance. We could also hypothesize that species like insects or plants should produce less pigmentation since the ambient temperature is higher and they do not need it for thermoregulation, or mammals and birds might reduce in size. However, one characteristic that lies close at hand and of which there exists large quantities of data for multiple species over a long time, is phenology. Phenology means the timing during the season when an individual expresses a certain central life-history stage, such as when birds migrate, when plants flower, or when adult butterflies fly and mate. Correctly timed phenology is critical for the overall success of an individual, since this timing determines whether the life history event is expressed during the time when the environment is most favorable for it, like their being plenty of insect larvae available for birds to feed their chicks with, or sunlight and lack of frost for new leaves to grow and start photosynthesizing. Several studies have shown that, under climate change, those species that advance their phenological timing in concert with advancing seasons tend to do better, and e.g., have more positive population trends (Møller et al 2008; Saino et al. 2011). Thus, concentrating on phenological change can be an informative lens through which we can understand how species are adjusting in place.

We know from previous studies that birds have advanced their spring migration and that some leave later in fall (Lehikoinen et al. 2019). Such changes would affect the time spent in breeding grounds and can, together with increased temperatures in the breeding sites, have affected both breeding timing and its duration. To study whether and how birds are changing their breeding phenology to altered seasons, we used a previously underutilized data set: the ringing data of bird chicks (Hällfors et al. 2020b). The banding or ringing time of bird chicks can be used as a proxy for breeding, since nestlings can be ringed when they are of a certain size. Thus, ringing time functions as an adequate surrogate for hatching time, and we can assume that if the hatching time has changed so too would the time of ringing have

shifted. Every year, about 100 000 bird chicks are ringed in Finland by trained bird enthusiasts. For this specific study we used 800 000 ringing events in unique nests for 73 species across four decades (data available in Hällfors et al. 2020c; Fig. 2). Because of the nature of these data, where bird chicks are continuously ringed throughout the occurrence of nestlings – we were able to define the beginning, the end, and the duration of breeding for each species (Fig. 2) within each of the four bioclimatic zones in Finland (Ahti et al. 1968).

The majority of the 73 bird species had advanced the timing of their breeding, both when it came to the beginning and the end of the breeding season. We saw an advance in the beginning of the breeding period by an average of 4.6 days. We also found that, for a third of the species, the duration of breeding had become shorter. Although only a minority of the species shortened the duration, this was enough to result in an average shortening of the breeding period across all species in the study: the average breeding period contracted by 1.7 days across all species. This contraction occurred since although the beginning of breeding had advanced, the end of breeding had advanced even more, by an average of 6.3 days. Because the timing of breeding was studied at a species level, in practice this means that, within a specific species, the latest individuals had advanced their breeding proportionally more than the early individuals. Among the species that shortened their breeding, almost all were resident or short distance migrants, which are the species that tend to breed earliest during the season. This suggests that residents and short-distance migrants may be better able to respond to increased temperatures in the spring and thus take better advantage of the earlier food and resource availability.

Our findings from this study using bird ringing data highlight the importance of quantifying phenological change across species and over the entire season to reveal shifts in the community-level distribution of bird reproduction. Our study also points out that evaluating changes throughout the season is crucial since changes may alter community-wide patterns of species co-occurrence and thereby trophic interactions: there might nowadays be more nestlings of the same species around at the same time, which would

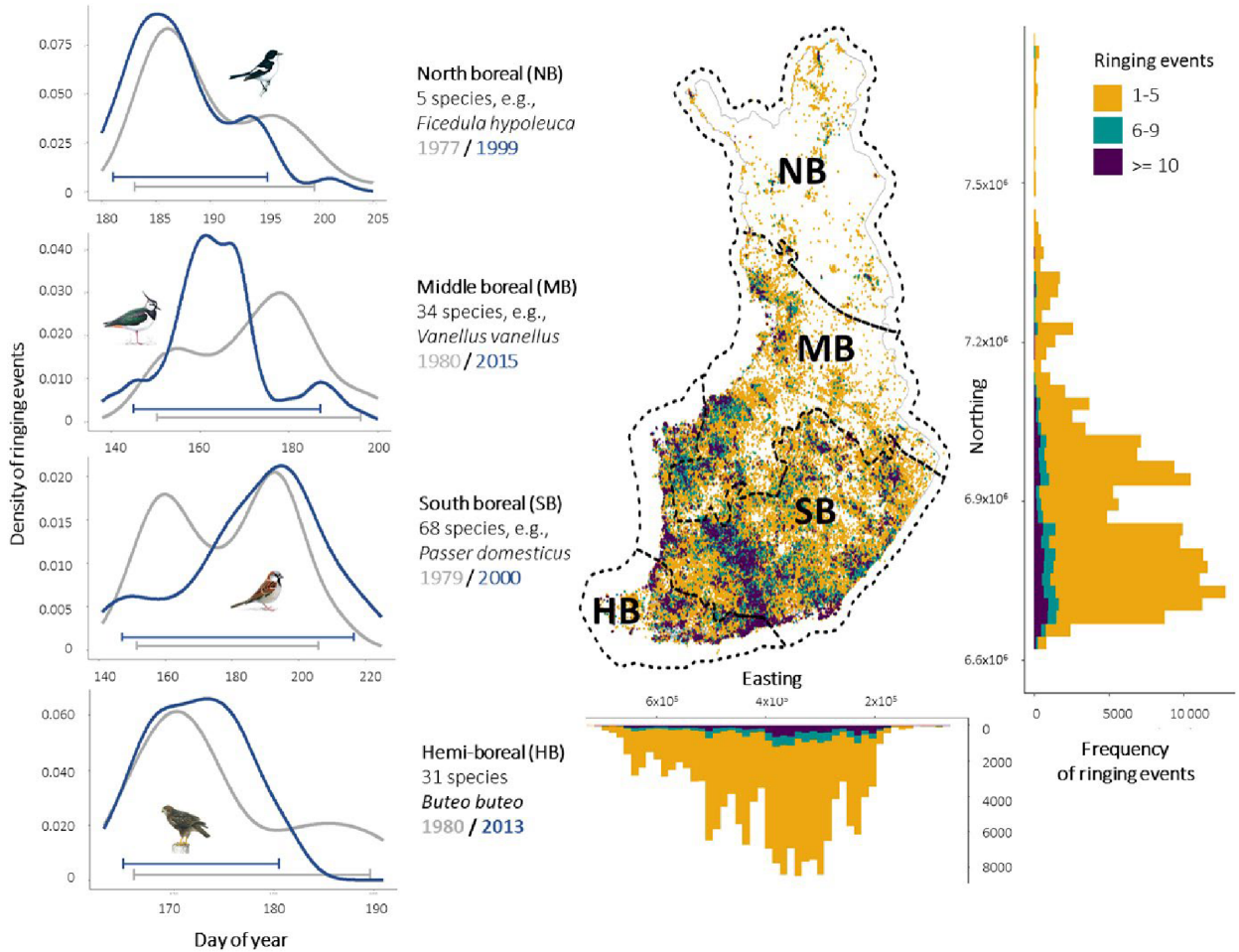


Figure 2. Spatial distribution of the nestling ringing data used in Hällfors et al. 2020b.

The map depicts the location of each ringing event across the four bioclimatic zones in Finland, and the marginal histograms show their distribution and sample size per spatial coordinate (European Terrestrial Reference System 1989 coordinate system).

The four side panels (Left) illustrate the distribution of ringing events over day of year for one selected species in each bioclimatic zone, showing two example years 20 to 25 y apart with different colors. Horizontal brackets indicate the phenological metrics calculated: beginning of breeding period (5th percentile), end of breeding period (95th percentile), and duration (difference between the end and the beginning). The number of species analyzed in each bioclimatic zone is shown beside each panel (73 species in total). There were 138 unique species-by-zone combinations as not all species were present in each of the four zones.

Bird illustrations are by Mike Langman (<https://www.rspb-images.com>).

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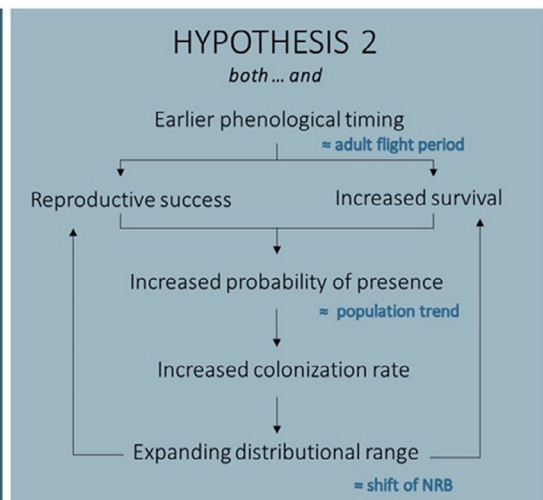
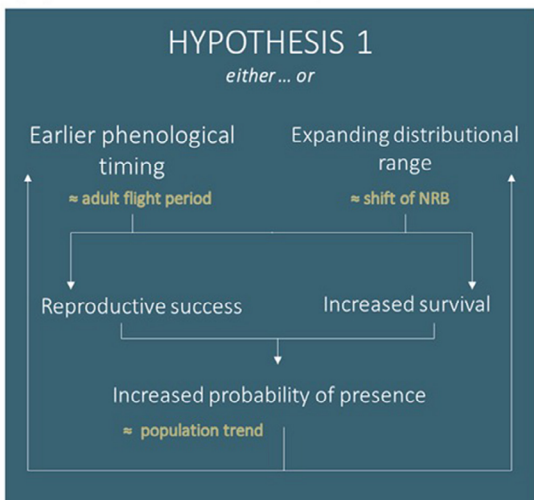
mean that there are more chicks needing similar food at the same time. Whether these resources are also shifting over the season is now the key question. Insects, e.g., is a main food source for many bird species, but we know very lit-

tle about how the temporal abundance of insects has changed. The potential loss of synchrony between interconnected species exemplifies one of the major uncertainties in the future functionality of ecosystems.

In another study we compared the pace of phenological shifts between different taxonomic groups. Here we used an enormous systematically collected dataset from long term monitored localities within eastern Europe and Russia (Ovas-kainen et al. 2020). We show, like so many other studies (Parmesan & Yohe 2003; Thackerey 2010; Cohen et al. 2018), that there is huge variation in phenological shifts across taxa (Roslin et al. 2020). But among this variation, we do find some generalities. Spring events showed the strongest shift towards earlier dates, whereas autumn shifted strongly towards later dates. This was particularly evident for plants, which advanced early or delayed late events faster than other trophic levels. Fastest of all changed the abiotic events such as the melting of snow cover, or the breakup of ice, which had also been observed in this phenological study. This shows that overall, organisms are failing to keep pace with the variable climate, and that there is large variation both within and among taxonomic groups in the capacity to advance phenology. Just as with the birds in our study using ringing data, although the average response was to advance breeding, not all of the studies species shifted in time. Does this mean that species that are failing to adjust will eventually face the same faith as what we fear is occurring for the Siberian primrose? There is still the second lifeline available: shifting in space.

**Figure 3 ▼►** (on pages 22 and 23). Chart describing processes and predictions of the hypotheses in Hällfors et al. 2021. ▼ 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. Assuming that these strategies are adaptive, being able to use either strategy 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 strategies to function. 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]). A successful colonization of new available habitat further increases the probability of survival and reproductive success of individuals, which again has a positive effect on species abundance. 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.

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



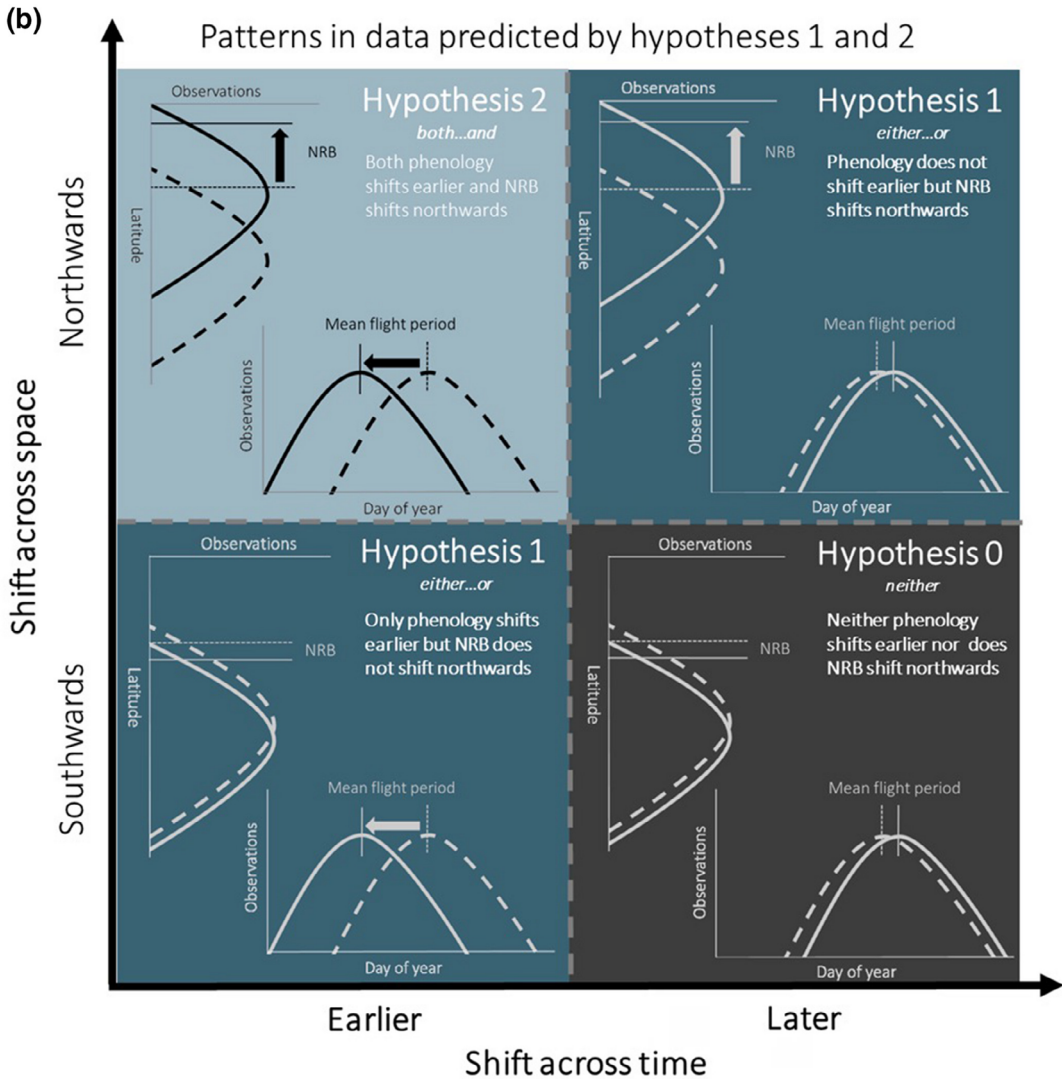


Fig. 3 cont.

▲ 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 likely 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 strategies.

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Palaeoecological evidence suggests that, during past changes in climate, most species have re-located rather than remained to face a new environment (Brook and Barnosky 2012). At the moment I am investigating range shifts of birds, moths, and butterflies in Finland. Finland is a good country to study range shifts within, since we have a long latitudinal extent and many species have their northern range boundaries in Finland. In this study under preparation, we want to find out how much the northern range edges have moved over the past decades and what characteristics describe species that are better able to utilize this response. Perhaps this propensity depends on their traits, like dispersal ability or over-

wintering stage. Or maybe their preadaptation to temperature conditions is the key: perhaps those more specialized to specific conditions are forced afoot while climatic generalist have more leverage to stay and adjust. In fact, as temperatures increase, both phenology shifts and range shifts can function to lower the experienced temperature (Socolar et al. 2017; Amano et al. 2014). Through phenology shifts populations can stay where they are but better match the new environment by, e.g., flowering or breeding earlier when the environmental window is favorable. The other option is to shift in space to other areas, often further north, and in that way keep the original phenological response in seasonal time. Could this explain why we do not see all species moving northwards or all species advancing their phenology – perhaps some use one strategy and some the other?

To find out, I tested the strategy choice of 237 moth species and 46 butterfly species by comparing temporal shifts in their flight period and spatial shifts in their northern range boundary (Hällfors et al. 2021a). For this study, I utilized data on Lepidoptera flight periods collected in two long-term monitoring projects coordinated by the Finnish Environment Institute (data available in Hällfors et al. 2021b). A dataset of citizen observations openly available through the Finnish Biodiversity Information Facility was utilized to calculate species range boundary shifts. The most straightforward hypothesis was that species would use one of the two strategies, as described above. But there is another possible scenario as well: responding adaptively by advancing one's phenology might actually induce a range shift response. As I already mentioned, species that advance their phenology tend to do better. We also know that stable or positive population trends, i.e., no change or increase in abundance, are often a prerequisite for species to expand their ranges, and that the dispersal rate from larger populations is higher and the probability of colonization increases with the summed contribution of individuals from neighboring source populations (Pärn et al. 2012; Hanski & Ovaskainen 2003). Thus, a competing hypothesis is, that species would combine both responses.

Like in so many other studies looking at range shifts or phenology shifts, we also found no overall direction in neither phenology nor range shifts:

equally many species responded by advancing their phenology as did not, and equally many species shifted their range boundaries northwards as stayed put. We did see however, that species tended to shift their ranges northwards more often than they advanced their phenology. Overall, our results supported the idea that there is some complementarity in the two responses, since roughly 45% of the species that we studied had either moved northward or advanced their flight period, but not done both. However, complementarity does not explain the lack of adaptive responses seen in studies concentrating on either range or phenological shifts, since as many as 40% of the species had still not responded in either way. On average, the populations of these poorly responding species had declined while the species responding in either way had positive population trends on average (Fig. 4). The largest increase in abundance was seen in the 15% of the species that both moved northward and advanced their flight, adding evidence to the notion that adaptive responses are connected with better thriving species.

A potential explanation for the infrequency of species responding optimally, that is, by both advancing their flight and moving northward or through either of the strategies could be a scarcity of suitable habitats. For organisms to be able to respond to climate change by shifting their ranges, enough suitable habitat of high-quality are needed. The amount of available habitat for many species has recently decreased (Kuussaari et al. 2007), resulting in many populations to decline. For example, many butterfly species have suffered from the decrease in meadows. Declining populations are usually not able to provide a sufficient basis for the species to spread to new areas. Small populations also contain less genetic diversity that could help the local populations adjust in place, e.g., by changing the timing of their flight.

Species have an amazing capacity to adjust, and nature is resilient and can buffer many disturbances and keep providing us with the ecosystem services that we depend on, but it cannot do this in a vacuum. With the rapid change we have brought about in the climatic environment, we cannot afford removing the very matrix that species need to respond appropriately: habitat. If we ensure sufficiently extensive and interconnected habitats



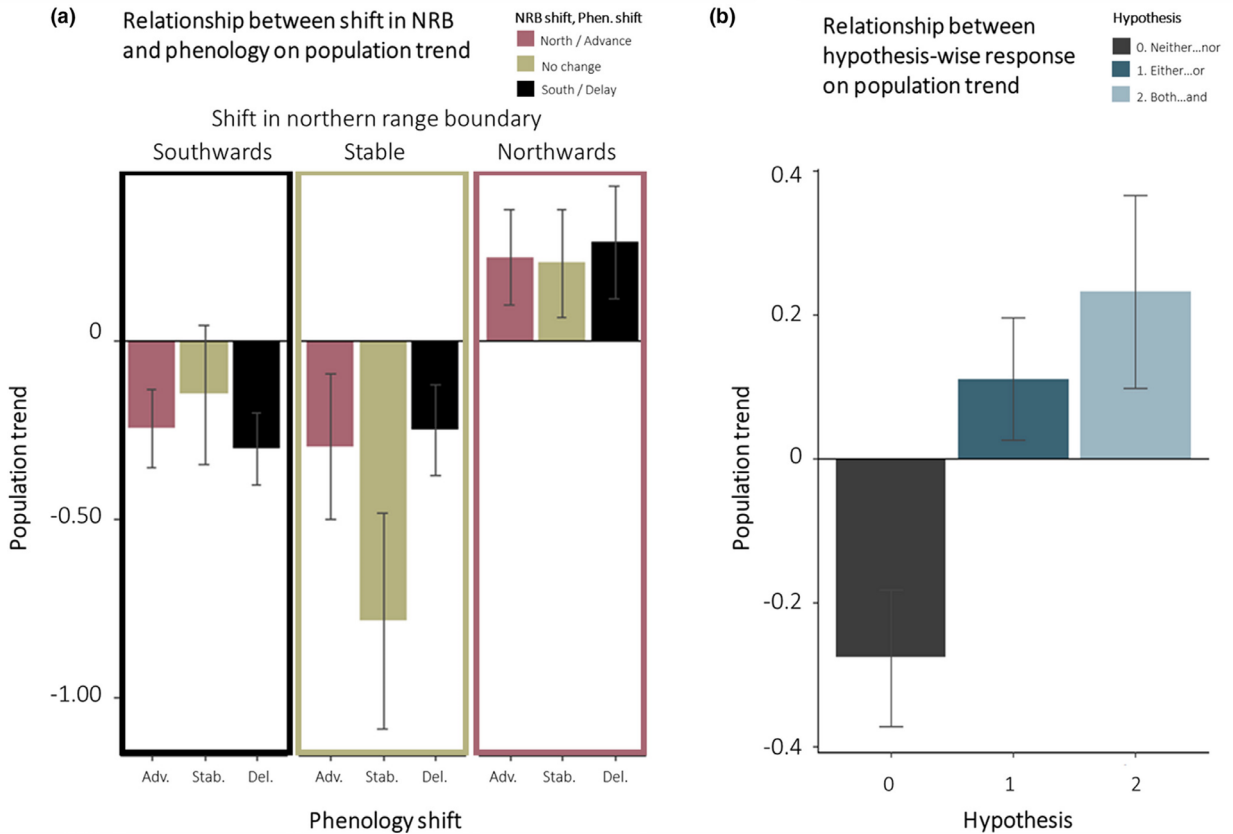


Figure 4. Relationship between responses and population trends found in Hällfors et al. 2021.

Panel (a) shows the mean population trend ( $\pm$ SEM) for species with different combinations of responses in phenology and NRB. The model (b) indicated that a shift in NRB had a significant positive effect on the population trend (Est. = 0.65;  $t = 3.36$ ;  $p < 0.001$ ).

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 1 showed stronger population trends (Est. 0.31;  $t = 2.51$ ;  $p < 0.05$ ), whereas species that responded according to Hypothesis 2 showed the strongest population trends (Est. = 0.52;  $t = 3.08$ ;  $p < 0.01$ ).

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of high-quality, species can more likely sustain sufficiently large and genetically variable populations which in turn can adjust in place when the environment changes. Safeguarding habitat will also allow species to move across space, dispersing through a habitat matrix and arriving in new habitat that they can colonize. Overall, to safeguard biodiversity as climate change intensifies, the best we can do is to allow nature room to make use of its resilience.

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