Space, time and climate change OR:

Shifts in time and space interact as climate warms

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Beetles found on Mediterranean shores in cold periods turned up in Finland in mild interglacials (1). Paleontologists see such range shifts as systematic responses to changing climate. No surprise, then, that recent global trends for poleward and upward range shifts are attributed to current warming (2,3). However, range shifts are not the only mechanism by which organisms can mitigate effects of warming. An organism's experience of climate can be modulated in situ by changes of microhabitat (4,5) or by phenological (timing) adjustment, which can dramatically alter climate space in seasonal habitats.

Phenology and species' range can be so intimately associated that understanding drivers of phenology can predict range limits. Morin et al. (6) predicted both poleward and equatorial range limits of temperate-zone trees from effects of climate on life history and phenology. They found equatorial limits where winter chilling was marginally adequate to vernalize the plants and trigger spring flowering, while poleward limits occurred where there was barely time to mature fruit before onset of winter. Demonstrations of this intimacy between range limits and phenology have been restricted to plants and insects (6). In contrast, Socolar et al (7) note that the ornithological literature has tended to view geography and phenology independently, with range shifts seen as responses to temperature change and shifts of breeding date driven more by changes of resource availability. On the one hand, bird range limits have been expanding polewards as climate warms (8), and on the other hand relative timing of bird nesting and peak abundance of caterpillar prey was both crucial to nestling survival and changing with climate warming (9).

Socolar et al. (7) give evidence that nestling survival is also sensitive to temperature, implying direct effects of climate distinct from indirect effects mediated by timing of resource peaks. Using a citizen-science database of >47,000 monitored nests across the USA, they show that cool temperature anomalies during nesting were associated with reduced nestling survival in cool parts of species' ranges, while warm anomalies had a similar negative effect in warm regions. Clearly, temperatures experienced by nestlings are important. Socolar et al. show that, across the entire bird community of the Californian Coast Ranges and Sierra Nevada, phenological advance (earlier nesting) has caused temperatures experienced by nestlings to remain essentially constant through the warming of the past century. Socolar et al. argue that this effect of phenology has been ignored by ornithologists.

Because phenological advance and range shifts both mitigate effects of warming, Socolar et al. (7) consider them as potential alternatives and advocate greater attention to this possibility. For example, they cite strong elevational range shifts of tropical birds in environments where phenological shifts would have little effect on temperature. Further, they critique DeVictor et al. (10) for ignoring phenology when concluding that birds had accumulated more "climate debt" than butterflies. Using data on changes of community composition across Europe, DeVictor et al (10) found that the mean observed poleward range shift was less in birds than in butterflies, and neither group had shifted as much as had the climate. Socolar et al. (7) suggest that if birds had greater phenological response than butterflies the conclusion that they have accumulated greater debt could be wrong.

It isn't simple to assess how widely Socolar et al's (7) claim to "reshape expectations" will apply. To begin evaluating the extent to which phenological shifts mitigate the need for range shifts and vice versa, note that three types of range shift are attributed to current climate warming: (A) shifts involving movement of absolute range limits; (B) shifts in which relative abundance changes within the established distribution of a species and (C) shifts in local community composition caused when warming allows species with more equatorial distributions to increase at the expense of those with more poleward distributions. I'll designate these three categories as "limit shifts," "internal shifts" and "community shifts" respectively.

All three types of shift have been invoked in the climate-change literature (8, 10-12). To think about how they might interact with phenology, begin by assuming a stylized geographic range in which both poleward and equatorial range limits are equally determined by climate and in which crucial reproductive activities - bird nesting, frog spawning, butterfly oviposition- occur earlier in the year in the warmer parts of the range. Also assume that climate warming is homogeneous across the species' range, that the species is most abundant in the range center and that resources exist beyond both range limits. How might we expect range limits and phenology to respond to climate warming?

At the center of this stylized range, phenological advance could occur through plastic response to warming or through a combination of natural selection and poleward gene flow. This advance should not be blocked by constraints because it would not take the population outside the species' existing phenological and climate envelopes. By this means the population would come to phenologically resemble one from closer to the equator and further from the range center. We would expect that the population would also come to resemble more equatorial regions in abundance, contributing to an "internal" range shift. If phenology failed to change adaptively, we'd expect the decline in abundance to be exacerbated, so in this case the phenological advance would indeed mitigate the expected range shift, but both would be expected to occur.

Now think about range limits. Individuals surely fail to perceive those limits and accidentally spill across them from time to time. In the past they will normally have failed to found persistent populations -thereby causing the limits to be where they are. Now, with recent warming, we expect some individuals that cross the poleward limit to succeed in founding new populations, and range expansion will result. If populations at the range-limit respond immediately to warming by plastic phenological advance, their ability to colonize poleward would be reduced: once again, an interaction between range shift and phenology. In contrast, we expect no such interaction at the equatorial limit, where the new climate lies outside the species' previous climate envelope. Phenological advance should not be capable of rescuing the range-limit populations. If it could, then the location of the range limit itself would be inexplicable. In general, we don't expect evolution of adaptation to hotter climates to rescue range-limit populations that are already experiencing the strongest natural selection to adapt to hot climates that they can endure without extinction (13). Instead, we expect range-limit retraction that cannot be modulated by phenological change.

In the real world species' ranges are complex not stylized, and range limits are evolutionarily dynamic (11). In the species on which I've worked longest (since 1967), Edith's checkerspot butterfly, populations far from the range limits have repeatedly and independently rendered themselves climate-change-vulnerable by adaptive evolution to the outer limits of their ecological tolerance (fig 1). Despite this peculiarity, by 1996 the species had shown an internal range shift of 89km polewards and 116m upwards in elevation during the 20th century, precisely as predicted from regional climate warming (12).

On the bright side, Edith's checkerspot provides a happy example of a species highly resilient to climate warming despite the vulnerability of individual populations and ecotypes (5). The butterflies mitigate thermal stress in situ by phenological advance and by increasing egg height above the ground. In a population with 2.5mm eggheight at 3171m elevation, we measured air temperatures 12.7°C cooler but eggspace temperatures 7°C hotter than at a site with 450mm eggheight at 213m elevation (5). The insects also have avenues to mitigate phenological stress, either by switching to a more long-lived host among the 5-6 genera that they can use, or by reducing the size of the adult and shortening the life cycle. Interpopulation variation of adult size is as dramatic as that of egg height: among the 15 populations we studied in detail, mean weight of females at eclosion varied from 92mg to 285mg.

CONCLUSION: In sum, we don't expect that poleward range shifts can be completely avoided by phenological advance, though the two processes interact. We expect to see changes in both space and time, which is exactly what we do see (2,3,13). The better we understand the options open to wild species to respond to climate change, the better we can mitigate impacts on natural systems (3). With respect to options for in situ mitigation and assisted migration, Socolar et al (7) have helped us along but lack of consensus about factors currently determining range limits (15) shows that we still need to hone our understanding.

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Figure 1: A female Edith's checkerspot butterfly from 2300m elevation in the Western Sierra Nevada of California. She is contemplating the options for host choice and phenology available in this habitat type, where her species occurs in a geographic mosaic of isolated metapopulations, some specialized on the ephemeral annual *Collinsia torreyi* (Plantaginaceae; blue flowers) and some on the longer-lived perennial *Pedicularis semibarbata* (Orobanchaceae; yellow flowers). Each specialization leads the insects to evolve to the limits of their ecological tolerance in ways that render them climate-sensitive, despite living far from any latitudinal or elevational range limit. *Pedicularis* is available for an extended period but is grazed by mammals, which has led the butterflies to evolve strong geotaxis and lay eggs on average <1cm above the ground (16). Eggs at this height experience temperatures 15-20°C above ambient, approaching their lethal limit of 48°C (5). Evolution of adaptation to *Pedicularis* has led the butterflies to operate close to their absolute limits of thermal tolerance. Populations adapted to *Collinsia* have a different climate sensitivity, evolving close to the limits of their phenological tolerance. Because the host is ephemeral the butterflies must lay eggs early in the year, generating a time-constrained life cycle with a tradeoff between maternal fecundity and offspring mortality. A female can achieve high fecundity by extended feeding as a larva, but later eclosion increases offspring starvation from host senescence. The result is evolution of high fecundity with consequent offspring mortality caused by adaptive asynchrony between insect and host life cycles. The extent of this asynchrony, and the proportion of larvae that die from it, is climate-sensitive (17).


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