Postprint version of the article published in *Trends in Ecology and Evolution*, DOI: 10.1016/j.tree.2021.02.008

How constraining are photic barriers to poleward range-shifts?

Tougeron Kévin

Earth and Life Institute, UCLouvain, croix-du-Sud 4-5, 1348 Louvain-la-Neuve, Belgium

tougeron.kevin@gmail.com

Keywords: light; climate-change; distribution range; adaptation

As species shift distributions to track their thermal niche, they face non-climatic abiotic factors that usually covary with thermal gradients. The recent article by Huffeldt [1] convincingly establishes that species extending distribution range poleward may encounter photic barriers. In this Letter, I argue that the strenght of the photic barrier restricting species climate-induced range shifts, described by Huffeldt, is not constant or uniform, but depends on (i) the selection constraint exerted by the new photic environment relatively to other factors [2], (ii) the amplitude of the photic change to adapt to, and (iii) the light-dependent phenotype considered.

Does a strong photic barrier exist?

The answer depends on the selection pressure exerted by light compared to each of the other environmental factors at play. If the photic environment is more constraining than other factors, then a strong photic barrier exists and it will be easier for some species to conserve the ancestral photic niche, and to locally adapt responses to climate-change. At the opposite, if it is easier for an organism to adapt to the new photic environment than to the shifting temperatures in the area of origin, then the photic barrier will likely be weak. Other factors that balance with light will then constrain range-shifts and preferentially drive selection [2].

The corollary question is how many species among those that actually expand poleward will really face such a photic barrier limiting range expansion? Species with large distribution ranges already show strong interpopulation variability in photoperiodic responses, demonstrating evolutionary adaptations to diverse light conditions [3]. Phenotype-environment mismatches may first occur, but individuals that best respond to the new photic environment will likely be rapidly selected. Because they are tracking their thermal niche, it is also likely that some organisms would already have their photoperiodic response matched with the annual cycle of temperatures in the shifted range. The existence of phenotypic responses already matching the new environment would be the third possible outcome of poleward expansion, in addition to the two others proposed by Huffeldt [1].

Where is the barrier, precisely?

The more abiotic constituents of the new environment differ from the original environment, the stronger are barriers to range-shifts [2]. I suggest that the strength of the photic barrier increases closer to the pole (in a non-linear way), and at some point, becomes too strong for some species to overcome. Abrupt changes in the photic environment (e.g., sea crossing events) would obviously be real barriers to distribution shifts, and this will be greater if the latitude gap is important. In most cases however, it is challenging to define a clear red-line after which a given phenotype would become maladapted.

For discrete life-histories responding to photoperiodic clines, the photic barrier would only be faced when a certain latitudinal threshold is reached within the thermal-tracked range, e.g., where an abrupt change in voltinism is necessary [4]. It could, for example, translate into populations being stuck in a development trap between two voltinism strategies [4,5]. Other light-dependent phenotypes may display more progressive changes, as species moving poleward adapt to photic conditions at the margin of their distribution range, making the photic barrier blurry. A tree currently growing at its distribution margin would likely be able to develop 1 km poleward if temperatures increase, but what about 10 or 100 km? To better predict limitations at shifting geographic ranges, the key point is to first define how the strength of the photic barrier varies with the latitudinal shifts (**Fig. 1**).

Phenotypic syndromes

As Huffeldt states [1], the question is which species will evolve fast enough to both track their optimal temperature poleward and persist in the novel photic conditions. Again, I suggest that the variety of selection factors should be considered in this general framework [2]. Evolution not only acts on the capacity to perceive the photic change itself, but also on the resulting phenotype produced by the response to photic changes, therefore potentially involving pleiotropy and trade-offs among the associated daily or seasonal syndromes.

I estimate that it is crucial to distinguish photic responses related to the biological rhythms, and the rest of the light-dependent phenotypes (visual systems, orientation, photosynthesis, thermoregulation, body-color, interactions with mates, predators, and prey). Species may respond in a timely manner to change in light conditions in the temperature-tracked area and match annual or daily activities to new photic environments, because biological rhythms are by definition plastic to local light conditions and can evolve quickly (e.g., diapause [3,6] or daily activity periods [7]). However, organisms would have to readapt the entire set of associated physiological and behavioral phenotypes to the new photic niche, and this is where the actual photic barrier could stand.

An estimation of the non-uniform constraining effect of photic barriers and corresponding eco-evolutionary responses of organisms will significantly improve our ability to predict and quantify range shifts.

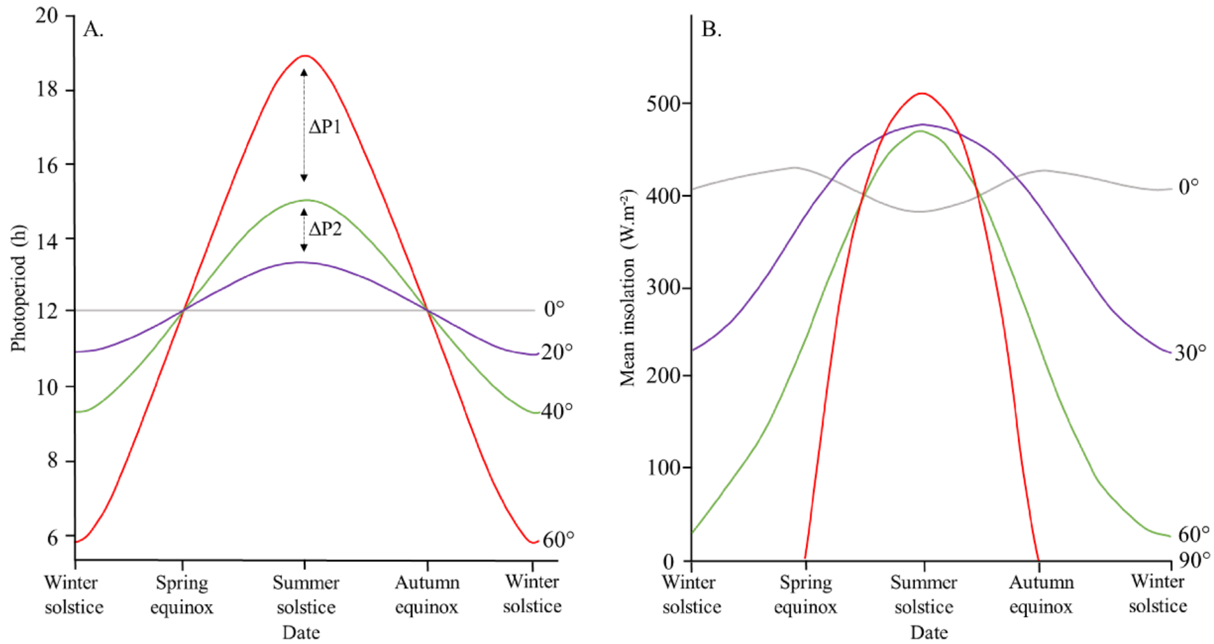

Figure 1. The non-linear patterns of photic changes in (**A**) photoperiod and (**B**) insolation with latitude and date strongly influence the ecology of organisms and are proxies of constraints to poleward range-shifts. (**A**) If we exclude latitudes >66° with continuous periods of light or dark, we can highlight three main points. (i) The greater the latitude gap between the origin area and the thermal-tracked area, the stronger the photic barrier; species moving from 20° to 30° face fewer constraints than species moving from 20° to 40°. (ii) Both the photoperiodic amplitude between the winter and the summer solstice, and the pace of annual photoperiodic change increase (non-linearly) with latitude, which are major constraints to adapt to. (iii) The closer to the poles, the more likely a species is to face a photic barrier to range-shift, because of the non-proportional change in photoperiod across latitudes. At any time of the year, other than the equinoxes, the delta-photoperiod is higher between 40° and 60° (ΔP1) than between 20° and 40° (ΔP2). (**B**) The higher the latitude, the greater the seasonal variations in insolation, and the faster the increase and decrease in insolation among seasons. This represents an important barrier, e.g., for animals relying on thermoregulatory behaviors to survive. Daily insolation levels averaged over the entire year (not shown here) are lower at higher latitudes, and the delta-insolation between two degrees of latitude increases towards the poles.

References

1 Huffeldt, N.P. (2020) Photic Barriers to Poleward Range-shifts. *Trends Ecol. Evol.* 35, 652–655
2 Spence, A.R. and Tingley, M.W. (2020) The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography* 43, 1571-1590.
3 Helm, B. *et al.* (2013) Annual rhythms that underlie phenology: biological time-keeping meets environmental change. *Proc. R. Soc. B Biol. Sci.* 280, 20130016–20130016
4 Kivelä, S.M. *et al.* (2013) Seasonality Maintains Alternative Life-History Phenotypes: Evolution Of Life-History Polyphenisms. *Evolution* 67, 3145–3160
5 van Dyck, H. *et al.* (2015) The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos* 124, 54–61
6 Bradshaw, W.E. and Holzapfel, C.M. (2001) Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci.* 98, 14509–14511
7 Sanders, D. *et al.* (2020) A meta-analysis of biological impacts of artificial light at night. *Nat. Ecol. Evol.*