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Photic barriers to poleward range-shifts

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Abstract

With climate warming, organisms are shifting their ranges towards the poles, tracking their optimal thermal environments. Day-length, the driver of daily and annual timing, is, however, fixed by latitude and date. Timing and photoreception mechanisms adapted to ancestral photic environments may restrict range-shift capacity, resulting in photic barriers to range-shifts.

Keywords: biological rhythm, global climate change, phenology, photoperiod, photoreception, range-shift

A thermal-photic mismatch

Organisms are shifting their ranges polewards at a median rate of 16.9 km decade\(^{-1}\) as they track their optimal thermal environment under climate warming [1]. Predictions of species’ abilities to establish and persist in these new ranges, however, rarely take into account that latitudinal range-shifts (see Glossary) result in exposure to novel photic environments. Many organisms have physiology and behavior (e.g., vision, circadian rhythms, and phenology) that optimize fitness under the photic environment of their ancestral latitude [2–4]. These adaptations integrate photic cues to allow for the successful anticipation of and response during the diel and annual cycles, and may, thereby, restrict range-shift capacity via a thermal-photic mismatch. A photic barrier would effectively cap the poleward range-shift of species that are unable to adapt to extremes in duration and annual transition in photoperiod. This mismatch may be especially problematic for species predicted to move into high-latitude photic environments [3], which have phases of continuous light and dark near and above the polar circles (66.6 °N and °S).
Both daily and annual aspects of the photic environment change with latitude and can underlie photic barriers to poleward range-shifts (Figure 1). First, the durations of the light and dark phases of the diel cycle increase with latitude during summer and winter, respectively, subjecting organisms to more extreme photoperiods as they move polewards (from 64 to 65 degrees latitude, photoperiod increases by 1.02 hours on the summer solstice and decreases by 0.62 hours on the winter solstice), and, in association, the 24-hour oscillation of light intensity attenuates greatly during phases of the annual cycle at high latitude (Figure 1A,B). Second, the annual transition in photoperiod becomes more rapid with increasing latitude (Figure 1A). These daily and annual aspects and their associated mechanisms are intertwined [3,5], but can have separate effects on the viability of species in new ranges.

Nearly all organisms have circadian rhythms that align with the predictable oscillation between light and dark across the diel cycle [2], and few, if any, organisms perform optimally under both light and dark. The changes in the photic environment with increasing latitude result in phases of low amplitude cycling of and low absolute light intensity (Figure 1B). Polar residents are thought to have increased sensitivity to changes in photic cues compared to low latitude organisms [6], and evidence from fish and humans describes latitudinal clines in photoreception, suggesting that their vision is adapted to the phases of longer twilight and lower light intensities nearer the poles [4]. Fitness depends on the appropriate integration of light for energy procurement in plants (via photosynthesis) and many animals (via sensory
perception during foraging) and on alignment of behavior and physiology with the environment.

A functioning circadian system is vital physiology and relies on the proper alignment of endogenous and environmental rhythms, of which the light-dark cycle is the primary entraining (i.e., synchronizing) agent [2,7]. Circadian rhythms have extensive influence over every level of organization within and among organisms [5,7]: up to one-third of plant and animal genomes cycle in sync with the 24-hour day [2] and competitive and breeding interactions depend often on time-of-day [5]. Misalignment between endogenous and environmental rhythms, as seen when photoperiod is extended by artificial light at night, results in increased risk of pathologies, for example, cancer and metabolic disease in mammals [5,7].

Experimental evidence indicates that competitive ability decreases when a species’ endogenous rhythm does not align with the environment [2] and that competitive relationships shift under contrasting photoperiods ([8],Box 1). Furthermore, plants and animals can have latitudinal clines in properties of their endogenous timing mechanisms (e.g., period length, amplitude, phase angle, and polymorphisms in circadian-clock genes) [4], indicating that a functioning timing mechanism that aligns with the photic environment of the current range confers a fitness advantage.

Species living at polar latitude have adaptations that allow them to live under extreme photic conditions [6]. These adaptations include loss of the circadian clock, entrainment to low-amplitude environmental cycles, and behavioral and physiological modifications allowing for appropriate relationships with the photic environment, such as migration and diapause [4–6]. For subpolar species lacking these adaptations, high-latitude photic environments may disrupt both ecological relationships, by prohibiting species interactions due to poor photoreception under extreme
photoperiods, and relationships between physiology and the environment, by a mismatch between the circadian system and the light-dark cycle (Figure 1).

Altogether, this could result in significant evolutionary barriers to persistence at high latitude.

Annual barriers to range-shifts

The annual change in photoperiod has selected for timing mechanisms that use this change to schedule the expression of the optimal phenotype for a season [3], and the mismatch between biological phenomena driven by annual change in temperature and photoperiod brought about by global climate change has been discussed elegantly and thoroughly (see [3,4], among others). Photoperiod affects phenological transitions across the annual cycle, with increasing strength at higher latitude [4]. This has resulted in heritable photoperiodic response profiles adapted to ancestral latitude ([3,4], Box 1). Misalignment and disruption of these photoperiodic responses can affect ecosystem services [5] and reduce fitness [3]. For example, organisms may either prematurely end diapause because of a misalignment between their photoperiodic response and resource availability or fail to reproduce because of an inherited photoperiodic response adapted to lower latitude [3,4]. If organisms are unable to adjust their photoperiodic response mechanisms appropriately to match annual photic conditions in a new range, then an annual photic barrier may inhibit latitudinal range-shifts.

Predicting the future and crossing the barrier

Limitations imposed by the photic environment may allow only the most adaptable species to track their optimal thermal environment polewards. Identifying which traits
facilitate passage of potential photic barriers will be instrumental in understanding latitudinal range-shifts and global changes in biodiversity in the face of global climate change [9]. In addition, a photic barrier has potential societal impacts: species introduced to higher latitude, intentionally or accidently, may be unable to establish [3] or may disrupt ecological relationships (e.g., [8]), which could affect food security and the economic potential of high-latitude regions [10]. This is especially relevant for polar regions, which are undergoing the most rapid warming and expecting associated economic development.

Altogether, the evidence illustrates that the physiology and ecology of many species will be affected by novel photic environments as species shift ranges polewards. Those species lacking the phenotypic plasticity or standing variation [11] needed to adapt to new photic environments will hit a photic barrier that blocks settlement at a new latitude, and, thus, not all species will successfully track their optimal thermal environment polewards. Using experimental and comparative methods, we can assess the underlying genetics and physiology necessary to persist successfully in temperature-tracked ranges shifted by latitude (Box 1).

The fact that some species have adapted previously to high-latitude photic conditions through a myriad of solutions [6], along with evidence of recent, rapid evolution of phenological traits (e.g., [12]), gives hope that species that shift ranges into novel photic environments can adapt. The question, however, remains: as global climate change progresses, which species will evolve quickly enough to both track their optimal temperature polewards and persist in the novel photic conditions of these new environments?

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Glossary

Circadian rhythm: temperature compensated, self-sustained rhythm with a duration of approximately 24 hours that persists in the absence of environmental cues and can be entrained to cues in the environment [2,3].

Phenology: timing of recurring seasonal processes [5].

Photic cue: characteristic of light originating from the sun, e.g., day-length, intensity, spectral composition, and solar position.

Photoperiod: duration of daylight across the diel cycle, i.e., day-length.

Photoperiodic response: mechanism used by an organism to track the annual cycle and schedule phenological transitions, e.g., photoperiodism, circannual rhythms, and critical photoperiods (see [3,4] for additional information and discussion).

Range-shift: extension of a margin of the area in which a species resides [9].

Box 1. Investigations of photic barriers to poleward range-shifts

Integrative investigations employing chronobiological, physiological, and ecological approaches will be valuable for identifying the mechanisms underlying photic barriers to latitudinal range-shifts [3–5], and studying many taxa will reveal which species can more effectively cross a potential photic barrier. Investigations of light integration and the salience of different photic cues will elucidate whether photoreception constrains range-shifts into high-latitude [3,4,6,9], while comparative genomics of populations under high- and low-latitude photic conditions can identify traits allowing for
successful range-shifts [11]. Common garden and transplant experiments along latitudinal gradients do not control for non-photic environmental factors that also change with latitude (especially temperature), and, thus, do not provide definitive evidence for or against photic barriers to range-shifts. Teasing apart the photic and thermal environments is, therefore, important and can provide surprising results. For example, the fitness of the mosquito *Wyeomyia smithii* from a high-latitude population increased when subjected to a low-latitude thermal-year under its ancestral photic-year, but this advantage was reversed under a low-latitude photic-year, indicating a thermal-photic mismatch [3]. In another experiment that controlled for temperature, a simulated high-latitude photoperiod facilitated reversal of the competitive advantage that the aphid *Acyrthosiphon pisum* had over the aphid *Megoura viciae* under a low-latitude photoperiod [8].
Figure 1. Changes in photic environment with latitude and date and how these may present a photic barrier to range-shifts. (A) The annual change in photoperiod at high- and low-latitude. (B) The insolation (a.k.a. direct solar radiation, light intensity) on the summer and winter solstices, respectively the yellow and grey lines. In (A) and (B), the brown dashes depict the photic environment at the equator (0° latitude), where the photic environment is stable annually. (C,D) The differences in photic environment with increasing latitude may cause daily and/or annual timing mechanisms adapted to ancestral ranges to either fail or become misaligned with environmental rhythms in temperature-tracked ranges. This may bring about cascading effects on the behavior, physiology, and/or phenology of species that result in poor health, decreased fitness, and/or disrupted ecology [2–5,7]. Within the temperature-tracked range, two non-mutually exclusive possibilities are depicted: 1) a functioning timing system unable to align to the environment due to poor or
maladaptive integration of photic cues by sensory systems [3–6] and 2) a non-functioning system that is directly inhibited or suppressed by the photic environment or that cannot appropriately integrate photic cues [3,4,6,7]. An organism’s annual and diel timing systems are intertwined [3,5], yet could be affected differently. Dotted connectors with a pointed head illustrate a photic cue that is integrated poorly or maladaptively into the timing mechanism and either is unable to affect the mechanism appropriately or results in misalignment with the environment. The solid connector with a flat head illustrates a direct inhibitory or suppressive effect. Solid connectors with pointed heads illustrate direct facilitatory effects.

**Literature cited**


