

Climate change-driven species' range shifts filtered by photoperiodism

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Forecasts of species range shifts as a result of climate change are essential, because invasions by exotic species shape biodiversity and therefore ecosystem functions and services. Ecologists have focused on propagule pressure (for example, the number of individuals and invasion events), the characteristics of an invading species, and its new abiotic and biotic environment to predict the likelihood of range expansion and invasion. Here, we emphasize the role of photoperiodic response on the range expansion of species. Unlike temperature, the latitudinal gradient of seasonal changes in day length is a stable, abiotic environmental factor that does not change with local or global climate. Predicting range expansions across latitudes and the subsequent consequences for native communities requires a more comprehensive understanding of how species use day length to coordinate seasonal growth, reproduction, physiology and synchronization of life cycles with interacting individuals and species.

Agriculture, forestry and climate change are among the most important forces driving species invasions globally and facilitating the establishment of species into new habitats^{1–4}. Climate change is predicted to facilitate range shifts of species especially across latitudes and altitudes^{5–8}. Expansion of species' ranges may enrich biota in the new environment⁹. However, accumulating evidence also suggests associated risks¹⁰. For example, native species may become locally extinct within their current ranges as a result of climate change and the presence of invading species, and globally biotas may become homogenized¹¹. Non-native species are among the major global threats to native biodiversity and the associated ecosystem functions and services, as they can consume, parasitize, hybridize with and outcompete native species^{9,10,12}. Economic losses due to invasion of non-native species are estimated as US\$13 billion and US\$137 billion in Europe and the United States, respectively^{12,13}.

Here, we focus on the importance of photoperiodism as a key to predicting climate change-induced range expansion of species across latitudes. Existing literature on species range shifts in changing climates has focused on abiotic and biotic ecological filters for invading species, but photoperiodism has been largely ignored. This is especially true for predictions about the impacts of climate change on species distributions and the community or ecosystem consequences^{1–3,14–20}. Changes in temperature or precipitation expand or contract the favourable climatic window for species across latitudes in ecological time. However, the gradient of seasonal changes in day length varies with latitude, and — as the energy source for primary producers and a seasonal cue for plants and animals — is a stable abiotic ecological filter²¹ at both ecological and evolutionary timescales (Fig. 1). The gradient of seasonal fluctuation in day length between summer and winter increases polewards owing to the tilt of the Earth's axis and elliptical orbit around the Sun²¹. The question we focus on here is: how well do predictions that fail to capture species' adaptations to day length, light intensity and spectral composition forecast the consequences of climate change?

Phenology, life cycles and the evolution of life histories

Phenological timing is crucial for individual fitness, particularly in higher latitudes where seasonal fluctuations in temperature and light intensity, duration and spectral composition (that is, 'quality') of light are great (Fig. 1). In temperate and polar zones, substantial temperature and light fluctuations between summer and winter determines the optimal time to grow, reproduce, migrate and become dormant. The relative importance of phenological events to different life forms depends largely on the life-history strategies of the organisms, such as length of life cycle, reproduction strategy and mobility. For example, timing of reproduction is crucial for annual plants²². The allocation of resources to storage organs, formation of winter buds and leaf abscission, timing of bud break and changes in cold hardiness are important for perennial plants^{21,23,24}. The timing of dormancy, hibernation and migration are also crucial for many animals^{25,26}. In general, the shorter the favourable season becomes towards the poles, the more important the timing of growth and reproduction, and adaptations to cope with or avoid cold winter temperatures. Although climate change may relax temperature barriers, constant latitudinal decrease and seasonality in day length and light quality remain a challenge for invading primary producers.

Photoperiodic cues provide accurate and consistent signals to optimally coordinate phenological events in higher latitudes relative to other more variable seasonal cues²⁵. Unlike temperature or precipitation, which can vary seasonally and yearly, day length is determined by the Earth's rotation, tilt and position. Responses to light are ubiquitous for nearly all life forms, and studies of photoperiodism in insects, endothermic vertebrates and plants are abundant^{21,25}. However, photoperiodic adaptation varies among species. For example, plants can be classified as 'short day', 'long day' and 'day neutral', and the phenology of many plants is regulated by changes in day length, particularly north and south of the tropics of Cancer and Capricorn²¹. However, documented examples of photoperiodism in microbes, most invertebrate groups other than insects and ectothermic vertebrates are scant^{21,25}.

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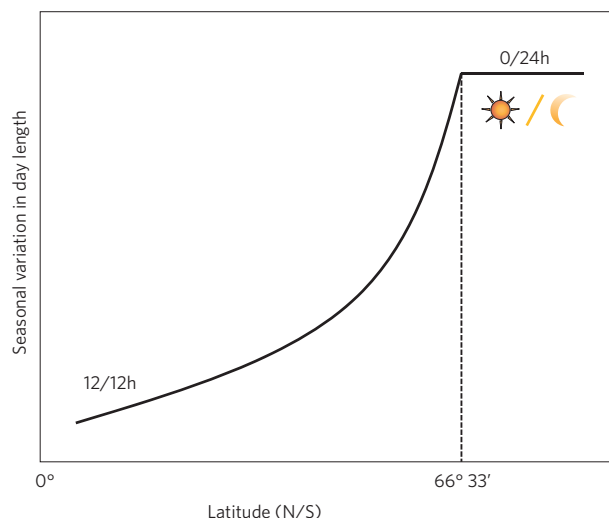


Figure 1 | The effect of latitude on the seasonality of day length. Day length varies insignificantly at lower latitudes, whereas the seasonality of day length increases polewards. Environments inside the Arctic and Antarctic circles are characterized by extremes of solar radiation ranging from the polar day in summer to the polar night in winter, and the shift between the extremes accelerates polewards^{26,51}. The reduced light availability is associated with a proportional increase in the amount of diffuse blue (400–500 nm) light, and a decrease in the red (660 nm) to far-red (730 nm) light ratio⁶⁶.

Other environmental cues, such as prevailing temperature, often play a modulating role in most species' adaptations to fluctuating seasonal changes, sometimes interactively with day length and light quality^{21,25}. For example, flowering of *Arabidopsis thaliana* is regulated by distinct but linked pathways detecting cues of light and temperature. Flowering can be accelerated by a decrease in the ratio of red to far-red light, but also requires vernalization and autonomous pathways²⁷.

We propose that the importance of photoperiodic responses in phenology mirror the organism's latitudinal distributional range, its dependence on the Sun as an energy source and the dependence of its interacting species on photoperiodic cues. Photosynthesizing plants as primary producers are directly and highly dependent on light, whereas herbivores, parasitic plants and other organisms are dependent on light through the food chain. Thus many heterotrophic species (for example, pollinators, herbivores and predators) can also be adapted to photoperiodic cues.

As photoperiodic life-history traits are heritable and polygenic²⁵, understanding their genetic regulation (for example, genetic variability, dominance, pleiotropy and epistasis) is needed to predict which species are likely to shift across latitudes. Genetically based and adaptive photoperiodic responses to climate change have been documented, for example, in the North American mosquito (*Wyeomyia smithii*), European blackcap (*Sylvia atricapilla*), Yukon red squirrel (*Tamiascurus hudsonicus*), European great tit (*Parus major*), European barn swallow (*Hirundo rustica*) and fruit flies (*Drosophila* spp.)^{28–37}. We propose that in some cases genetic mechanisms may promote or constrain the adaptive evolution of the species^{27,38–43}, and thereby range shifts of the species.

Climate change increases mistiming?

Climate change has been demonstrated to produce trophic desynchronization in herbivorous insects, migratory birds and aquatic communities^{44–48}. Phenologies of many species have changed in response to climate change, particularly in higher latitudes in the Northern Hemisphere. However, the degree of phenological shift varies among species because they use different environmental cues

to time phenological events^{44,46}. For example, climate change can cause local extinction of herbivores that are adapted to feed on very young host leaves as larvae, if larval emergence tracks temperature but budburst is triggered by photoperiodism⁴⁴. Similarly for migratory birds, increased mismatches between the timing of migration and the availability of prey insects can be detrimental to bird populations⁴⁸. Here, we propose that mistiming is also likely to modify plant communities through competition between native and invading species in changing climates. We expect invasions across latitudes to increase the mistiming of phenologies in communities. This is because photoperiodism and other environmental cues may have different importance in the timing of seasonal activities in invading species compared with native species.

Constraints on invading species and perturbations to native food webs depend on the potential of traits to evolve rapidly. Recent evidence suggests that phenological traits have this potential^{30,49,50}. However, little is known about evolutionary responses to seasonal changes in day length and light quality. Therefore, it is unclear how photoperiodism constrains adaptive expansion of individual species across latitudes.

Invasions from Europe to North America more common?

Although Europe and North America are biogeographically similar, weed and insect species invasions have been more common from Europe to North America than the reverse⁵¹. This asymmetric exchange is considered to result from disproportionate propagule pressure (the number of individuals introduced and the frequency of introductions), the competitive ability of invaders and the ecological filters of the destination area^{51,52}. We propose that adaptations to seasonal changes in day length and light quality is one of the key factors limiting the distribution of species invading from North America to Europe, because comparable climate zones are present at higher latitudes with higher seasonal variation in day length and light quality in Western Europe compared with those in North America owing to Gulf Stream effects (Figs 1 and 2).

Although we expect invasions across latitudes to increase the mistiming of phenologies in communities, migration to lower latitudes should be more successful than vice versa. Successful migration to higher latitudes requires adaptations to cope with or avoid cold winter temperatures and extreme seasonality in day length and light quality, which can be more critical to successful invasion compared with a limited ability to fully exploit the longer favourable season in lower latitudes⁵³.

Milder winters are predicted in the future under most scenarios of global climate change⁵⁴, which may equalize the trans-Atlantic exchange of species. However, the successful colonization of North American species to the climatically equivalent, but higher latitude, habitats of northern Europe (Fig. 2) may still be inhibited because of seasonal differences in light energy and quality that affect key elements of photoperiodism.

Shifts of human-modified habitats

Climate change will geographically shift ecosystem services for the continuously growing human population. Accumulating evidence suggests that climate change will increase natural disasters (for example, cyclones, droughts and flooding) and lead to increasing degradation of environments (for example, sea-level rise, coastal erosion and desertification) especially in the tropics and subtropics, while climate becomes milder in the high-latitude subarctic and Arctic regions^{54,55}. Thus, distribution of many plant and animal species, as well as environments suitable for agriculture and forestry, will shift to higher latitudes and altitudes⁴ particularly in the Northern Hemisphere, which has the greater land area (Fig. 2).

A poleward shift in arable environments as a result of climate change is likely to provide opportunities for the use of unique crop species and crop-production technologies in higher latitudes. However,

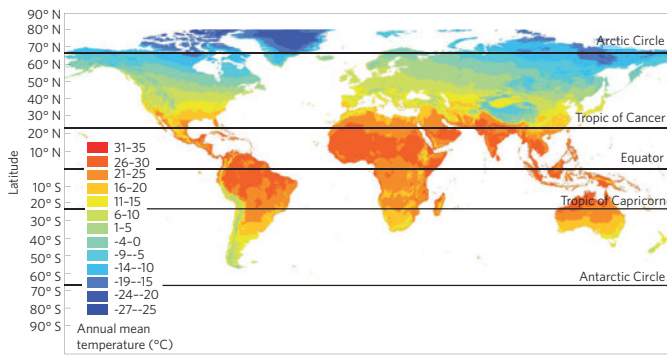


Figure 2 | World climate map demonstrating that comparable climate zones are present at higher latitudes in Western Europe compared with those in North America. Data taken from the WorldClim Database (<http://www.worldclim.org/>).

benefits to food production do not come without associated risks, such as increasing opportunities for invading species and their likely negative impacts on system biodiversity and function. Agriculture and forestry increase habitat attractiveness to invaders by increasing ecosystem productivity through the energy inputs inherent in crop production, and by loss of initial genetic, species and habitat richness of the ecosystems^{56,57}. Many invading species are serious pests and pathogens affecting both human-made and natural environments. The success of the invaders in new habitats depends on their ability to adapt to seasonal changes (largely determined by phenotypic plasticity, genetic variation and gene flow), intra- and interspecific competition, and timing of trophic interactions.

In the Northern Hemisphere, many tree species were able to expand their distribution ranges northwards and circumpolarly into areas scoured by the last major glaciation. This is because temperature largely determines overwintering, growth and reproduction of trees^{23,58}. However, we propose that photoperiodism may slow or constrain poleward plant invasions, particularly in the case of trees with long life cycles, because their phenologies (for example, bud break, growth, reproduction, leaf senescence) are commonly well-adapted and timed to prevailing day length and light quality⁵⁹. Although cross-latitudinal transplantations of forest trees show some species can successfully grow in broader geographical areas, their fitness is often highest at the home site^{60–62}. At higher latitudes, the consequences can be fatal if species are not adapted to short growing seasons in combination with cold winters^{53,60,61}. Climate change may relax some of the temperature constraints. However, native species may still retain a competitive edge because they are adapted to strictly track the photoperiodic cues at that latitude, which remain the same.

Ultimately, the community-level consequences will largely depend on the adaptive ability of different species to use altered environmental cues for seasonal timing of their phenological traits^{30,34,36}. The species-specific adaptations of phenological tracking of temperature and/or photoperiodic cues^{63,64} play a significant role in the ability of woody plants to invade polewards and shape plant communities following climate change. These adaptations also do apply to silviculture, horticulture and landscaping. For example, in the horticulturally important family *Rosaceae*, many tree species track temperature cues instead of photoperiodic cues in growth cessation and subsequent adaptation to winter⁶⁴. In contrast, many conifers are well known for their adaptations for responding to light quality and day length^{60,61,65,66}. Empirical evidence indicates strong, population- and species-specific adaptations and show that northern populations are more sensitive in changes in the light environment, in terms of both day length and light quality⁶⁷.

The successful use of crop species in temperate and boreal regions largely depends, however, on harvested product (for example, seeds,

tuber, vegetative biomass). For example, plants adapted to long days, such as wheat, barley and oat, are widely cultivated in boreal regions, but short-day plants such as potato and field corn (for animal feed and bioenergy) can also be cultivated in environments where sweet corn fails because of a short growing season^{68–70}. A more comprehensive understanding of photoperiodism may provide invaluable insights for plant-breeding strategies, which will undoubtedly be needed for local breeding programmes designed to develop varieties adapted to the prevailing environmental conditions.

Invasions of pests and pathogens are more difficult to accurately predict based on photoperiod than plants⁷¹. Arthropod pests often have light- and temperature-driven complex life cycles with phases adapted to different habitats and behaviours⁵⁵. In contrast, the success of microbial pathogens seems to be determined by propagule pressure and presence of a susceptible host in a favourable environment, and not by day length. For example, many pathogens such as potato late blight (*Phytophthora infestans*) and coffee rust (*Hemileia vastatrix*) have been shown to be capable of following host plant introductions into new areas worldwide⁷².

Conclusions

Day length is the most accurate and consistent environmental cue in northernmost seasonal environments. Thus, we propose that the predictions of species invasion success across the latitudes as a result of climate change are more reliable if photoperiodism is included in the models. Species' adaptations to seasonality can readily be empirically tested and incorporated into existing models forecasting species range shifts due to climate change. Determining the success of invading species in new environments, and how they shape biodiversity and ecosystem functions and services will require studies testing (1) how species respond individually and within the context of the community to increasing seasonal fluctuations in day length, (2) the genetic bases and phenotypic plasticity of photoperiodism, and (3) how photoperiodism interacts with climate change to affect the evolution of life histories, biodiversity and species–species interactions in communities.

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Author contributions

K.S. led the creation and writing of the paper with inputs from all authors. All authors participated in the literature survey of their expertise (K.S.: climate change, and general ecology and evolution; K.T.: photoperiodism; T.H.: climate change, weeds; P.E.G.: crop species; C.E.H.: crop species; I.V.: pests; A.N.: pests; M.H.: pathogens).

Additional information

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