Greening up the mountain

V. Vandvik[a,b,1], A. H. Halbritter[a,b], and R. J. Telford[a,b]

The progression of key plant life-history events, such as spring leaf-out and flowering, along bioclimatic gradients in elevation and latitude is one of the more conspicuous patterns in nature, and, as such, it has served as a source of opportunity, industry, inspiration, and wonder for farmers, natural scientists, and artists alike (1–3). For example, in many regions across the world, transhumance, traditional land-use practices that involve the seasonal movement of people and their livestock between fixed summer and winter pastures, has developed to exploit such phenological gradients across the landscape (2, 4, 5). These phenological patterns are tightly linked to temperature, leading to the formulation of bioclimatic "laws" about phenology (6). Advancing spring phenologies were also among the first clear empirical examples of biotic responses to a warming climate (7, 8).

In PNAS, Vitasse et al. (9) show convincingly that climate change is now altering not only the timing of the phenological events but also the underlying patterns in phenology along environmental gradients, to an extent where these patterns are no longer in concordance with "Hopkins bioclimatic law" (6). In particular, the elevation-induced shift in the time of leaf-out in four common tree species in the Swiss Alps between low and high elevation has contracted by 35% from the 1960s until today (i.e., an increase in the rate of progression of spring leaf-out with elevation). Vitasse et al. (9) investigated three possible explanations for the observed discrepancy: (*i*) stronger warming at high elevation, (*ii*) stronger warming later in the season affecting plants at high elevation more because of later leaf-out, and (*iii*) changes in the number of chilling days (mean temperature of 0–8 °C between November and mean leaf-out date). Their analyses show that the number of chilling days during warmer winters has decreased at low elevation but increased at high elevation, suggesting that lowland trees are not keeping up with the pace of phenological advance of their upland conspecifics, and that this is happening because they are receiving insufficient chilling during the winter.

Hopkins' bioclimatic law (6) was developed for broad climatic gradients, such as elevation and latitude. An interesting question, therefore, is to what extent the observed contraction in the elevation-induced shifts in the time of leaf-out is a local pattern in the European Alps or whether this is also happening regionally or even globally along elevation and latitudinal gradients? To explore this, we compared the patterns in chilling days in the 1960s and 2000s from sites with contrasting climates across Europe from *ca.* 46–70°N including an elevational gradient comparable to that in the study by Vitasse et al. (9) (Fig. 1 *A* and *B*) and two oceanic to continental climate gradients in Fennoscandia (Fig. 1 *C*–*F*). These data illustrate, firstly, how and why climatic warming drives opposing trends in winter chilling at low and high elevations in the Alps. In the temperate climates found at low elevations, chilling occurs throughout winter, and since the winter temperatures were already at the high end of the chilling spectrum in the 1960s, the number of effective chilling days has decreased with climatic warming (increasing number of observation points falling outside the blue box in Fig. 1*A*). At high elevation, in contrast, the winter months are too cold for effective chilling, which therefore primarily occurs in autumn and spring; here, the number of effective chilling days has increased with climate warming (more observation points falling into the blue box in Fig. 1*B* during autumn to early spring).

Inspection of climatic data across Europe further suggests that the change in Hopkins' bioclimatic law observed by Vitasse et al. (9) in the Alps may also occur at broader scales. In particular, regions with temperate and oceanic climates, exemplified by Lugano and Bergen, where winters are mild and most days fall within the 0–8 °C chilling window are likely to be experiencing a decreasing trend in effective winter chilling with warming, and hence less pronounced phenological shifts (Fig. 1 *A* and *C*). In contrast, areas with colder winter climates, such as higher elevation areas (Feldberg), continental boreal climates (Nesbyen), and northern

[a]Department of Biological Sciences, University of Bergen, N-5020 Bergen, Norway; and [b]Bjerknes Centre for Climate Research, University of Bergen, N-5020 Bergen, Norway

Author contributions: V.V. designed research; V.V. and A.H.H. performed research; A.H.H. and R.J.T. analyzed data; V.V. and A.H.H. wrote the paper; and R.J.T. edited the paper.

The authors declare no conflict of interest.

See companion article on page 1004.

[1]To whom correspondence should be addressed. Email: vigdis.vandvik@uib.no.

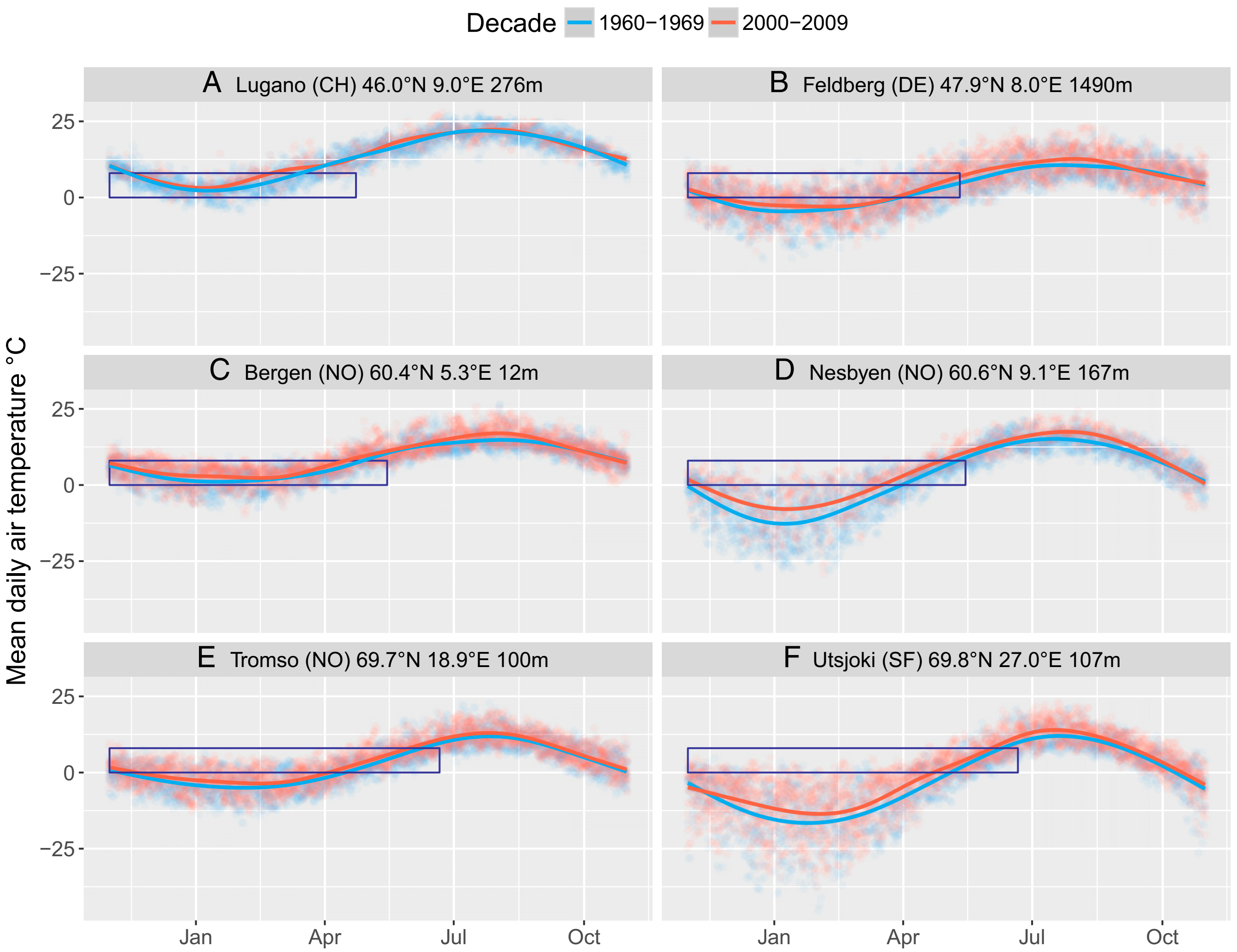

Fig. 1. Mean daily air temperature (2 m) from six European weather stations (data from KNMI Climatological Service; https://climexp.knmi.nl) in the decades 1960–1969 (blue) and 2000–2009 (red). The points show the individual observations, and the blue box indicates the approximate chilling period per site, observations with temperatures from 0–8 °C from first of November until mean leaf-out day: April 23 (*A*), May 11 (*B*), May 15 (*C* and *D*), and June 21 (*E* and *F*). The mean leaf-out dates were extracted from the study by Vitasse et al. (9) (*A* and *B*) and calculated from available data from three stations in southern Norway (Njos, As, and Fana) (*C* and *D*) and five in northern Finland (Pallasjärvi, Hetta, Saariselkä, Muddusjärvi, and Kevo) (*E* and *F*) from four common tree species (*Betula* sp., *Picea abies*, *Fagus sylvatica*, and *Pinus sylvestris)* in the period 1964–2015 (Pan European Phenology Network; www.pep725.eu/). CH, Switzerland; DE, Germany; m, metres above sea level; NO, Norway; SF, Finland.

areas [both oceanic (Tromsø) and continental (Utsjoki)], will be experiencing increasing effective winter chilling with climatic warming, and hence more pronounced phenological shifts (Fig. 1 *B* and *D*–*F*). Together, these results suggest that we should be seeing a general contraction of both elevational and latitudinal phenological gradients, and hence a significant weakening of Hopkins' bioclimatic law with climatic warming. Far from being the "paradox" that Vitasse et al. (9) suggest, our climate data illustrate how these contrasting responses in areas with mild vs. cold winter climates emerge simply because the chilling requirement is satisfied within a window of temperatures, with both a high- and low-temperature limit, rather than as a linear response to temperature.

Based on this, we would expect to find systematic changes in Hopkins' bioclimatic law in response to global warming broadly across the northern and southern mid- to high latitudes, but not in the tropics (where chilling and/or seasonality is lacking) and not in regions where seasonality and phenological patterns are driven by patterns other than temperature (e.g., in drylands and monsoonal climates). There may be regional differences driven by the underlying patterns in chilling and temperature relative to the requirements for bud break; for example, the contraction of phenological shifts along elevational gradients is likely to be pronounced in oceanic climates at mid- but not high latitudes (compare Fig. 1 *C* and *D*). There may also be other sources of regional variation; for example, the contraction of the latitudinal phenological shift may be further exacerbated by faster warming in the high north (10), illustrating how the alternative explanations put forward by Vitasse et al. (9) may also come into play in some regions.

Shifts in the spatial patterns of the timing of leaf-out can have far-reaching consequences for species, communities, and ecosystems, because they can affect community composition, trophic interactions, or biochemical cycling (11–13). For example, as illustrated by the prevalence of transhumance farming systems in seasonal climates worldwide (2, 4, 5), tracking phenological shifts, and thus feeding on the high-quality early-season growth for an extended period during summer, can offer substantial energetic advantages to grazers (14), with potential knock-on effects on their predators. Earlier leaf-out in upland and high-latitude trees over a broad scale can also impact ecosystem processes, such as carbon dynamics, by extending the growing season, and hence increasing the carbon accumulation and accelerating the uphill and northward expansion of the tree line at high elevations and latitudes. A climate change-driven contraction of the seasonal availability of this resource could thus negatively affect both higher and lower trophic levels. It is therefore crucial to understand phenological responses of different taxa to climate change, especially at a broad scale.

The alterations of phenological gradients could also vary within trophic levels, such as across plant growth forms. For example, while the change in Hopkins' bioclimatic law along elevation is currently demonstrated for trees (9), it could also be valid for other plant growth forms, such as field-layer plants, provided that the same drivers, chilling and spring temperature, are also controlling the timing of leaf-out in these groups. There are a number of reasons why this might not be the case. First, a number of ground-layer plants are herbaceous, and thus protect their meristems from frost by keeping them underground during the cold season (15). Adding to this, snow, which is common in winter across the boreal zone, effectively decouples the apical meristems of field-layer plants from the cold winter temperatures. Hence, chilling requirements are unlikely to be controlling leaf-out in field-layer growth forms; indeed, spring ephemerals are regulated primarily by spring temperature (16). If leaf-out in trees and field-layer plants are regulated by different climatic drivers, then climate change could result in phenological mismatches between growth forms. For example, if upland and northern trees experience increasing numbers of chilling days, leading to earlier and faster spring leaf-out, the time window between snow melt and tree canopy closure may narrow, presenting a challenge to the characteristic spring ephemerals of the forest understory, which may not be able to reproduce before the canopy closes (17).

The change in Hopkins' bioclimatic law due to climate change is thus expected to lead to widespread contraction of elevation- or latitude-induced shifts in the time of leaf-out, but with variations depending on the bioclimatic starting point, the specifics of the regional climate changes, plant growth forms, and landscape structure. As illustrated by Vitasse et al. (9), long-term datasets are extremely valuable to understand patterns in how species are responding to climate change, and, with careful analysis, such data can also be used in testing alternative hypotheses about the processes underlying these patterns. We encourage more studies from other regions, species, plant-functional groups, climatic gradients, and carefully selected "natural experiments" to explore and understand biogeographical patterns in phenological response to climate change.

1 Hopkins AD (1918) *Periodical Events and Natural Law as Guides to Agricultural Research and Practice* (US Government Printing Office, Washington, DC).
2 Ruiz M, Ruiz JP (1986) Ecological history of transhumance in Spain. *Biol Conserv* 37:73–86.
3 Astrup NJ (1915) Soleienatt, Nasjonalmuseet, billedkunstsamlingene. Available at https://digitaltmuseum.no/011041100735/soleienatt-egenhendig-trykk. Accessed December 19, 2017.
4 Paine R (1994) *Herds of the Tundra: A Portrait of Reindeer Pastoralism* (Smithsonian Institution Press, Washington, DC).
5 Moktan MR, et al. (2008) Ecological and social aspects of transhumant herding in Bhutan. *Mt Res Dev* 28:41–48.
6 Hopkins AD (1920) The bioclimatic law. *J Wash Acad Sci* 10:34–40.
7 Menzel A, et al. (2006) European phenological response to climate change matches the warming pattern. *Glob Change Biol* 12:1969–1976.
8 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669.
9 Vitasse Y, Singarbieux C, Fu YH (2018) Global warming leads to more uniform spring phenology across elevations. *Proc Natl Acad Sci USA* 115:1004–1008.
10 Stocker TF, et al. (2014) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Stocker T, et al. (Cambridge Univ Press, Cambridge, UK).
11 Keeling CD, Chin J, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO2 measurements. *Nature* 382:146–149.
12 CaraDonna PJ, Iler AM, Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proc Natl Acad Sci USA* 111:4916–4921.
13 Thackeray SJ, et al. (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535:241–245.
14 Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency: An experiment. *Oecologia* 95:164–170.
15 Raunkiær CC (1907) *Planterigets livsformer og deres betydning for geografien* (Gyldendalske Boghandel-Nordisk Forlag, København, Denmark). Danish.
16 Lindsey AA, Newman JE (1956) Use of official weather data in spring time: Temperature analysis of an Indiana phenological record. *Ecology* 37:812–823.
17 Lapointe L (2001) How phenology influences physiology in deciduous forest spring ephemerals. *Physiol Plant* 113:151–157.