Version dated: May 12, 2022

Integrating experiments to predict interactive cue effects on spring phenology with warming

E. M. Wolkovich[1,2,3], C. J. Chamberlain[1,2], D. M. Buonaiuto[1,2],
A. K. Ettinger[3] & I. Morales-Castilla[5]

[1] *Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4*

[2] *Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, 02131, USA*

[3] *Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, 02138, USA*

[4] *The Nature Conservancy, 74 Wall Street, Seattle, Washington USA*

[5] *Global Change Ecology and Evolution Group, Department of Life Sciences, University of Alcalà, Alcalà de Henares 28805, Spain*

Article acceptance date: 21 April 2022

Methods S1: OSPREE database

We built the Observed Spring Phenology Responses in Experimental Environments (OSPREE) database, by searching both ISI Web of Science and Google Scholar the following terms:

1. TOPIC = (budburst OR leaf-out) AND (photoperiod or daylength) AND temperature*, which yielded 85 publications

2. TOPIC = (budburst OR leaf-out) AND dorman*, which yielded 193 publications

We extracted data (using ImageJ for figures, transcribing values from tables and extracting date, location and other methods from the text) from papers on woody plants that test for photoperiod and/or temperature effects on budburst, leafout, or flowering (Fig. S1). Ettinger *et al.* (2020) used a subset of these data (studies on budburst for which we could estimate forcing, chilling and photoperiod treatments), while here we present the full database, capturing data from 84 papers (see Table S1 for a list), of which 21 are focused on crops (*Malus domestica, Vitis vinifera, Ribes nigrum, Vaccinium ashei, Vaccinium corymbosum, Prunus persica*). Most papers focused on only one species, with data on a total of 226 species (in contrast, long-term observational data often have far more data, for example the PEP725 and NECTAR databases together have multi-site data for more than 2500 species, Wolkovich *et al.*, 2012; Templ *et al.*, 2018). Papers often reported more than one experiment, which we refer to as a 'study.'

OSPREE includes 136 studies (with the earliest study was conducted in 1947, see Lamb, 1948), which spanned a variety of plant materials, though studies on 'seedlings' (51 studies) and 'cuttings' (55 studies) were most common. The most reported events were related to vegetative phases (days until or percent budburst or leafout, 66% of events across studies), followed by flowering (12% of events across studies). This is unsurprising given that species often leafout before flowering and most species' cuttings become resource limited after leafout and fail to reach flowering or later phenological stages. Our search terms and focus on woody species means few of the studies focused on molecular pathways for phenological events, though an extension of this database to include such studies would likely provide important insights into drivers of budbreak.

Methods S2: Comparing experimental treatments to forecasted trends

To compare the magnitude of experimental treatments to forecasted changes in temperature we calculated treatment differences as the differences within varying forcing and chilling treatments within a single study (e.g., a study with a 1 and 4°C chilling treatment would yield a value of 3°C). We did this across all studies (136 total) and for the 19 studies of *Fagus sylvatica* and 17 studies of *Betula pendula*. We calculated forecasted changes in minimum and maximum average daily temperatures over a 60 day window using RCP8.5 from the NCAR Large Ensemble (LENS, a multi-member ensemble of a single general circulation model, GCM, the Community Earth System Model Kay *et al.*, 2015).

Notes S1: The chilling enigma of over-winter temperatures

Our poor understanding of chilling makes estimating historical and predicted shifts in chilling difficult (Chuine *et al.*, 2016). Research to date suggests chilling only accumulates in a certain range of temperatures with low (e.g., <0°C) temperatures generally not contributing to accumulated chilling (but see Baumgarten *et al.*, 2021), and higher temperatures (e.g., >12°C) potentially decreasing previously accumulated chilling (see Fig. S2 and Richardson, 1974; Fishman *et al.*, 1987). Long-term studies generally focus on the warmer part of this chilling accumulation curve, suggesting that chilling should decrease with warming (Fu *et al.*, 2015; Piao *et al.*, 2017; Gauzere *et al.*, 2019). However, considering the cooler part of this curve (corresponding to where post-warming winter temperatures go from below to above 0°C), chilling could also increase with warming, which would yield earlier budburst, potentially far earlier than last frost dates (Guy, 2014).

Unfortunately, these predictions for chilling are based on models developed almost solely for agricultural crops (but see Harrington & Gould, 2015), especially stone fruits (even for stone fruits, there have been few advances on the possible mechanisms and pathways that underlie these models over decades of research, see Erez & Lavee, 1971; Rageau *et al.*, 1998), and have rarely been robustly adapted to forest trees. While the development of classic models of chilling for peaches and related fruit trees benefited from data where these species were planted far outside their range, into regions with extremely low or potentially no chilling (Erez & Lavee, 1971; Richardson, 1974), equivalent data on forest trees is almost never available (Dennis, 2003). Thus most chilling models use limited observational and experimental data from forest trees to try to re-parametrize the basic stone fruit models (Chuine, 2000; Chuine *et al.*, 2016). This limited understanding of the physiology and process of chilling in trees, makes any current observations of shifts in 'chilling'—and all forecasts with warming—uncertain. Thus, both increases and decreases of chilling should be considered as potential outcomes of warming (Fig. S2).

These issues are partly why many studies use 'field chilling,' which take tissue (e.g., cuttings of adult dormant trees) from the field progressively across the fall and/or winter (see Weinberger *et al.*, 1950). However, this design may assign changes in other cues to chilling. This is because such studies often equate tissue removed later as having received more chilling and thus often treat 'time of cutting' as interchangeable with 'chilling,' though forcing and photoperiod conditions also change sequentially in the field.

Physiological insights into the controllers of chilling—or more specifically endo- and ecodormancy–lag far behind our understanding of flowering and other developmental events (Azeez & Sane, 2015; Azeez *et al.*, 2021). Recent work has shown that the sugar callose blocking plasmodesmata may proximately lead to endodormancy (Rinne *et al.*, 2011; van der Schoot *et al.*, 2014), which relates to previous studies that suggested restricted water movement correlates with dormancy induction (Kalcsits *et al.*, 2009), but this is still far downstream of the molecular and genetic controls. The few studies to date, however, suggest multiple pathways that include both temperature and photoperiod may underlie the same event timings (Azeez *et al.*, 2021), with potential variation in the pathway used across populations (Tanino *et al.*, 2010). Multiple layered pathways would explain decades of contrasting results (Erez & Lavee, 1971; Rageau *et al.*, 1998) and suggest most current models of chilling may be compromises across these pathways. Such an outcome would point to the possibility that no current model captures the underlying mechanisms of 'chilling.'

Notes S2: Trends in experimental treatments over cue levels and space

Photoperiods of 12, 16 and 24 hours represented 65% of all photoperiod treatments, while almost half (47%) of all forcing treatments were 10, 20 or 25°C. This suggests we have greater inference at these cue levels, but also more limited understanding beyond them, which could limit forecasting. Chilling treatments were far more varied. Of the studies that reported chilling temperatures, 4°C was the most common (14% of all studies), followed by 0°C and 3°C (11% and 9%, respectively).

Treatments (cue levels) varied across latitude, with a general trend toward more extreme values at higher latitudes. Forcing and chilling treatments decline 0.1°C per 1° of latitude (for forcing, min is -0.1, for max it is -0.06, see Fig S4; for chilling it is -0.06 for min and -0.09 for max); and the maximum studied photoperiod increases with latitude (0.09 hr per ° latitude, see Fig S4).

1 References

Ashby, W. (1962) Germination capacity in American Basswood *Tilia americana*. *Transactions of the Illinois State Academy of Science* **55**, 120–3.

Azeez, A. & Sane, A.P. (2015) Photoperiodic growth control in perennial trees. *Plant signaling & behavior* **10**, e1087631.

Azeez, A., Zhao, Y.C., Singh, R.K., Yordanov, Y.S., Dash, M., Miskolczi, P., Stojkovic, K., Strauss, S.H., Bhalerao, R.P. & Busov, V.B. (2021) Early bud-break 1 and early bud-break 3 control resumption of poplar growth after winter dormancy. *Nature Communications* **12**.

Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* **165**, 73–81.

Basler, D. & Körner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology* **34**, 377–388.

Baumgarten, F., Zohner, C.M., Gessler, A. & Vitasse, Y. (2021) Chilled to be forced: the best dose to wake up buds from winter dormancy. *New Phytologist* **230**, 1366–1377.

Biasi, L., Zanette, F. & Carvalho, R. (2012) Dormancy dynamics of grape and kiwifruit buds in a region of low chill occurrence. *XXVIII International Horticultural Congress on Science and Horticulture for People (IHC2010): International Symposium on Plant 932*, pp. 507–512.

Boyer, J. & South, D. (1986) Dormancy, chilling requirements, and storability of container-grown loblolly pine seedlings .

Caffarra, A. & Donnelly, A. (2011) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International Journal of Biometeorology* **55**, 711–721.

Caffarra, A., Donnelly, A., Chuine, I. & Jones, M.B. (2011) Modelling the timing of *Betula pubescens* bud-burst. I. Temperature and photoperiod: A conceptual model. *Climate Research* **46**, 147.

Calmé, S., Bigras, F.J., Margolis, H.A. & Hébert, C. (1994) Frost tolerance and bud dormancy of container-grown yellow birch, red oak and sugar maple seedlings. *Tree Physiology* **14**, 1313–1325.

Campbell, R.K. & Sugano, A.I. (1975) Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* pp. 290–298.

Cannell, M. & Smith, R. (1983) Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *Journal of applied Ecology* pp. 951–963.

Charrier, G., Bonhomme, M., Lacointe, A. & Améglio, T. (2011) Are budburst dates, dormancy and cold acclimation in walnut trees (juglans regia l.) under mainly genotypic or environmental control? *International journal of biometeorology* **55**, 763–774.

Chavarria, G., Herter, F.G., Raseira, M.d.C.B., Rodrigues, A.C., Reisser, C. & Silva, J.B.d. (2009) Mild temperatures on bud breaking dormancy in peaches. *Ciência Rural* **39**, 2016–2021.

Chuine, I. (2000) A unified model for budburst of trees. *Journal of Theoretical Biology* **207**, 337 – 347.

Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. & Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology* **22**, 3444–3460.

Cook, C. & Jacobs, G. (2000) Progression of apple (malus× domestica borkh.) bud dormancy in two mild winter climates. *The Journal of Horticultural Science and Biotechnology* **75**, 233–236.

Cook, N.C., Bellen, A., Cronjé, P.J., De Wit, I., Keulemans, W., Van den Putte, A. & Steyn, W. (2005) Freezing temperature treatment induces bud dormancy in 'granny smith'apple shoots. *Scientia horticulturae* **106**, 170–176.

Cronjé, P., Jacobs, G., Sadie, A. & Cook, N. (2003) Quantification of the dormancy progression in terminal apple buds. changes in growth rate and water status. *Advances in horticultural science* pp. 105–110.

Dantec, C.F., Vitasse, Y., Bonhomme, M., Louvet, J.M., Kremer, A. & Delzon, S. (2014) Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range. *International journal of biometeorology* **58**, 1853–1864.

De Vries, D., Smeets, L. & Dubois, L.A. (1982) Interaction of temperature and light on growth and development of hybrid tea-rose seedlings, with reference to breeding for low-energy requirements. *Scientia Horticulturae* **17**, 377–382.

Dennis, F. (2003) Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience* **38**, 347–350.

Erez, A. & Lavee, S. (1971) Effect of climatic conditions on dormancy development of peach buds. i. temperature. *Journal of the American Society for Horticultural Science* .

Ettinger, A., Chamberlain, C., Morales-Castilla, I., Buonaiuto, D., Flynn, D., Savas, T., Samaha, J. & Wolkovich, E. (2020) Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change* pp. 1–6.

Falusi, M. & Calamassi, R. (1990) Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree Physiology* **6**, 429–438.

Falusi, M. & Calamassi, R. (1996) Geographic variation and bud dormancy in beech seedlings (*Fagus sylvatica* L). *Annales des Sciences forestières*, vol. 53, pp. 967–979, EDP Sciences.

Falusi, M. & Calamassi, R. (1997) Bud dormancy in *Fagus sylvatica* L. II. The evolution of dormancy in seedlings and one-node cuttings. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology* **131**, 143–148.

Falusi, M. & Calamassi, R. (2003) Dormancy of *Fagus sylvatica* L. buds III. Temperature and hormones in the evolution of dormancy in one-node cuttings. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology* **137**, 185–191.

Fishman, S., Erez, A. & Couvillon, G. (1987) The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. *Journal of Theoretical Biology* **124**, 473–483.

Fu, Y.H., Campioli, M., Deckmyn, G. & Janssens, I.A. (2013) Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agricultural and Forest Meteorology* **181**, 125–132.

Fu, Y.S.H., Zhao, H.F., Piao, S.L., Peaucelle, M., Peng, S.S., Zhou, G.Y., Ciais, P., Huang, M.T., Menzel, A., Uelas, J.P., Song, Y., Vitasse, Y., Zeng, Z.Z. & Janssens, I.A. (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107.

Gansert, D. (2002) Betula ermanii, a dominant subalpine and subarctic treeline tree species in japan: ecological traits of deciduous tree life in winter. *Arctic, Antarctic, and Alpine Research* pp. 57–64.

Gauzere, J., Lucas, C., Ronce, O., Davi, H. & Chuine, I. (2019) Sensitivity analysis of tree phenology models reveals increasing sensitivity of their predictions to winter chilling temperature and photoperiod with warming climate. *Ecological Modelling* **441**, 108805.

Ghelardini, L., Santini, A., Black-Samuelsson, S., Myking, T. & Falusi, M. (2010) Bud dormancy release in elm (*ulmus* spp.) clones—a case study of photoperiod and temperature responses. *Tree physiology* **30**, 264–274.

Gianfagna, T. & Mehlenbacher, S. (1985) Importance of heat requirement for bud break and time of flowering in apple. *HortScience* **20**, 909–911.

Gömöry, D., Foffová, E., Longauer, R. & Krajmerová, D. (2015) Memory effects associated with early-growth environment in Norway spruce and European larch. *European Journal of Forest Research* **134**, 89–97.

Granhus, A., FlØistad, I.S. & SØgaard, G. (2009) Bud burst timing in *Picea abies* seedlings as affected by temperature during dormancy induction and mild spells during chilling. *Tree physiology* **29**, 497–503.

Guak, S., Olsyzk, D.M., Fuchigami, L.H. & Tingey, D.T. (1998) Effects of elevated CO2 and temperature on cold hardiness and spring bud burst and growth in douglas-fir (*Pseudotsuga menziesii*). *Tree Physiology* **18**, 671–679.

Guerriero, P., Scalabrelli, G. & Grazzini, G. (1990) Chilling effect on inhibition removal in kiwifruit dormant lateral buds. *I International Symposium on Kiwifruit 282*, pp. 79–86.

Gunderson, C.A., Edwards, N.T., Walker, A.V., O'Hara, K.H., Campion, C.M. & Hanson, P.J. (2012) Forest phenology and a warmer climate–growing season extension in relation to climatic provenance. *Global Change Biology* **18**, 2008–2025.

Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.

Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy requirements for pacific northwest tree species. *Frontiers in Plant Science* **6**, 120.

Hawerroth, F.J., Herter, F.G., Petri, J.L., Marafon, A.C. & Leonetti, J.F. (2013) Evaluation of winter temperatures on apple budbreak using grafted twigs. *Revista Brasileira de Fruticultura* **35**, 713–721.

Hawkins, C.D. & Dhar, A. (2012) Spring bud phenology of 18 *Betula papyrifera* populations in British Columbia. *Scandinavian Journal of Forest Research* **27**, 507–519.

Heide, O. (1993a) Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* **88**, 531–540.

Heide, O. (1993b) Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum* **89**, 187–191.

Heide, O. (2003) High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology* **23**, 931–936.

Heide, O. & Prestrud, A. (2005) Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. *Tree Physiology* **25**, 109–114.

Heide, O.M. (2008) Interaction of photoperiod and temperature in the control of growth and dormancy of *Prunus* species. *Scientia Horticulturae* **115**, 309–314.

Heide, O.M. (2011) Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus* species. *Journal of Experimental Botany* **62**, 5397–5404.

Heide, O.M. & Sønsteby, A. (2012) Floral initiation in black currant cultivars (*Ribes nigrum* L.): Effects of plant size, photoperiod, temperature, and duration of short day exposure. *Scientia Horticulturae* **138**, 64–72.

Heide, O.M. & Sonsteby, A. (2015) Simultaneous dormancy induction interferes with short day floral induction in black currant (*Ribes nigrum* L.). *Scientia Horticulturae* **185**, 228–232.

Howe, G.T., Hackett, W.P., Furnier, G.R. & Klevorn, R.E. (1995) Photoperiodic responses of a northern and southern ecotype of black cottonwood. *Physiologia Plantarum* **93**, 695–708.

Jones, H., Hillis, R., Gordon, S. & Brennan, R. (2012) An approach to the determination of winter chill requirements for different *Ribes* cultivars. *Plant Biology* **15**, 18–27.

Junttila, O. & Hänninen, H. (2012) The minimum temperature for budburst in Betula depends on the state of dormancy. *Tree physiology* **32**, 337–345.

Kalcsits, L., Kendall, E., Silim, S. & Tanino, K. (2009) Magnetic resonance microimaging indicates water diffusion correlates with dormancy induction in cultured hybrid poplar (populus spp.) buds. *Tree Physiology* **29**, 1269–1277.

Karlsson, P., Bylund, H., Neuvonen, S., Heino, S. & Tjus, M. (2003) Climatic response of budburst in the mountain birch at two areas in northern fennoscandia and possible responses to global change. *Ecography* **26**, 617–625.

Kay, J.E., Deser, C., Phillips, A., Mai, A., Hannay, C., Strand, G., Arblaster, J.M., Bates, S.C., Danabasoglu, G., Edwards, J., Holland, M., Kushner, P., Lamarque, J.F., Lawrence, D., Lindsay, K., Middleton, A., Munoz, E., Neale, R., Oleson, K., Polvani, L. & Vertenstein, M. (2015) The Community Earth System Model (CESM) Large Ensemble Project A community resource for studying climate change in the presence of internal climate variability. *Bulletin of the American Meteorological Society* **96**, 1333–1349.

Lamb, R.C. (1948) Effect of temperatures above and below freezing on the breaking of rest in the Latham raspberry. *Proceedings of the American Society for Horticultural Science*, vol. 51, pp. 313–315.

Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014a) Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.

Laube, J., Sparks, T.H., Estrella, N. & Menzel, A. (2014b) Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist* **202**, 350–355.

Li, C., Welling, A., Puhakainen, T., Viherä-Aarnio, A., Ernstsen, A., Junttila, O., Heino, P. & Palva, E.T. (2005) Differential responses of silver birch (*Betula pendula*) ecotypes to short-day photoperiod and low temperature. *Tree physiology* **25**, 1563–1569.

Linkosalo, T. & Lechowicz, M.J. (2006) Twilight far-red treatment advances leaf bud burst of silver birch (*Betula pendula*). *Tree Physiology* **26**, 1249–1256.

Man, R. & Lu, P. (2010) Effects of thermal model and base temperature on estimates of thermal time to bud break in white spruce seedlings. *Canadian Journal of Forest Research* **40**, 1815–1820.

Manson, P. & Snelgar, W. (1991) Effect of time of budburst and apical shoot growth on flower production in kiwifruit. *New Zealand Journal of Crop and Horticultural Science* **19**, 441–445.

Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010) Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist* **186**, 900–910.

Myking, T. (1997) Effects of constant and fluctuating temperature on time to budburst in *Betula pubescens* and its relation to bud respiration. *Trees* **12**, 107–112.

Myking, T. (1998) Interrelations between respiration and dormancy in buds of three hardwood species with different chilling requirements for dormancy release. *Trees* **12**, 224–229.

Myking, T. & Heide, O. (1995) Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiology* **15**, 697–704.

Nienstaedt, H. (1966) Dormancy and dormancy release in white spruce. *Forest Science* **12**, 374–384.

Nishimoto, N. & Fujisaki, M. (1994) Chilling requirement of buds of some deciduous fruits grown in southern japan and the means to break dormancy. *Dormancy and the related Problems of Deciduous Fruit Trees 395* pp. 153–160.

Okie, W.R. & Blackburn, B. (2011) Interactive effects of light and chilling on peach flower and leaf budbreak. *HortScience* **46**, 1056–1062.

Pagter, M., Andersen, U.B. & Andersen, L. (2015) Winter warming delays dormancy release, advances budburst, alters carbohydrate metabolism and reduces yield in a temperate shrub. *AoB plants* **7**, plv024.

Partanen, J., Hänninen, H. & Häkkinen, R. (2005) Bud burst in Norway spruce (*Picea abies*): preliminary evidence for age-specific rest patterns. *Trees* **19**, 66–72.

Partanen, J., Koski, V. & Hänninen, H. (1998) Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). *Tree Physiology* **18**, 811–816.

Partanen, J., Leinonen, I. & Repo, T. (2001) Effect of accumulated duration of the light period on bud burst in Norway spruce (*Picea abies*) of varying ages. *Silva Fennica* **35**, 111–117.

Pettersen, H. (1972) Effect of temperature and daylength on shoot growth and bud formation in azaleas. *Journal of the American Society for Horticultural Science* **97**, 17.

Piao, S., Liu, Z., Wang, T., Peng, S., Ciais, P., Huang, M., Ahlstrom, A., Burkhart, J.F., Chevallier, F., Janssens, I.A. *et al.* (2017) Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nature climate change* **7**, 359.

Pop, E.W., Oberbauer, S.F. & Starr, G. (2000) Predicting vegetative bud break in two arctic deciduous shrub species, salix pulchra and betula nana. *Oecologia* **124**, 176–184.

Rageau, R., Bonhomme, M., Richard, J.P. & Erez, A. (1998) The climatic determinism of vegetative bud break on peach trees with no exposure to chilling: Some experimental results. *Acta Horticulturae: 4th International Peach Symposium*, pp. 511–519.

Ramos, A. & Rallo, L. (1999) Effect of the bearing condition of the tree, chilling and defoliation on the forced budburst of olive cuttings at different tempeartures. *III International Symposium on Olive Growing 474* (eds. I.T. Metzidakis & D.G. Voyiatzis), pp. 251–254.

Richardson, E. (1974) A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience* **9**, 331–332.

Rinne, P., Hänninen, H., Kaikuranta, P., Jalonen, J. & Repo, T. (1997) Freezing exposure releases bud dormancy in *Betula pubescens* and *B. pendula*. *Plant, Cell & Environment* **20**, 1199–1204.

Rinne, P., Saarelainen, A. & Junttila, O. (1994) Growth cessation and bud dormancy in relation to ABA level in seedlings and coppice shoots of *Betula pubescens* as affected by a short photoperiod, water stress and chilling. *Physiologia Plantarum* **90**, 451–458.

Rinne, P.L.H., Welling, A., Vahala, J., Ripel, L., Ruonala, R., Kangasjarvi, J. & van der Schoot, C. (2011) Chilling of dormant buds hyperinduces FLOWERING LOCUS T and recruits GA-Inducible 1,3-beta-Glucanases to reopen signal conduits and release dormancy in *Populus*. *Plant Cell* **23**, 130–146.

Ruesink, J. (1998) Long day treatment prevents flower bud formation in pieris. *Gartenbauwissenschaft (Germany)* .

Sanz-Pérez, V. & Castro-Díez, P. (2010) Summer water stress and shade alter bud size and budburst date in three Mediterranean *Quercus* species. *Trees* **24**, 89–97.

Sanz-Perez, V., Castro-Diez, P. & Valladares, F. (2009) Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring Mediterranean oaks. *Plant Biology* **11**, 142–51.

Schnabel, B.J. & Wample, R.L. (1987) Dormancy and cold hardiness in *Vitis vinifera* L. cv. White Riesling as influenced by photoperiod and temperature. *American Journal of Enology and Viticulture* **38**, 265–272.

Skre, O., Taulavuori, K., Taulavuori, E., Nilsen, J., Igeland, B. & Laine, K. (2008) The importance of hardening and winter temperature for growth in mountain birch populations. *Environmental and experimental botany* **62**, 254–266.

Skuterud, R. & Dietrichson, J. (1994) Budburst in detached birch shoots (*Betula pendula*) of different varieties winter-stored in darkness at three different temperatures. *Silva Fennica* **28**, 223–224.

Søgaard, G., Johnsen, Ø., Nilsen, J. & Junttila, O. (2008) Climatic control of bud burst in young seedlings of nine provenances of norway spruce. *Tree Physiology* **28**, 311–320.

Sønsteby, A. & Heide, O. (2013) Variation in seasonal timing of flower bud initiation in black currant (ribes nigrum l.) cultivars of contrasting geographic origin. *The Journal of Horticultural Science and Biotechnology* **88**, 403–408.

Sønsteby, A. & Heide, O.M. (2014) Chilling requirements of contrasting black currant (*Ribes nigrum* L.) cultivars and the induction of secondary bud dormancy. *Scientia Horticulturae* **179**, 256–265.

Spiers, J. & Draper, A. (1974) Effect of chilling on bud break in rabbiteye blueberry cultivars. *Journal American Society for Horticultural Science* .

Swartz, H. & Powell Jr, L. (1981) The effect of long chilling requirement on time of bud break in apple. *Symposium on Growth Regulators in Fruit Production 120*, pp. 173–178.

Tanino, K.K., Kalcsits, L., Silim, S., Kendall, E. & Gray, G.R. (2010) Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant Molecular Biology* **73**, 49–65.

Templ, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., Rutishauser, T., Busto, M., Chmielewski, F.M., Hájková, L., Hodzić, S., Kaspar, F., Pietragalla, B., Romero-Fresneda, R., Tolvanen, A., Vučetič, V., Zimmermann, K. & Zust, A. (2018) Pan European Phenological database (PEP725): a single point of access for European data. *International Journal of Biometeorology* **62**, 1109–1113.

Thielges, B. & Beck, R. (1976) Control of bud break and its inheritance in *Populus deltoides*. *Tree Physiology and Yield Improvement* **14**, 253–259.

van der Schoot, C., Paul, L.K. & Rinne, P.L.H. (2014) The embryonic shoot: a lifeline through winter. *Journal of Experimental Botany* **65**, 1699–1712.

Viherä-Aarnio, A., Häkkinen, R. & Junttila, O. (2006) Critical night length for bud set and its variation in two photoperiodic ecotypes of *Betula pendula*. *Tree Physiology* **26**, 1013–1018.

Webb, D.P. (1977) Root regeneration and bud dormancy of sugar maple, silver maple, and white ash seedlings: effects of chilling. *Forest Science* **23**, 474–483.

Weinberger, J.H. *et al.* (1950) Chilling requirements of peach varieties. *Proceedings. American Society for Horticultural Science*, vol. 56, pp. 122–28.

Wolkovich, E.M., Cook, B.I. & Regetz, J. (2012) NECTAR: Network of Ecological and Climatological Timings Across Regions, http://knb.ecoinformatics.org/knb/metacat/nceas.988/knb.

Worrall, J. & Mergen, F. (1967) Environmental and genetic control of dormancy in *Picea abies*. *Physiologia Plantarum* **20**, 733–745.

Yazdaniha, A. (1967) *Effects of Chilling, Chemicals and Pruning on the Rest Period of Peach Trees*. Master's thesis, Utah State University, http://digitalcommons.usu.edu/etd/3596.

Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123.

Supplemental Tables

Table S1: **Dataset names and references for papers in the OSPREE database.**

Dataset	Reference
ashby62	(Ashby, 1962)
basler12	(Basler & Körner, 2012)
basler14	(Basler & Körner, 2014)
biasi12	(Biasi *et al.*, 2012)
boyer	(Boyer & South, 1986)
caffarra11a	(Caffarra & Donnelly, 2011)
caffarra11b	(Caffarra *et al.*, 2011)
calme94	(Calmé *et al.*, 1994)
campbell75	(Campbell & Sugano, 1975)
cannell83	(Cannell & Smith, 1983)
charrier11	(Charrier *et al.*, 2011)
chavarria09	(Chavarria *et al.*, 2009)
cook00b	(Cook & Jacobs, 2000)
cook05	(Cook *et al.*, 2005)
cronje03	(Cronjé *et al.*, 2003)
dantec14	(Dantec *et al.*, 2014)
devries82	(De Vries *et al.*, 1982)
falusi03	(Falusi & Calamassi, 2003)
falusi90	(Falusi & Calamassi, 1990)
falusi96	(Falusi & Calamassi, 1996)
falusi97	(Falusi & Calamassi, 1997)
fu13	(Fu *et al.*, 2013)
gansert02	(Gansert, 2002)
ghelardini10	(Ghelardini *et al.*, 2010)
gianfagna85	(Gianfagna & Mehlenbacher, 1985)
gomory15	(Gömöry *et al.*, 2015)
granhus09	(Granhus *et al.*, 2009)
guak98	(Guak *et al.*, 1998)
guerriero90	(Guerriero *et al.*, 1990)
gunderson12	(Gunderson *et al.*, 2012)
hawerroth13	(Hawerroth *et al.*, 2013)
hawkins12	(Hawkins & Dhar, 2012)
heide03	(Heide, 2003)
heide05	(Heide & Prestrud, 2005)
heide08	(Heide, 2008)
heide11	(Heide, 2011)
heide12	(Heide & Sønsteby, 2012)
heide15	(Heide & Sonsteby, 2015)
heide93	(Heide, 1993a)
heide93a	(Heide, 1993b)
howe95	(Howe *et al.*, 1995)
jones12	(Jones *et al.*, 2012)
junttila12	(Junttila & Hänninen, 2012)
karlsson03	(Karlsson *et al.*, 2003)
lamb37	(Lamb, 1948)
laube14a	(Laube *et al.*, 2014a)
laube14b	(Laube *et al.*, 2014b)

Table S1: **Dataset names and references for papers in the OSPREE database.**

Dataset	Reference
li05	(Li *et al.*, 2005)
linkosalo06	(Linkosalo & Lechowicz, 2006)
man10	(Man & Lu, 2010)
manson91	(Manson & Snelgar, 1991)
morin10	(Morin *et al.*, 2010)
myking95	(Myking & Heide, 1995)
myking97	(Myking, 1997)
myking98	(Myking, 1998)
nienstaedt66	(Nienstaedt, 1966)
nishimoto95	(Nishimoto & Fujisaki, 1994)
okie11	(Okie & Blackburn, 2011)
pagter15	(Pagter *et al.*, 2015)
partanen01	(Partanen *et al.*, 2001)
partanen05	(Partanen *et al.*, 2005)
partanen98	(Partanen *et al.*, 1998)
pettersen71	(Pettersen, 1972)
pop2000	(Pop *et al.*, 2000)
ramos99	(Ramos & Rallo, 1999)
rinne94	(Rinne *et al.*, 1994)
rinne97	(Rinne *et al.*, 1997)
ruesink98	(Ruesink, 1998)
sanz-perez09	(Sanz-Perez *et al.*, 2009)
sanzperez10	(Sanz-Pérez & Castro-Díez, 2010)
schnabel87	(Schnabel & Wample, 1987)
skre08	(Skre *et al.*, 2008)
skuterud94	(Skuterud & Dietrichson, 1994)
sogaard08	(Søgaard *et al.*, 2008)
sonsteby13	(Sønsteby & Heide, 2013)
sonsteby14	(Sønsteby & Heide, 2014)
spiers74	(Spiers & Draper, 1974)
swartz81	(Swartz & Powell Jr, 1981)
thielges75	(Thielges & Beck, 1976)
viheraaarnio06	(Viherä-Aarnio *et al.*, 2006)
webb78	(Webb, 1977)
worrall67	(Worrall & Mergen, 1967)
yazdaniha64	(Yazdaniha, 1967)
zohner16	(Zohner *et al.*, 2016)

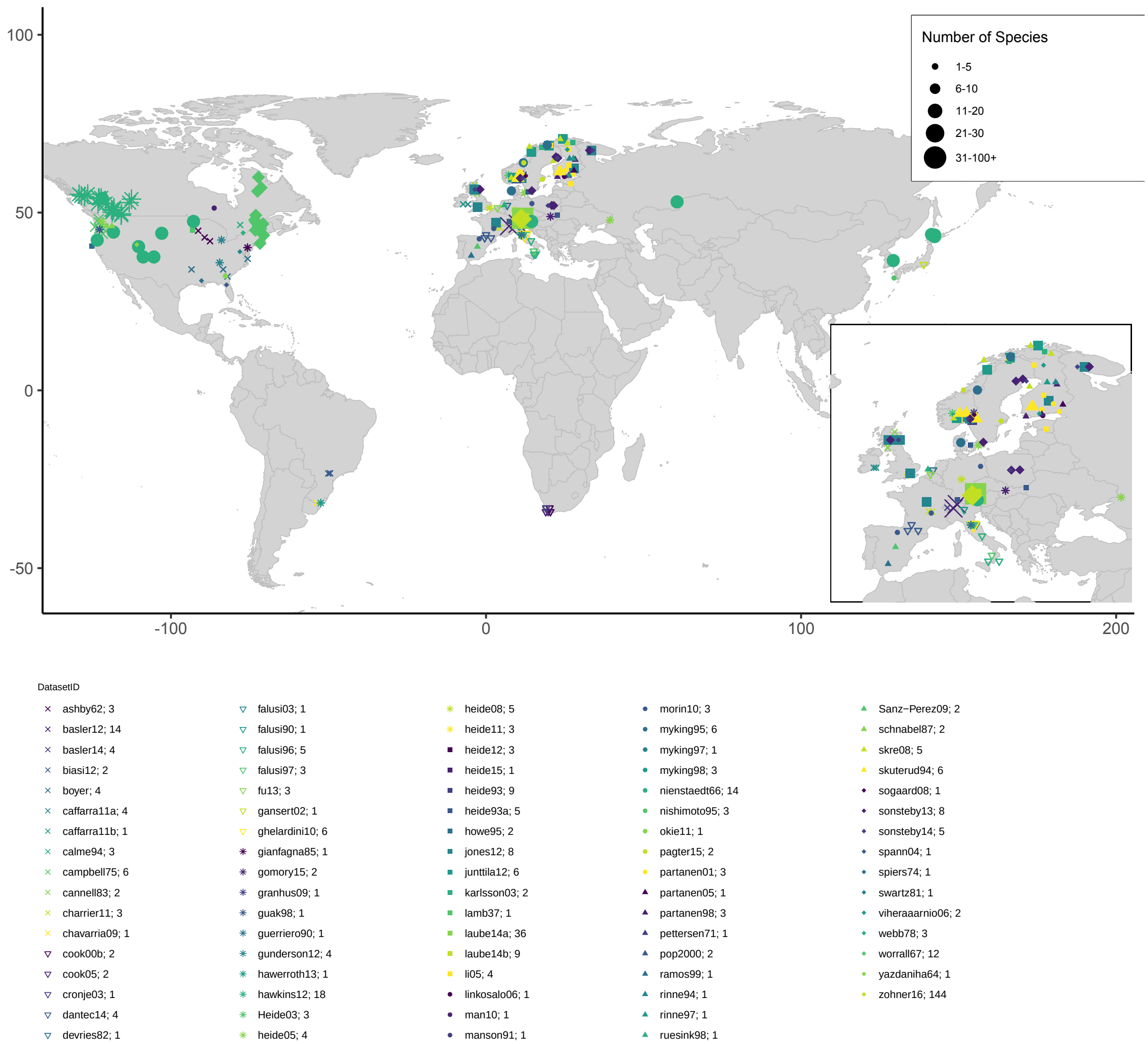

Figure S1: We reviewed seven decades of controlled environment studies, from Lamb (1948) to Zohner *et al.* (2016), conducted across the globe generally on 1-3 species in each experiment (size of circles and exact number of species given after each each study). See Table S1 for references for each 'Dataset.'

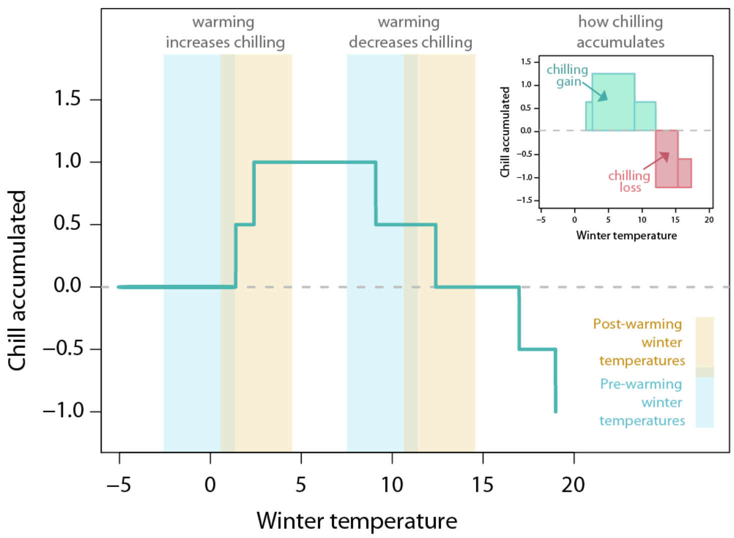

Figure S2: Current models of chilling suggest it may decrease or increase with winter warming. Here we show a common version of the Utah chilling model (top right inset and also turquoise line in main figure) with two conceptual scenarios of mean daily winter temperatures. When temperatures are generally below zero warming may increase accumulated chilling, while if pre-climate change temperatures are generally higher (near where chilling accumulates most per °C) then warming may decrease accumulated chilling.

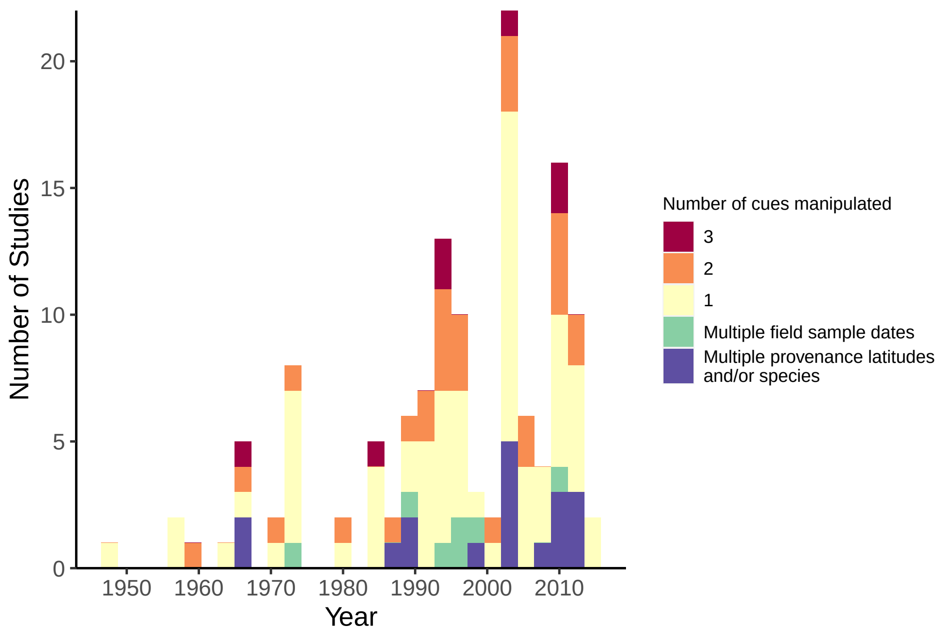

Figure S3: Prevalence of number of cues (1-3 possible: chilling, forcing, photoperiod) manipulated in studies over time. Studies that had multiple field sample dates but did not otherwise manipulate experimental chilling were counted as manipulating the chill cue. We separately counted the number of studies that had multiple field sample dates and manipulated experimental chilling (shown in green). Some studies had only multiple provenance latitudes and/or species (shown in blue).

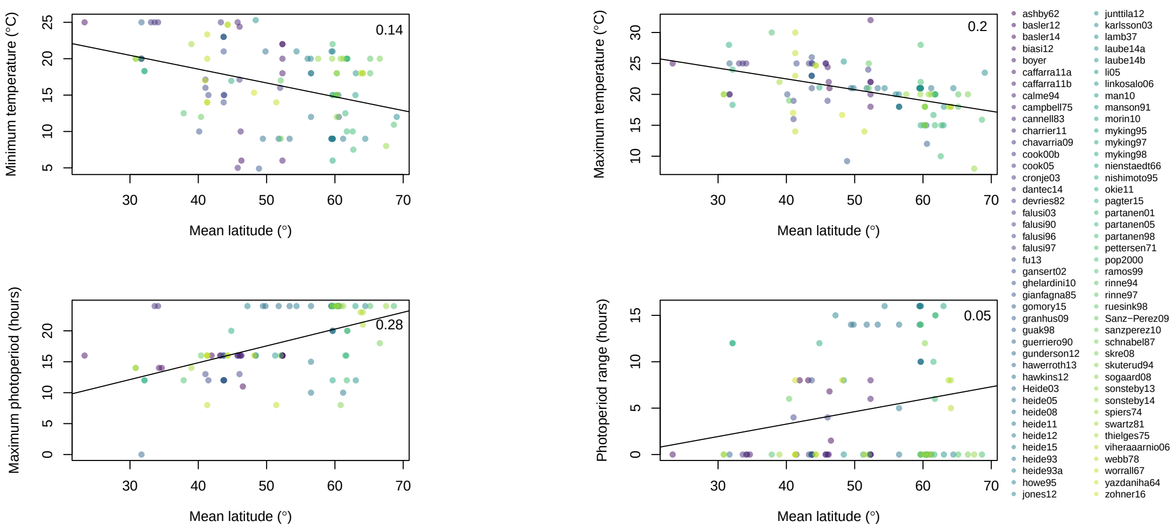

Figure S4: Experimental treatments correlate with latitude. Here we show the average latitude of a study (averaged over all latitudes from which tissue was taken) versus the minimum (upper left) and maximum (upper right) forcing treatments and the maximum (lower left) photoperiod treatment and range of photoperiod treatments (lower right, range calculated as maximum versus minimum treatments in a study). Colors represent unique datasets (see Table S1) and R^2 values are given in the upper-right corner of each plot.