

# Earlier and more variable spring phenology projected for eastern Canadian boreal and temperate forests with climate warming

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## ABSTRACT

Climate change affects timing and variability of spring phenology, as well as occurrence of spring frosts, and therefore influences forest structure, function, and management practices. In this study, we evaluated changes in budburst timing, sequential order of budburst, budburst temperatures, and frosts, from 1981–2010 baseline to different future climates (+2, +4, and +6 °C for moderate, high, and extremely high warming) for selected boreal and temperate species in eastern Canada. We used species-specific budburst models that are developed from large-scale forcing experiments.

Budburst averaged 10–15 days earlier per 2 °C increase of temperatures, except for temperate yellow birch and eastern white pine that slowed down to 5–7 days in budburst advancement from +4 to +6 °C. Earlier budburst was associated with greater annual and interspecific variations in budburst timing, lower budburst temperatures, more frosts, and less annual variations in sequential order of budburst. Compared to temperate trees, boreal trees had greater budburst advances and annual variations, but less interspecific variations in timing and sequential order of budburst. Early flushing species had greater phenological changes and annual variations, as well as more frosts. Our results suggest that budburst advance that has occurred will continue with greater among years/species variability but is unlikely to converge between boreal and temperate regions in eastern Canada under anticipated levels of climate warming.

## 1. Introduction

Timing of plant phenology in spring is shifting due to rising temperatures caused by climate change (Badeck et al., 2004; Schaber and Badeck, 2005; Schwartz et al., 2006; Delbart et al., 2008; Beaubien and Hamann, 2011). These phenological changes differ spatially and among species with differing spring phenology. Among geographic regions, phenological changes tend to be greater in colder climates, leading to “more synchronized spring phenology” across latitudes and altitudes (Ziello et al., 2009; Prévay et al., 2017; Post et al., 2018; Vitasse et al., 2018a; Liu et al., 2019). Among species, plants that start early in spring generally have greater responses to warming, resulting in increasing interspecific discrepancy (Murray et al., 1989; Abu-Asab et al., 2001; Fitter and Fitter, 2002; Beaubien and Hamann, 2011; Shen et al., 2014). It is not clear, however, if or how these spatial and interspecific differences might change with different levels of climate warming anticipated for the rest of this century (IPCC, 2014).

Occurring simultaneously with the changes in timing of spring phenology are inherent variabilities among years and among species (Roberts et al., 2015; Yang et al., 2020). Comparatively, annual and interspecific variations are much less studied, but likely critical to understanding dynamics of plant communities (Montgomery et al., 2020). For example, sequential order of spring phenology, i.e., the phenology of one tree species relative to others, may influence competitive interactions among trees (Kramer et al., 2000; Primack and Gallinat, 2016; Roberts et al., 2015; Cole and Sheldon, 2017), as well as plant–herbivore and trophic interactions in forest communities (Strode, 2015).

Trees in North American boreal and temperate forests have been observed to start growing earlier in spring (Beaubien and Freeland, 2000; Schwartz et al., 2006; Zhang et al., 2007; Beaubien and Hamann, 2011; Polgar et al., 2014; Primack and Gallinat, 2016) and therefore may experience longer growing seasons (Badeck et al., 2004; Schwartz et al., 2006; Gunderson et al., 2012). However, it is not clear if these phenological advances would continue with the further anticipated

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**Table 1**  
Deterministic budburst models for selected boreal and temperate trees in eastern Canada.

Species group	Model <sup>a</sup>	Parameters (a, b, c, d)
<b>Boreal species (Man et al., 2017a)</b>		
<i>Pinus banksiana</i> Lamb.	3-exponential	2013, 10993, 0.0049
<i>Populus balsamifera</i> L.	4-sigmoid	3266, 51776, 247, -107
<i>Betula papyrifera</i> Marsh.	3-exponential	5819, 50394, 0.0054
<i>Populus tremuloides</i> Michx.	4-sigmoid	6217, 53076, 304, -115
<i>Picea glauca</i> (Moench) Voss	3-exponential	6505, 21558, 0.0080
<i>Picea mariana</i> (Mill.) B. S. P.	3-exponential	8768, 18145, 0.0118
<b>Temperate species (Man et al., 2020a)</b>		
<i>Betula alleghaniensis</i> Britton	4-sigmoid	1311, 88151, 332, -263
<i>Pinus strobus</i> L.	4-sigmoid	1438, 29274, 429, -165
<i>Larix laricina</i> (Du Roi) K. Koch)	4-sigmoid	2769, 199142, -297, -248
<i>Pinus resinosa</i> Ait.	4-sigmoid	5175, 113800, 17, -221
<i>Thuja occidentalis</i> L.	4-sigmoid	5742, 80365, 376, -124
<i>Picea rubens</i> Sarg.	4-sigmoid	10771, 59227, 430, -176

<sup>a</sup> 3-parameter exponential decay,  $y=a + b*\exp(-cx)$  and 4-parameter sigmoid curve,  $y=a + b*(1 + \exp((x-c)/d))^{-1}$ ; balsam poplar and trembling aspen data were refitted with sigmoid models for better fitting.

climate warming caused by climate change (IPCC, 2014) and how they would differ between boreal and temperate regions and among species with differing spring phenology. In these northern climates (Liu et al., 2018; Ma et al., 2019), there is also a concern that earlier spring phenology is associated with increasing frosts, a climate-related stress that can be devastating in these areas (Gu et al., 2008; Man et al., 2009, 2013) and can counterbalance the benefits of longer growing seasons (Man et al., 2013; Marquis et al., 2020; Chamberlain and Wolkovich, 2021). Limited modelling and projections for future phenology are based either on single species (Colombo, 1998; Laskin et al., 2019) or phenological models developed from short-term field observations

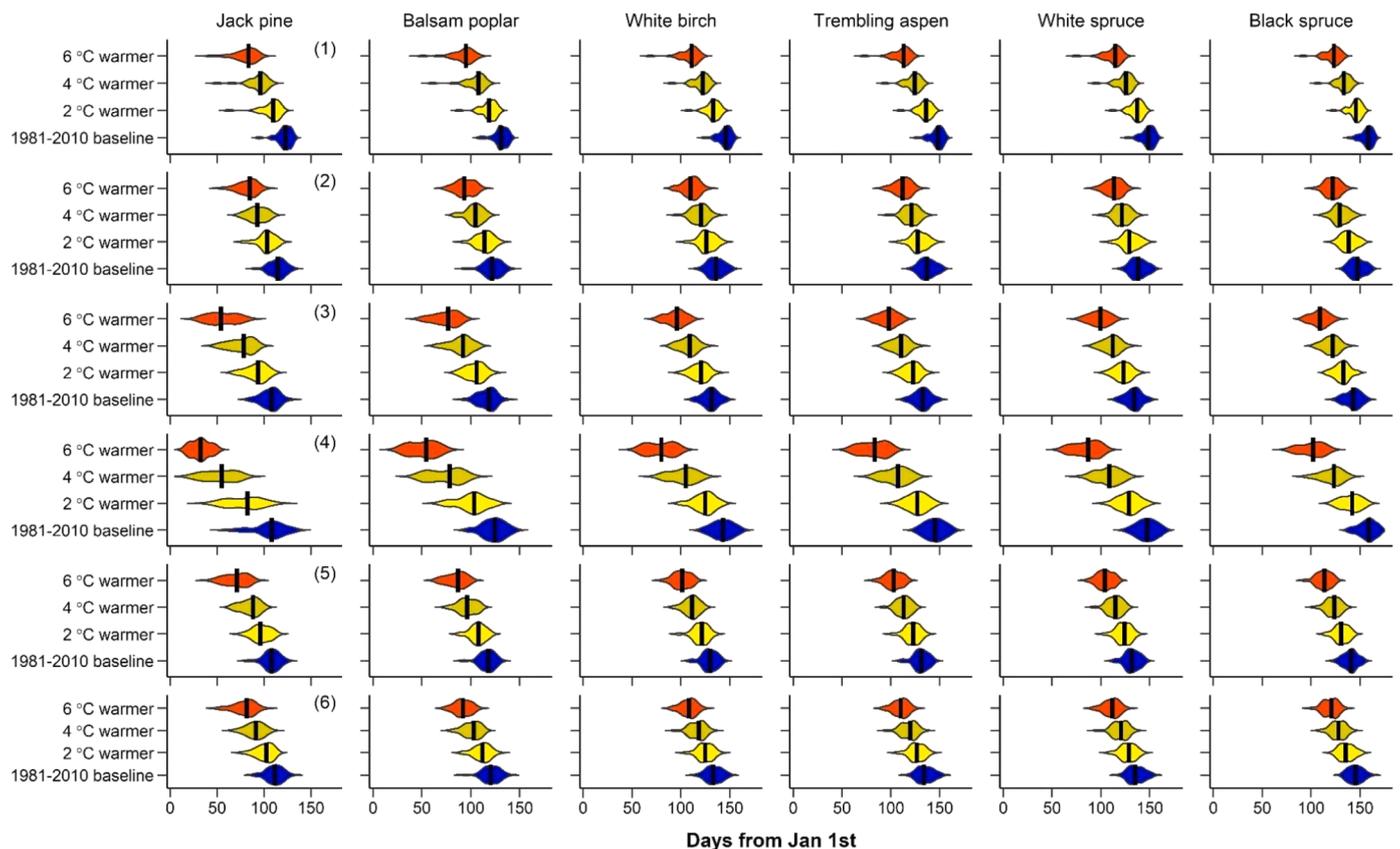
(Morin et al., 2009).

In this study, we examined changes in timing of bud phenology for selected boreal and temperate trees in eastern Canada, across an area of large natural forests in northern North American forests (Rowe, 1972), from 1981–2010 baseline to different scenarios of future warmer climates. We took advantage of species-specific deterministic budburst models that are developed from large-scale forcing experiments under a wide range of winter chilling conditions (Man et al., 2017a, 2020a) that would provide reliable predictions for varying temperatures (Guak and Neilsen, 2013; Chuine et al., 2016; Man et al., 2017a) over multiple years and geographic locations. Our working hypotheses are: (a) budburst would continue to advance with rising temperatures due to long and cold winter and likely sufficient winter chilling (Man et al., 2017a, 2020a); (b) phenological responses would vary among species of different spring phenology, i.e., early vs. late spring phenology (Murray et al., 1989; Morin et al., 2009; Polgar and Primack, 2011), due to different chilling and forcing requirements (Man et al., 2017a, 2020a), and between boreal and temperate regions due to different chilling and forcing regimes (Zhang et al., 2007; Fu et al., 2015; Asse et al., 2018); (c) interspecific variations in timing and sequential order of budburst would increase, due to interspecific differences in phenological responses; and (d) frosts would occur more frequently with advance of budburst into early and cold spring.

**2. Materials and methods**

**2.1. Phenological models**

Our species-specific budburst models include six boreal trees, jack pine (*Pinus banksiana* Lamb.), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus*



**Fig. 1.** Violin plots of 30-year budburst distributions by boreal locations (1 to 6), species (from early (left) to late (right) spring phenology), and levels of climate warming (from 1981–2010 baseline to three 2 °C warming increments) in eastern Canada. Median timing of budburst is shown as a black vertical line. The six locations are (1) Baie Comeau (Quebec), (2) Kapuskasing, (3) Sault Ste. Marie, (4) St. Johns (Newfoundland), (5) Sudbury, and (6) Timmins.

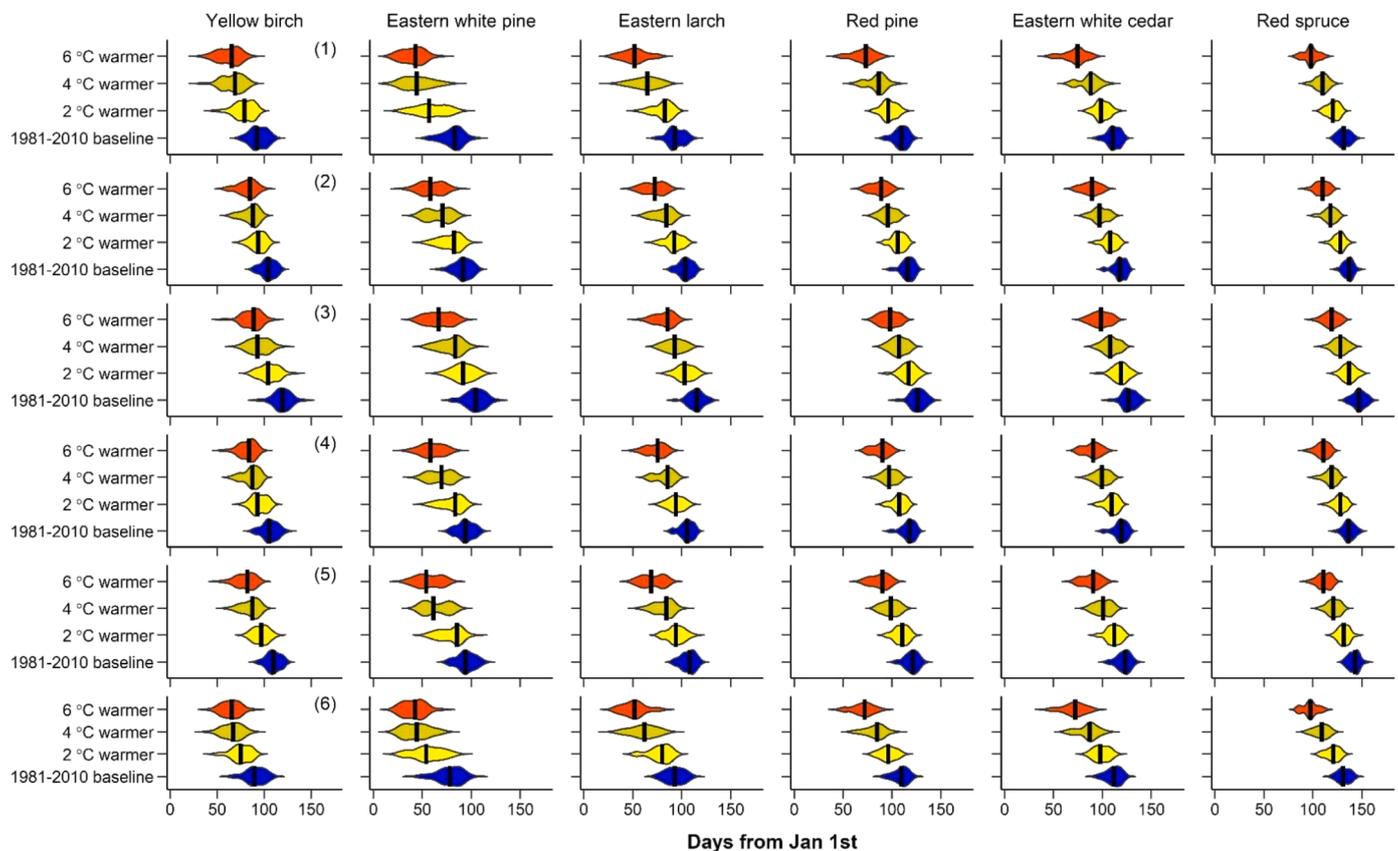


Fig. 2. Violin plots of 30-year budburst distributions by temperate locations (1 to 6), species (from early (left) to late (right) spring phenology), and levels of climate warming (from 1981–2010 baseline to three 2 °C warming increments) in eastern Canada. Median timing of budburst is shown as a black vertical line. The six locations are (1) London, (2) Montreal (Quebec), (3) North Bay, (4) Ottawa, (5) Sherbrooke (Quebec), and (6) Toronto.

tremuloides Michx.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) B. S. P.), and six temperate trees, yellow birch (*Betula alleghaniensis* Britton), eastern white pine (*Pinus strobus* L.), eastern larch (*Larix laricina* (Du Roi) K. Koch), red pine (*Pinus resinosa* Ait.), eastern white cedar (*Thuja occidentalis* L.), and red spruce (*Picea rubens* Sarg.) (Table 1). The trees used for determinations of chilling–forcing relationships were grown from seeds collected from a boreal or a temperate climate region in Ontario (Man et al., 2017a, 2020a). The timing of budburst was assessed in greenhouse conditions after exposure to a range of natural winter chilling from extremely insufficient to fully satisfied (Man et al., 2017a, 2020a). This is in contrast with studies that are based on narrow ranges of winter chilling, i.e., forcing does not stabilize within the range of chilling examined (Cannell and Smith, 1986; Murray et al., 1989; Harrington and Gould, 2015; Zhang et al., 2018) and would not provide reliable projections for future climates when winter chilling regimes may be substantially different (Zhang et al., 2007; Fu et al., 2015; Asse et al., 2018).

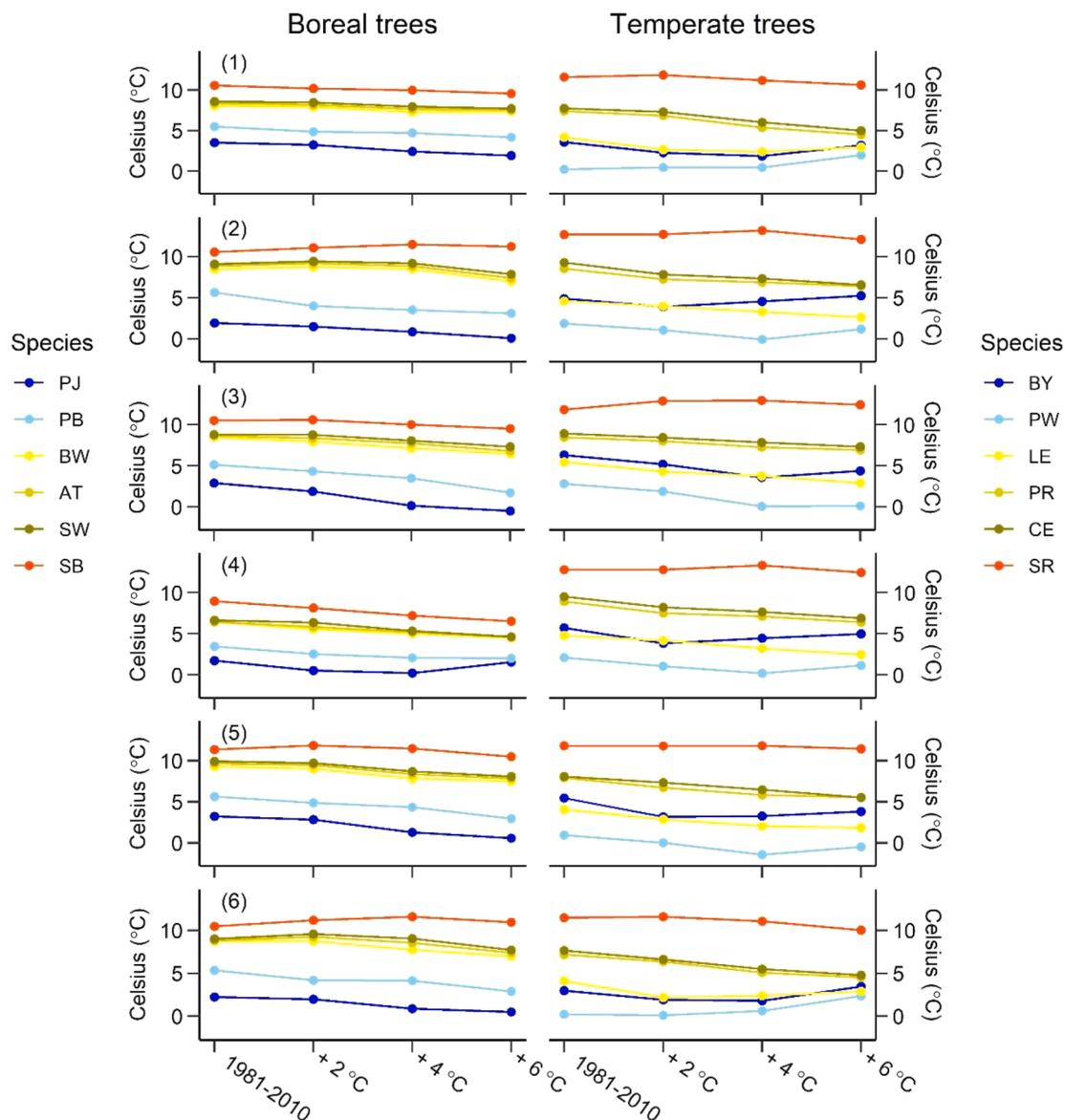
## 2.2. Predicting phenological changes and spring forcing conditions

The hourly temperatures required by the models were downloaded from the Environment Canada historical data portal ([http://climate.weather.gc.ca/historical\\_data/search\\_historic\\_data\\_e.html](http://climate.weather.gc.ca/historical_data/search_historic_data_e.html)) for six locations in each boreal and temperate region in eastern Canada (Table S1). To maintain the current within- and among-year variability, the hourly temperatures of 1981–2010 baseline were uniformly raised by 2, 4, and 6 °C, representing moderate, high, and extremely high warming by the end of this century (IPCC, 2014). The timing of budburst was determined for each species, year, location, and level of climate warming when the chilling–forcing relationships of the 12 tree species crossed the chilling–forcing curves of weather data (Figs. S1 and S2). Winter chilling

was calculated by hours using the Sarvas model (Sarvas, 1974) and accumulated from October 1<sup>st</sup> of the previous year. Spring forcing was calculated as cumulative growing degree hours above 0 °C since January 1<sup>st</sup> of the current year (Man et al., 2017a, 2020a). The average budburst temperatures (10 days prior to budburst, a period when most spring forcing occurs) were calculated and the occurrence of spring frosts after budburst was estimated at temperatures  $\leq -4$  °C, threshold temperatures known to damage opening buds and young tissues (Bigras and Hébert, 1996; Bigras et al., 2001).

Species budburst timing, annual variations (standard deviation and coefficient of variation), and changes were determined by locations and levels of climate warming. Similarly, interspecific variations in budburst timing (standard deviation and coefficient of variation), calculated for each year, were averaged by locations and levels of climate warming. The interspecific variations in sequential order of budburst were assessed at two levels, annual variations and deviations from 1981–2010 baseline; the two types of variations are related to each other and influenced by warmer climates. The annual variations within climate scenario were assessed by deviations from the dominant order of budburst determined with the colRanks function in R statistical software (R Foundation for Statistical Computing & R Core Team, 2019) and averaged by species and locations. The deviations from 1981–2010 baseline were assessed by the differences in sequential order of budburst each year between 1981–2010 baseline and warmer climates, which were then averaged by species and locations. Both chronological variations were expressed in proportion of the maximum change a species can achieve (5 in this study).

Budburst timing and variations, budburst temperatures, and frosts were subjected to a 1- or 2-way analysis of variance, separately by species groups (boreal and temperate). Species was treated as a fixed factor, location as a random factor, and level of climate warming as a



**Fig. 3.** Changes in budburst temperatures (10-day averages prior to budburst) with levels of climate warming (from 1981–2010 baseline to three 2 °C warming increments) by species groups, locations (1 to 6), and species in eastern Canada. Species abbreviations, ranked from early to late spring phenology, are PJ (jack pine), PB (balsam poplar), BW (white birch), AT (trembling aspen), SW (white spruce), and SB (black spruce) for boreal trees, and BY (yellow birch), PW (eastern white pine), LE (eastern larch), PR (red pine), CE (eastern white cedar), and SR (red spruce) for temperate trees. The six locations are (1) Baie Comeau (Quebec), (2) Kapuskasing, (3) Sault Ste. Marie, (4) St. Johns (Newfoundland), (5) Sudbury, and (6) Timmins for boreal trees and (1) London, (2) Montreal (Quebec), (3) North Bay, (4) Ottawa, (5) Sherbrooke (Quebec), and (6) Toronto for temperate trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

repeated factor (using compound symmetry in the covariance structure). Thirty-year data were averaged prior to analyses with Proc Mixed available in SAS 9.4 (SAS Institute Inc., Cary, NC). All other calculations and predictions were done using R statistical software with the RStudio IDE (RStudio Team, 2019).

### 3. Results

#### 3.1. Phenological responses to warming

Species budburst averaged 10–15 days earlier and had greater annual variation per 2 °C increase of temperatures (Figs. 1 and 2; Tables 2 and S2). Within each species group, early flushing species (species with smaller forcing requirements, see Figs. S1 and S2) showed greater budburst advances and annual variations, except for early flushing temperate yellow birch and eastern white pine that slowed down to 5–7

days in budburst advancement from +4 to +6 °C (significant species by climate interaction). Between the two species groups, boreal trees had more phenological changes (averaged 12.6 days with every 2 °C increase of temperatures) but less annual variations (8.9 days and 9.2% by SD and CV), compared to temperate trees (11.0 days, 8.9 days, and 10.7% for phenological changes and annual variations by SD and CV).

Interspecific variations in timing of budburst, relatively smaller with boreal compared to temperate trees, increased with levels of climate warming, except for a drop in SD from +4 to +6 °C with temperate trees (Figs. 1 and 2; Tables 2 and S2). The annual variations in sequential order of budburst averaged 0.5% in boreal trees and 2.3% in temperate trees and generally decreased with climate warming, except for an increase from +4 to +6 °C with temperate trees. Comparatively, the deviation in budburst order from 1981 to 2020 baseline did not change with warming in boreal trees, but generally increased in temperate trees (Figs. 1 and 2; Tables 2 and S2). Differences in variation in budburst

**Table 2**

Summary for statistical analyses on effects of species and climate warming on budburst timing and variations, budburst temperatures, and frosts. Location in boreal or temperate region was treated as a random factor and timing of estimated budburst for 30 years was averaged before statistical analyses.

Species group	Species	Climate warming	S x C interaction
	Species budburst — timing (Julian days)		
Boreal	<0.001	<0.001	0.943
Temperate	<0.001	<0.001	<0.001
	Species budburst — annual variation (SD, days)		
Boreal	<0.001	<0.001	0.989
Temperate	<0.001	<0.001	<0.001
	Species budburst — annual variation (CV, %)		
Boreal	<0.001	<0.001	0.003
Temperate	<0.001	<0.001	<0.001
	Species budburst — change (days)		
Boreal	<0.001	0.001	0.661
Temperate	<0.001	<0.001	<0.001
	Interspecific variation (SD, days)		
Boreal		<0.001	
Temperate		<0.001	
	Interspecific variation (CV, %)		
Boreal		<0.001	
Temperate		<0.001	
	Budburst order — annual variation (%)		
Boreal	<0.001	<0.001	<0.001
Temperate	<0.001	0.007	<0.001
	Budburst order — deviations from baseline (%)		
Boreal	<0.001	0.558	0.887
Temperate	<0.001	0.007	<0.001
	Budburst — temperatures (°C)		
Boreal	<0.001	<0.001	0.003
Temperate	<0.001	<0.001	<0.001
	Frosts after budburst ( $\leq -4^\circ\text{C}$ )		
Boreal	<0.001	<0.001	<0.001
Temperate	<0.001	<0.001	<0.001

order occurred mostly between white birch and trembling aspen in boreal trees and among yellow birch, eastern larch, red pine, and eastern white cedar in temperate trees (Figs. 1 and 2; Table S2).

### 3.2. Spring temperature conditions

Budburst temperatures (10-day averages prior to budburst) generally decreased with increases in climate warming, particularly for early flushing species (Fig. 3; Table 2). Early flushing temperate yellow birch and eastern white pine, however, showed a different trend, having the lowest budburst temperature at  $+4^\circ\text{C}$ . The number of frosts per year after budburst ( $\leq -4^\circ\text{C}$ ) increased with warming, particularly for early flushing species, i.e., jack pine and balsam poplar in boreal trees and yellow birch, eastern white pine, and eastern larch in temperate trees (Fig. 4; Table 2).

## 4. Discussion

### 4.1. Changes in species bud phenology

As expected, budburst advanced with warming in all species, due to the general adequacy of winter chilling in both boreal and temperate regions of eastern Canada (Fig. S3), relative to species chilling requirements (Man et al., 2017a, 2020a). The winter months in the study areas are generally below the optimum range of temperatures for effective winter chilling (Man et al., 2017a, 2020a). Warmer temperatures would shift winter temperatures from less effective (below optimum) to more effective (within optimum) ranges and therefore increase both winter chilling and spring forcing and promote early dormancy release and budburst. In contrast, warming in fall and spring months could move temperatures from more effective (within optimum) to less effective (above optimum) ranges and reduce winter chilling and negatively affect dormancy release (Fig. S3). Although some high

chilling temperate trees showed a slower advance of budburst, the reversed trend of later budburst with warming climate observed in areas with mild winters (Zhang et al., 2007; Asse et al., 2018) will not occur with the levels of climate warming expected for eastern boreal and temperate forests in Canada.

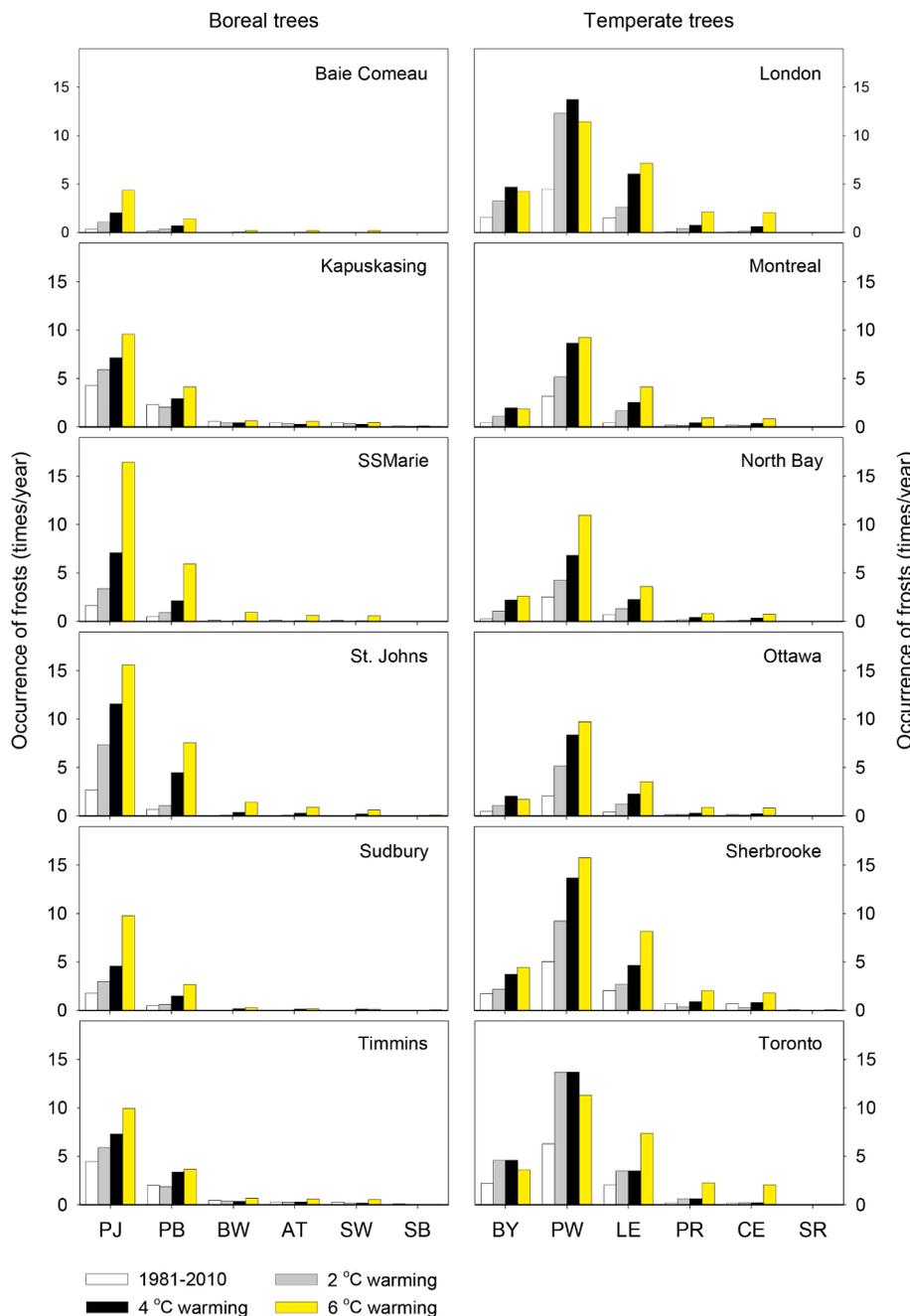
The rates of budburst advances projected for the different future climates are similar to those by Laskin et al. (2019) on a boreal shrub *Shepherdia canadensis* in western Canada and by Colombo (1998) on white spruce across boreal Canada based only on cumulative spring forcing. The results, however, are substantially larger than those by Morin et al. (2009) based on both chilling and forcing needs of southern temperate species and populations. For trembling aspen, Morin et al. (2009) projected a slightly delay (0.1 days) and advance (1.9 day) for  $+1.0$  and  $+3.2^\circ\text{C}$ , respectively, compared to the predicted 11.3-day and 23.1-day advances for  $+2.0$  and  $+4.0^\circ\text{C}$  of this study. Southern species and populations may have higher chilling and forcing requirements (Hannerz et al., 2003; Howe et al., 2003; Guy, 2014), as shown for temperate species in this study (Man et al., 2017a, 2020a), and therefore experience greater chilling deficiency and restricted phenological responses to warming (Zhang et al., 2007; Morin et al., 2009). It is also possible that phenological models based on short-term field observations go beyond the chilling and forcing ranges observed during model development when projecting for future climates of likely different chilling and forcing regimes (Zhang et al., 2007; Fu et al., 2015; Asse et al., 2018). Nevertheless, our projections are comparable to the observed phenological changes in the North American boreal and temperate forests due to climate warming (Schwartz et al., 2006; Zhang et al., 2007; Beaubien and Hamann, 2011; Polgar et al., 2014; Primack and Gallinat, 2016).

Our expectation on the responses of species with differing spring phenology was supported by the data, but with likely mechanisms different from what are commonly suggested. The greater responses by early flushing species are mainly due to their early spring phenology and therefore lower budburst temperatures (Fig. 3), rather than their smaller chilling needs. In this study, early flushing species, on average, had higher chilling requirements in both boreal and temperate species groups (Man et al., 2017a, 2020a). Because of lower budburst temperatures, early flushing species need a longer period of time to accumulate forcing temperatures needed for budburst and are more sensitive to changes in temperatures in terms of day-per-degree sensitivity (Keenan et al., 2020) not only by climate warming (Fitter and Fitter, 2002; Wolkovich et al., 2012; Shen et al., 2014; Zhang et al., 2015a, 2015b), but also by interannual variations in temperatures (Table S2). The common explanations that species of smaller chilling requirements are less restricted by insufficient chilling induced by warming climate (Murray et al., 1989; Morin et al., 2009; Polgar and Primack, 2011) do not help explain differential responses between early and late flushing species in this study, but seem to be accountable for the differences between boreal and temperate species (Zhang et al., 2007; Morin et al., 2009; Man et al., 2017a, 2020a). Indeed, insufficient chilling at high warming ( $> +2.0^\circ\text{C}$ ) apparently restricted the responses of some early flushing, high chilling temperate species (i.e., yellow birch), which has been suggested for late flushing species elsewhere (Morin et al., 2009; Primack and Gallinat, 2016; Asse et al., 2018).

In this study, the uniform warming did not change annual variability in temperatures. The increasing annual variations must be due to differential efficiencies of spring forcing ( $>0^\circ\text{C}$ ) and winter chilling with temperatures (Sarvas, 1974), which would lead to increasing chilling and forcing variations among years. This speculation is supported by the fact that temperate trees with higher chilling requirements had greater annual variations than boreal trees (Table S2).

### 4.2. Interspecific variations

As expected, increasing interspecific variations in budburst timing with climate warming result from differential phenological responses



**Fig. 4.** Occurrence of frosts (times per year  $\leq -4$  °C after estimated budburst) with levels of climate warming (from 1981–2010 baseline to three 2 °C warming increments) by species groups, locations, and species in eastern Canada. Species abbreviations are PJ (jack pine), PB (balsam poplar), BW (white birch), AT (trembling aspen), SW (white spruce), and SB (black spruce) for boreal trees, and BY (yellow birch), PW (eastern white pine), LE (eastern larch), PR (red pine), CE (eastern white cedar), and SR (red spruce) for temperate trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

between early and late flushing species (Figs. 1 and 2), i.e., greater advance of budburst by early flushing species (Murray et al., 1989; Morin et al., 2009; Caffarra and Donnelly, 2011; Polgar and Primack, 2011; Montgomery et al., 2020). Temperatures that help the early fulfilment of chilling and forcing requirements would promote early budburst (Cannell and Smith, 1983; Hänninen, 1990; Polgar and Primack, 2011) and therefore interspecific variations, but those in three winter months were more closely related to interspecific variations in timing of budburst for both boreal and temperate forest trees in eastern Canada (Table S3). Thus, interspecific phenological variations would be even greater if warming occurs more intensively in these winter months (Bonsal et al., 2001; Robeson, 2004; Beaubien and Hamann, 2011).

The greater variability in timing of spring phenology did not increase annual variations in sequential order of budburst (Wesolowski and Rowiński, 2006), contrary to our expectation. Instead, the sequence of budburst generally varied less with warming, despite increasing

deviations from baseline chronology in temperate trees. This is, again, due to more stable order of species forcing needs at high winter chilling (Figs. S1 and S2) and general increases of winter chilling from 1981–2010 baseline to +4 °C (Fig. S3). The relatively greater and increasing deviations from +4 °C to +6 °C with temperate trees are therefore a combination of species high chilling needs and reduced winter chilling (Fig. S1, S2, and S3). This suggests that phenological asynchrony among species and deviation from baseline chronology would be greater if climate warming induces severe chilling deficiency (Laube et al., 2014; Roberts et al., 2015; Man et al., 2017a, 2020a), as has been found in areas with mild winters (Zhang et al., 2007; Fu et al., 2015; Asse et al., 2018).

Between boreal and temperate regions in eastern Canada, spring phenology is unlikely to converge given expected levels of climate warming. The average difference in budburst timing between boreal and temperate trees was about 21 days at 1981–2010 baseline and the 2 °C

warming and dropped to 20 days at the 4 °C warming and 16 days at the 6 °C warming. The narrowing in the difference resulted primarily from reduced advance of early flushing, high chilling temperate yellow birch and eastern white pine. Even if boreal regions experience more warming than temperate regions (i.e., +3 °C vs. +2 °C), as is observed and projected (IPCC, 2014; Post et al., 2018), the average difference would be 15 days, far from the “synchronized spring phenology” or the convergence of spring bud phenology suggested by others (Prevéy et al., 2017; Post et al., 2018; Liu et al., 2019).

#### 4.3. Occurrence of frosts

Slightly different from our expectation, more incidence of frosts with earlier spring phenology occurred mostly with early flushing species, despite a general decrease of budburst temperatures in all species (Fig. 3). These results are somewhat consistent with the projections by Colombo (1998) on white spruce, a late flushing, low chilling boreal conifer (Fig. S1), and suggestions by others on early vs. late flushing species (Murray et al., 1989; Morin et al., 2009; Primack and Gallinat, 2016; Ma et al., 2019) and high vs. low elevations (Asse et al., 2018; Vitasse et al., 2018b; Bigler and Bugmann, 2018), but different from the predictions of decreasing frosts with climate warming (Pohl et al., 2019; Zohner et al., 2020). For both early and late flushing species, however, frosts would occur more often if temperature variability increases, i.e., more alternations of warm and cold winter days with warming climate, as has been suggested from conifer winter injury at high elevations (Lazarus et al., 2006), large-scale freezing events (Gu et al., 2008; Man et al., 2009), warming experiments (Norby et al., 2003; Man et al., 2014), and phenological studies (Augsburger, 2013).

Frosts not only generate visual tissue damage, but also cause internal physiological shock and delay budburst (Bailey and Harrington, 2006; Man et al., 2014, 2020b), resulting in disadvantages for early flushing species. The actual impacts of frosts, however, may be less, due to slow development of early flushing species in early and cold springs (Polgar and Primack, 2011). The occurrence of frosts could also be less if species-specific critical values of cold hardiness, instead of threshold daily minimum temperatures, are used in frost assessments. For instance, previous observations indicated that early flushing pine trees are nearly as hardy as late flushing spruce trees during spring dehardening due to different structures of flushing tissues (Glerum, 1973; Man et al., 2017b, 2020b).

#### 5. Conclusion and outlook

The advance of budburst in eastern boreal and temperate forests likely continues with rising temperatures under the levels of climate warming expected. Although reversed trends of advanced budburst will not occur, the responses of some high chilling temperate species would start to slow down at high warmings (+6 °C) when chilling gain in winter months does not compensate for loss in fall and spring. This explains the altered trends of multiple phenological attributes including budburst timing and advances, interspecific variations in both timing and sequential order of budburst, budburst temperatures, and occurrence of frosts for temperate trees.

Comparatively, early flushing species have greater phenological changes, but likely experience lower budburst temperatures and more frosts, with greater advance of budburst into early and cold spring. This may prevent some early flushing species from exploiting an earlier spring and taking advantage of longer growing season and would require protective measures to reduce the impacts of frosts at the vulnerable stage of stand development (Man et al., 2009).

Our results indicate that climate warming will increase variations in timing of budburst among years and among species in eastern boreal and temperate regions. This suggests generally more diverse spring phenology and therefore ecosystem function. While greater annual variation may be difficult for some organisms to adapt to (Strode, 2015),

more interspecific variations in timing and less variation in sequential order of budburst would be beneficial to species dependent on diverse phenological resources (Cole and Sheldon, 2017).

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2021.100127.

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