The early bud gets the cold: Diverging spring phenology drives exposure to late frost in a Picea mariana [(Mill.) BSP] common garden

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Abstract

Under climate change, the increasing occurrence of late frost combined with advancing spring phenology can increase the risk of frost damage in trees. In this study, we tested the link between intra-specific variability in bud phenology and frost exposure and damages. We analysed the effects of the 2021 late frost event in a black spruce (*Picea mariana* (Mill.) BSP) common garden in Québec, Canada. We hypothesised that the timing of budbreak drives the exposure of vulnerable tissues and explains differences in frost damage. Budbreak was monitored from 2015 to 2021 in 371 trees from five provenances originating between 48° and 53° N and planted in a common garden at 48° N. Frost damages were assessed on the same trees through the proportion of damaged buds per tree and related to the phenological phases by ordinal regressions. After an unusually warm spring, minimum temperatures fell to $-1.9°$C on May 28 and 29, 2021. At this moment, trees from the northern provenances were more advanced in their phenology and showed more frost damage. Provenances with earlier budbreak had a higher probability of damage occurrence according to ordinal regression. Our study highlights the importance of intra-specific variability of phenological traits on the risk of frost exposure. We provide evidence that the timings of bud phenology affect sensitivity to frost, leading to damages at temperatures of $-1.9°$C. Under the same conditions, the earlier growth reactivation observed in the northern provenances increases the risks of late frost damage on the developing buds.

1 | INTRODUCTION

In cold-exposed areas, woody plants alternate phases of intense activity, growth and reproduction with dormancy (i.e. low metabolic activity) to survive under unfavourable conditions (Junttila, 2007). Temperature is a limiting factor in temperate and boreal ecosystems, mainly during winter. When temperatures drop below zero, ice is formed within the living tissues, leading to cell death by frost desiccation and disruption of the plasma membrane (Dowgert & Steponkus, 1984; Uemura et al., 2006). Frost damage happens when the exposure to cold temperatures (environmental factor) exceeds the plant's sensitivity (endogenous factor) (Burke et al., 1976; Charrier et al., 2015, 2018).

Trees adopt two strategies to reduce the risk of frost damage: avoidance and tolerance (Charrier et al., 2011). Avoidance is achieved through the synchronisation of phenological processes (dormancy) with the unfavourable season, thus preventing the exposure of sensitive growing tissues to damaging temperatures (Chamberlain et al., 2019). Tolerance is achieved by increasing frost hardiness (i.e. the ability of tissues to withstand cold temperatures by

preventing ice formation inside the cells) in the overwintering organs during the dormant season (Atucha Zamkova et al., 2021). Therefore, frost hardiness of trees changes according to the organ (variation in space) and phenological phase (variation in time) (Charrier et al., 2013; Sakai & Larcher, 1987). Current scientific knowledge suggests that trees at high latitudes withstand temperatures lower than −40°C during dormancy, but their developing shoots can be damaged at −4°C (Dang et al., 1992; Glerum, 1973).

The two strategies of frost tolerance and frost avoidance are closely linked and depend on a good synchronisation with the seasonal variations between favourable and unfavourable temperatures. Frost hardiness is generally at a minimum during the growing season when most resources are allocated to growth (Lang et al., 1987). Growing tissues have a high water content to achieve the cell turgor necessary for cell enlargement (Steppe et al., 2015) and are, therefore, more likely to freeze intracellularly, resulting in frost damage (Charrier et al., 2013). As days get shorter and temperatures decrease, secondary growth stops and the primary meristems become protected from cold temperatures by the formation of winter bud scales, entering into dormancy (i.e. frost avoidance; Charrier, 2022). This phase of dormancy, endodormancy, is internally regulated by growth inhibitors, and released by exposure to accumulated cold temperatures (i.e. chilling requirement) (Chuine et al., 2016). As temperatures get colder, the frost hardiness of overwintering organs (i.e. frost tolerance) increases through physiological mechanisms aimed at lowering the freezing point of the living cells and favouring the formation of extracellular ice (Baffoin et al., 2021; Charrier et al., 2013; Deslauriers et al., 2021). Once the chilling requirements are fulfilled, the trees enter the ecodormancy phase. In this phase, frost hardiness decreases in response to warm temperatures (Charrier et al., 2011, 2015; Kovaleski, 2022; Kovaleski et al., 2018; North et al., 2022). After being exposed to a certain amount of warm temperatures (i.e. forcing requirement), trees resume growth through the phenological event of budbreak. The forcing requirement can be measured as heat unit accumulation, for example with the commonly used growing degree-days (GDD) calculated by subtracting daily mean temperatures from a pre-determined base threshold (Snyder et al., 1999).

The ongoing warming conditions produced by climate change are shifting the timing of phenological events by fulfilling forcing requirements earlier (i.e. accelerating ecodormancy release), potentially exposing plants to an increasing risk of frost damage due to late frost events (Gu et al., 2008; Liu et al., 2018; Vitasse et al., 2018; Zohner et al., 2020). Late frost events are characterised by freezing temperatures after plant leaf-out in the spring, often causing significant damage to crops and forests (Chamberlain et al., 2019; Rigby & Porporato, 2008). Under climate change, the combination of warmer spring conditions and increased variability in temperature values make late frosts a serious threat, which has received increasing attention in the scientific literature (Chamberlain et al., 2021; Marquis et al., 2022). However, late frosts are discrete weather events, more difficult to predict than long-term climatic trends and mean values (Jentsch et al., 2007). This makes field measurements of such events challenging to design in advance, limiting empirical evidence about

this topic and generating uncertainty in predicting future consequences (Atucha Zamkova et al., 2021; Chuine et al., 2016; Warrington & Rook, 1980).

A relevant source of uncertainty is that species with a wide distribution can exhibit ecotypes with different responses to environmental drivers, resulting in variations in phenological traits. For example, when growing in the same conditions, northern provenances of some species show earlier budbreak than southern provenances (Ren et al., 2020b; Rossi & Bousquet, 2014). These diverging responses point to differences in plant sensitivity to environmental cues, for example lower forcing requirements in a provenance can lead to earlier budbreak. Since growing tissues are more vulnerable to frost damage, different timings of budbreak entail a different sensitivity to frost within the same species (Charrier et al., 2013). Understanding the link between these intra-specific differences in phenology and the risk of exposure to late frosts can both improve predictions of climate change impacts on forests (both natural and managed) and help adopt management strategies to minimise the risk of frost damage in the spring, for example by provenance selection. Given its wide distribution across the boreal region of North America and its ecological and economic importance, black spruce [*Picea mariana* (Mill.) B.S.P.] is a relevant model species to study this problem. The current scenario of increasing risk of late frost would entail negative impacts on growth, carbon uptake and survival of boreal species by loss of photosynthetic and reproductive tissue (Hufkens et al., 2012) and potentially increase the susceptibility to other stressors, such as drought (Charrier et al., 2021).

This study investigated the impact of a late frost event in spring 2021 in a common garden hosting five *P. mariana* provenances originating from a temperature gradient in the boreal forest of Quebec, Canada. The common garden is located on the southernmost margin of the closed-canopy boreal forest, representing a warmer condition for most provenances. The aim of our work was to understand the relationship between phenological patterns in tree provenances and the potential exposure to frost damage. We tested the hypothesis that under the same conditions, provenances from colder climates are more damaged by the frost because of an earlier budbreak, which exposes growing shoots to freezing temperatures.

2 | MATERIALS AND METHODS

2.1 | Common garden and phenological observations

Black spruce [*Picea mariana* (Mill.) B.S.P.] seeds from natural stands were collected from five provenances located along a latitudinal and climatic gradient between 48° and 53° N in the boreal forest of Quebec, Canada (Figure 1, Table 1). The term "provenance" is used to indicate the site of origin, that is the natural *P. mariana* stand in which the seeds were collected. Simoncouche (SIM) and Bernatchez (BER) are located in the *A. balsamea–B. papyrifera* (balsam fir-white birch) bioclimatic domain. Mistassibi (MIS) and Camp Daniel (DAN) belong
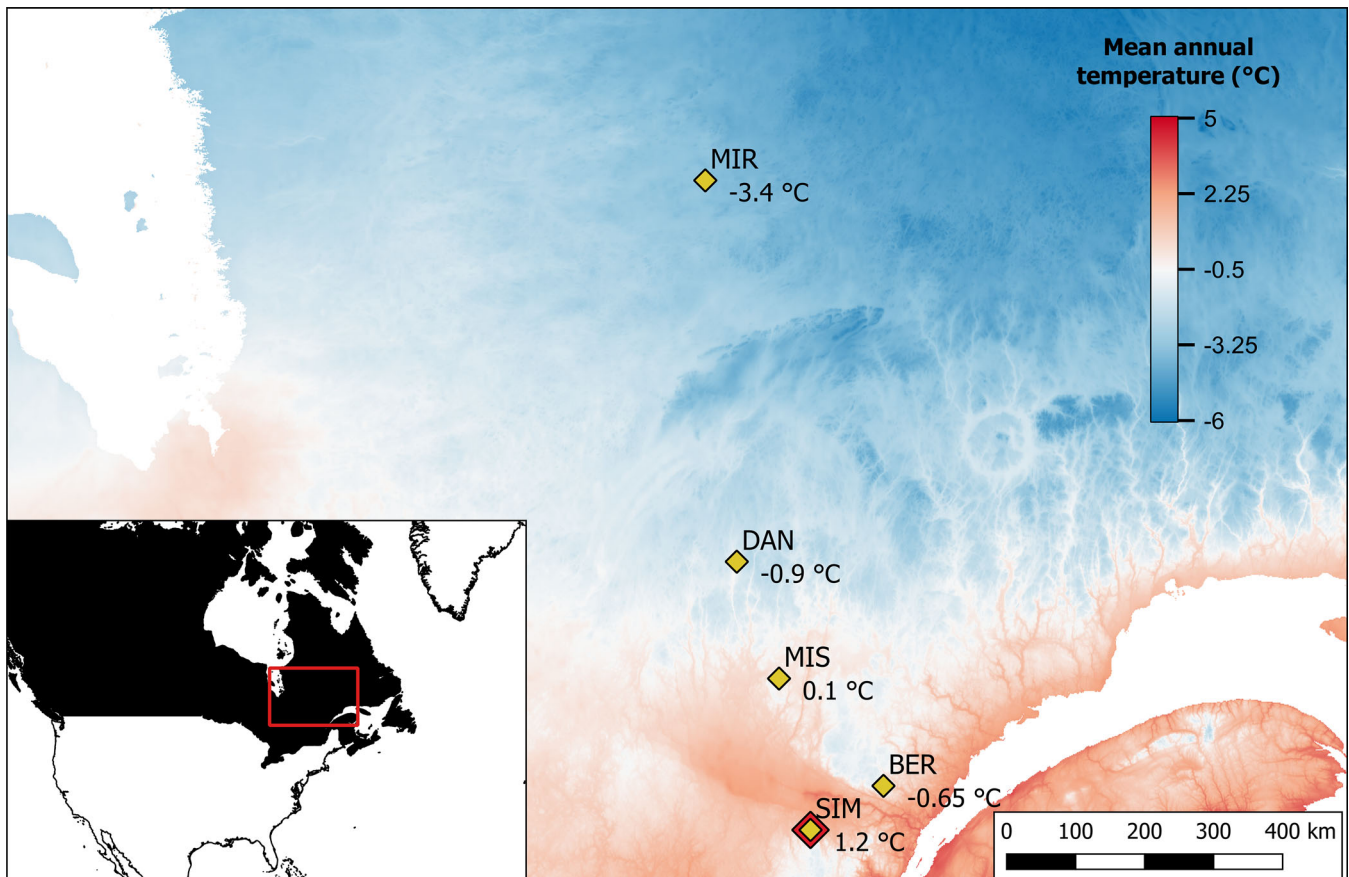
FIGURE 1 Geographical location of the five *P. mariana* provenances in Québec, Canada. Provenance origins (yellow diamonds) are shown with their mean annual temperature. All provenances were planted in a common garden located in the southernmost provenance site, SIM (diamond with red border).

TABLE 1 Characteristics of the five sites where black spruce provenances were collected

Site	Location	Total trees	Latitude (N)	Longitude (W)	Altitude (m a.s.l.)	Annual T (°C)	Min T (°C)
SIM	Simoncouche	89	48°13′	71°15′	338	1.2	−21.6
MIS	Mistassibi	56	49°43′	71°56′	342	0.1	−25.2
BER	Bernatchez	86	48°51′	70°20′	611	−0.6	−23.3
DAN	Camp Daniel	71	50°41′	72°11′	487	−0.9	−26.6
MIR	Mirage	69	53°47′	72°52′	384	−3.4	−28.8

Note: Annual T (°C) refers to the annual mean temperature; min T (°C) to the average minimum temperature for the coldest month. Temperature data are calculated for the 30-year period 1990–2020.

to the *P. mariana*−moss bioclimatic domain. Mirage (MIR) is located in the *P. mariana*−lichen domain, characterised by lower density and growth rates (Morneau, 2021). All sites are natural forests, that is no forestry operations or other anthropogenic disturbances are recorded. We, therefore, consider these stands to be representative of locally adapted and naturally occurring *P. mariana*. The climate of the area is typically boreal, with long, cold winters and short, cool and wet summers. Temperatures decrease with increasing latitude and elevation, with mean annual temperatures ranging from 1.2°C to −3.4°C (Table 1). In this work, we use mean annual temperature at the site of origin to define the climatic gradient to account for the effect of elevation. For example, site BER is further south than MIS, but being at a higher elevation the annual temperature is lower (Figure 1, Table 1).

Using mean annual temperature to define the gradient allows us to consider the effective environmental conditions in the provenance's site of origin instead of only considering the geographical position.

A common garden was established in July 2014 in Simoncouche (SIM), the southernmost site, using seeds collected from the five provenances (Silvestro et al., 2019). Apart from SIM, all the other provenances were transferred to warmer conditions. Seedlings were planted in a 0.5 ha clearcut forest patch, following a grid design with a random distribution of provenances and distances of 2 m × 2 m. On each side of the common garden, two rows of non-experimental spruces were planted to prevent the edge effect of the nearby forest.

Bud phenology was observed weekly from May to October 2015 and from 2017 to 2021 (Guo et al., 2021). Measurements in 2016

were not performed due to logistical constraints. A total of 371 trees were measured for budbreak phenology. During weekly visits, the apical bud of each tree was observed to assess the phenological stage. Seven ordinal phases of budbreak were identified: (0) closed bud; (1) open bud with a lightly coloured tip; (2) elongated bud, with scales stretching; (3) swollen bud with smooth scales; (4) translucent bud with needles visible through the scales; (5) bud broken, with needles exposed but not yet spread; (6) exposed shoot and spread needles (Dhont et al., 2010).

2.2 | Environmental conditions

Environmental conditions for the spring of 2021 were compared with historical averages to understand and contextualise the weather leading to the late frost. A weather station in Simoncouche (500 m from the study area) recorded the temperatures for 2021. The nearest weather station providing long-term data (1990–2020) of temperature and snow cover was in Bagotville, QC, 23 km from the study site (Environnement Canada, 2022). Daily temperature data were recorded at two stations (Simoncouche and Bagotville) from 2010 to 2015. The relationship between the temperatures recorded at the two sites was modelled using linear regressions (Table S1). Slope and intercept of the regression were used to calculate the long-term temperature in the study site by imputation, allowing long-term (1990–2020) averages to be computed for the study area in Simoncouche. Growing degree days (GDD) were used to represent warming conditions leading to spring and allow for a quantitative comparison between 2021 and the historical average (Gilmore & Rogers, 1958; Snyder et al., 1999). GDD were also used to assess differences in forcing requirements between provenances. We defined the forcing requirement as the mean GDD accumulation necessary to complete budbreak (i.e. reach phase 6), based on our 6 years of phenological observations. To select the base threshold for GDD calculation, we tested different base temperatures to compute the GDD necessary for budbreak and selected the one which produced less variability between years (Snyder et al., 1999). Variability was calculated as the coefficient of variation of the yearly mean GDD value necessary to reach budbreak. Four provenances out of five had a best base threshold (i.e. producing the lowest coefficient of variation) of $-3°C$ (Figure S1a). The warmest provenance (i.e. SIM) had very similar variability values using both $-2°C$ and $-3°C$, that is 0.0676 and 0.0677, respectively. For consistency, we used $-3°C$ as the base threshold for all GDD calculations in this work.

2.3 | Frost damage measurement

After the occurrence of damages in the field, a pilot survey was conducted to establish a protocol for frost damage assessment and train the observer to perform the measurement. We based our protocol on the browning method used to visually assess frost damages in conifers by observing tissue browning after frost treatments (Burr et al., 2001; Glerum, 1985). During the pilot survey, the repartition of brown buds on

individual trees was also visually assessed to exclude spatial variations in frost damages (e.g. more damage on one side of the tree). Based on the proportion of damaged brown buds on each tree, we defined four frost damage levels: (0) no damaged buds; (1) low, <5% of buds damaged; (2) medium, 5%–15% of buds damaged; (3) high, >15% of buds damaged. Observations of frost damages were performed on 11 June 2021, that is 2 weeks after the late frost event. Each tree in the plantation was assigned a score for frost damage, for a total of 371 trees.

2.4 | Statistical analyses

To test for differences in the occurrence of frost damage between provenances (i.e. presence or absence of damage), we applied a chi-squared (χ^2) test followed by a post-hoc pairwise comparison using Fisher's exact test. We applied an ordinal regression to model the relationship between phenology and frost hardiness. We set the frost damage level (i.e. 0–3) as an ordinal response variable and the phenological phase at the time of frost occurrence (i.e. 0–6) as an ordinal explanatory variable. The Lipsitz goodness of fit test was applied to evaluate the model, with non-significant p-values indicating that the model is reliable (Fagerland & Hosmer, 2016; Lipsitz et al., 1996). Finally, we used the ordinal model to predict the probability of observing each frost damage level based on a given phenological phase. All statistical analyses were performed in R (R Core Team, 2020) using chisq.posthoc.test (Ebbert, 2019), MASS (Venables & Ripley, 2002), generalhoslem (Jay, 2019) and pollen (Nowosad, 2019).

3 | RESULTS

3.1 | Phenology across *P. mariana* provenances

During 2015–2020, budbreak varied in duration and timing. In general, it lasted from mid-May until the end of June. The bud phase
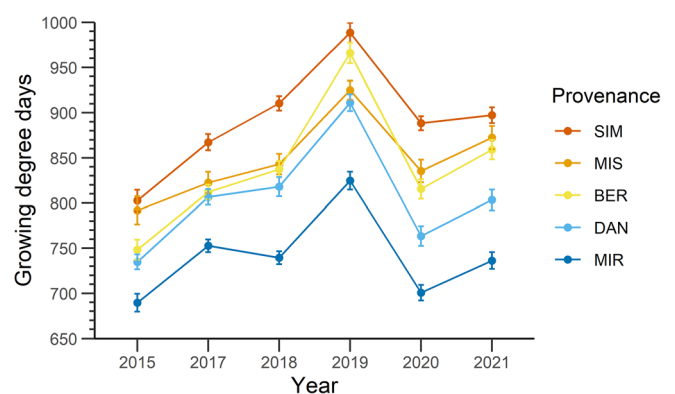

FIGURE 2 Mean growing degree days (GDD) necessary to complete budbreak for each year of observation. Colours indicate the five P. mariana *provenances*, points and whiskers the mean ± SE.

succession was longer in 2015 (35 days), and shorter in 2019 (55 days). Regardless of the lower threshold temperature used to calculate GDD, provenances from colder climates had lower forcing requirements (Figure S1b). The mean value of GDD necessary to complete budbreak (i.e. reach phase 6) varied between provenances along the temperature gradient, with a minimum of 741 ± 47.9 (SD) degree-days for the coldest provenance (i.e. MIR) and a maximum of 892 ± 60.5 (SD) degree-days for the warmest provenance (i.e. SIM). Across

years, and despite the inter-annual variation, colder provenances required less GDD to perform budbreak (Figure 2). With lower GDD requirements (i.e. forcing requirements), provenances from colder sites showed a consistently earlier budbreak than provenances from warmer sites (Figure S2). Averaging 6 years of observations, the coldest provenance (i.e. MIR) completed budbreak (i.e. reached phase 6) on DOY 161 (early May), 8 days earlier than the warmest provenance (i.e. SIM).
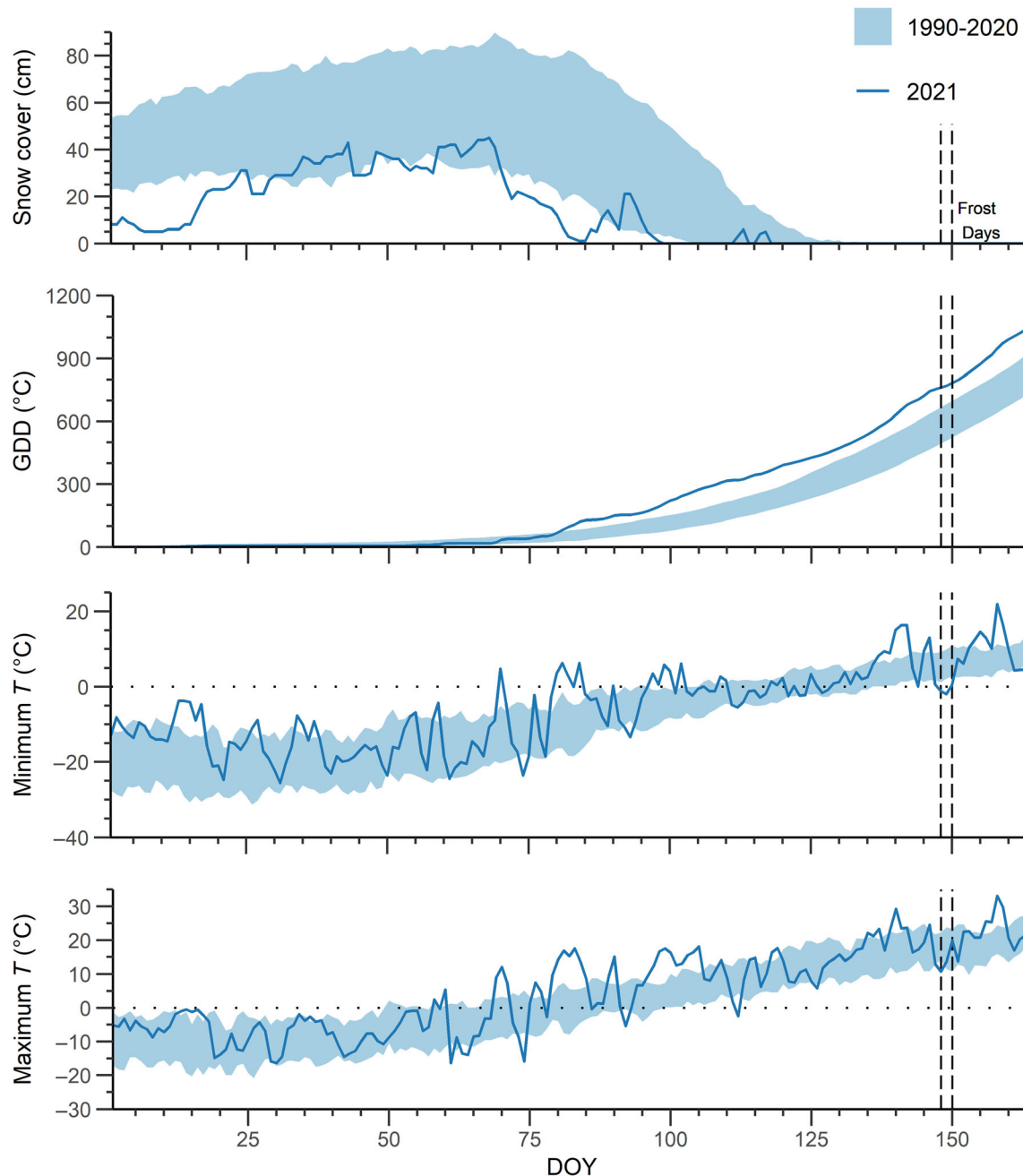
FIGURE 3 Climatic conditions of 2021 (blue line) compared to the average for the 30-year period 1990–2020 (mean ± SD, light-blue shaded area). The vertical dashed lines indicate when the frost days occurred. The horizontal dotted lines indicate the reference of 0°C. Temperature data and GDD for 2021 was measured at a weather station located 500 m from the study area. Temperature data and GDD for the 30-year period were estimated for the study area by imputation, from the weather station of Bagotville (23 km from study area). Snow cover data was measured at the weather station of Bagotville.

3.2 | The late frost event of 2021

Snow cover in the winter of 2020/2021 started on 27 October 2020 (DOY 301), similar to the 30-year average (DOY 304 ± 10 SD). Snow effectively disappeared on 8 April 2021 (DOY 98), with only a minor accumulation afterwards (Figure 3). Conversely, on the long-term average, the snowpack lasts 20 more days, up to DOY 118 (±10 SD). The snowpack was thin throughout the winter, reaching a maximum snowpack height of 45 cm on 9 March (DOY 68), 15 cm lower than the 30-year average for the same day. GDD (base threshold $-3°C$) accumulated faster compared with the historical average, reaching 753 degree-days on 27 May (DOY 147), the day before the start of the frost events. This GDD sum was 187 degree-days higher than the 30-year historical average for the same day, indicating the particularly warm conditions of this year ($+33\%$ GDD). Maximum temperatures in the late winter peaked twice, 24 March (DOY 83) and 9 April (DOY 99). On both occasions, temperatures reached $17.5°C$, respectively, $17.8°C$ and $13.8°C$ higher than the long-term average. This indicates two warm periods early in the season (Figure 3). Minimum temperatures showed a marked increase after 15 May, culminating at a value of $16.4°C$ on 22 May (DOY 142). This value is $11.7°C$ higher than the average, marking another warm period. The late frost event occurred on 28 and 29 May 2021 (DOY 148–149), when minimum temperatures measured at the study site (Simoncouche) fell abruptly, reaching minimum values of $-1.1°C$ and $-1.9°C$, respectively, on the 2 days. Sub-zero temperatures lasted 6 h on 28 May (2–8 AM) and 4 h on 29 May (3–7 AM). Wind conditions during the event were calm, averaging 0.55 and 0.02 m s^{-1} during the freeze hours of 28 and 29 May, respectively.

3.3 | Timings of spring phenology in 2021

Budbreak was already advanced at the time of frost because of the warm conditions of the 2021 spring. On 28 May (DOY 148), the first

FIGURE 5 The appearance of the developing buds after the late frost occurred on 28 and 29 May. The brown buds killed by the frost are also visible.

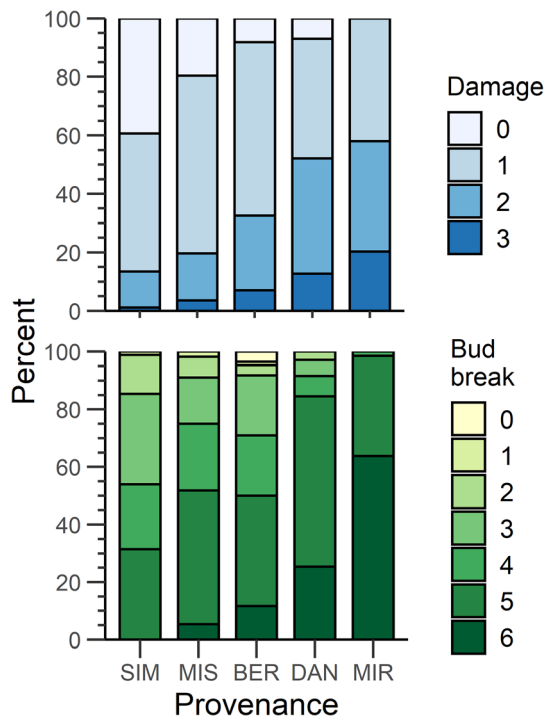**FIGURE 4** Distribution of frost damage levels (upper) and budbreak phenological phases at the time of frost occurrence (lower) between trees, by site of provenance. Darker colours indicate a higher proportion of damaged buds and a more advanced budbreak phase, respectively.
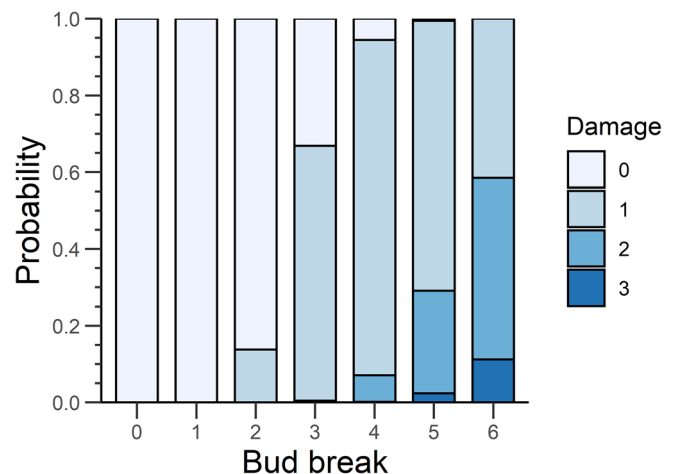

FIGURE 6 Probability of frost damage occurring at different phases of budbreak, as predicted by an ordinal regression model.

day on which temperatures dropped below 0°C, 61.5% of the observed trees were at phases 5 or 6 (i.e. the final phases of bud phenology). Provenances originating from colder climates exhibited more advanced phases of budbreak, as observed in 2015–2020 (Figure 4). Indeed, 58.7% of all trees at phase 6 (i.e. the final phenological phase for budbreak) before the frost event were those from MIR, the coldest provenance. In contrast, no tree from SIM, the warmest provenance, had reached phase 6 at the time.

3.4 | Frost damage

Frost damages resulted in collapsed, dead brown buds (Figure 5). The survey confirmed that frost was most likely the cause of bud mortality, as no sign of other causes (e.g. insects, parasites) was observed. Visual assessment of the repartition of frost damages on individual trees did not identify any spatial variation (i.e. damages appeared well distributed on the tree). Bud mortality rate did not exceed 30%.

The percentage of damaged trees (i.e. frost damage level >0) followed the provenance temperature gradient, varying between 60.7 to 100% for the warmest (i.e. SIM) and coldest (i.e. MIR), respectively (Table 2). The chi-square test confirmed differences among the provenances ($\chi^2 = 58.98$, $p < .0001$). The post hoc test indicated that provenances from warmer sites were less damaged than provenances from colder sites, with differences being more marked for the provenances at the extremes of the temperature gradient (Table 2).

Intermediate levels of damage (i.e. levels 1 and 2) were more frequent, accounting for 75.7% of the observations. Only 15.6% of the trees had no damage (i.e. level 0); of these, 79.3% belonged to the two warmer provenances (i.e. SIM and MIS). On the other hand, the two coldest provenances (i.e. MIR and DAN) accounted for 71.8% of all observed higher-level damages (i.e. level 3).

The observed distribution of damages matched the phenological phase observed at the time of the frost event, that is coldest provenances were more advanced in their timing of budbreak and exhibited more severe damages on their buds (Figure 4). Consistently, the ordinal model predicted higher probabilities of observing damage on more

advanced budbreak phases (Figure 6). Goodness of fit indicated that the model is reliable (LR = 3.63, $df = 9$, $p = .9339$).

4 | DISCUSSION

This study quantified the effects of a late frost event on *P. mariana* provenances growing in a common garden. We used 6 years of phenological observations to understand budbreak dynamics in five provenances originating from a thermal gradient along the latitudinal distribution of the boreal forest in Quebec, Canada. We compared the progression of budbreak in 2021 with the resulting levels of frost damage. Provenances from colder sites had an earlier and faster budbreak and showed more frost damages. We provided field-based evidence that, despite its well-known winter frost hardiness, *P. mariana* can experience damages at air temperatures as mild as −1.9°C in the case of a failure in frost avoidance.

4.1 | The late frost event of 2021

Overall, the spring of 2021 showed the typical characteristics of a false spring event, that is early warm conditions preceding a late cold spell (Gu et al., 2008). This is evident by looking at GDD accumulation, which started earlier and progressed faster in 2021 compared with the 30-year average. Moreover, snow cover during winter was scarce and melted 20 days earlier than usual (Figure 3). Temperatures reveal three warm spells, with temperatures higher than the norm contributing to hasten budbreak in the trees. Afterwards, there was a return of cold weather, with freezing minimum temperatures recorded on 27 and 28 May in calm air conditions (wind speed <6 m s^{-1}), indicating a radiative-type frost event (Kalma et al., 1992).

Frost damages were observed after mild temperatures (minimum recorded hourly temperature −1.9°C). While *P. mariana* can withstand temperatures below −40°C during the winter (Glerum, 1973), the growing shoots can be damaged by air temperatures of −4°C (Dang et al., 1992). In the present case, the frost happened during budbreak, and we found the most damage on more advanced buds (i.e. with exposed shoots; Figure 4). In this phase, the cells are highly hydrated to reach the turgor pressure necessary for cell enlargement, have a low concentration of solutes, which act as cryoprotectants in winter, and thinner cell walls (Charrier et al., 2013; Pantin et al., 2012) all factors that increase the likelihood of intracellular ice formation, which is lethal for the cell in natural conditions (Charrier et al., 2015; Wolfe & Bryant, 2001). Moreover, the restoration of water fluxes between the stem and bud favours ice propagation between organs (Neuner & Beikircher, 2010; Villouta et al., 2022). The less densely packed configuration of elongating buds may also contribute to increase bud vulnerability to frost. For these reasons, shoots in the first elongation phase have lower frost hardiness than closed buds and fully formed shoots (Lenz et al., 2013). This shows the importance of matching budbreak with favourable environmental conditions. To our knowledge, this is the first time that damages on immature *P. mariana*

TABLE 2 Frost damage occurrence for each provenance of the common garden

Provenance	No. damaged trees/no. trees	Damaged trees (%)
SIM	54/89	60.7 (a)
MIS	45/56	80.4 (b)
BER	79/86	91.9 (b)
DAN	66/71	93 (bc)
MIR	69/69	100 (c)

Note: Trees are considered damaged if the ordinal level of frost damage is 1 or higher (see Section 2.3). The total number of measured trees in the common garden is 371. Letters in brackets indicate significantly different groups, according to post hoc pairwise comparison using Fisher's exact test.

shoots have been quantified at air temperatures above $-2°C$. The literature found similar thresholds for other species, indicating that spring temperatures of $-2°C$ are able to damage the growing tissues of trees in temperate areas of North America and Europe (Chamberlain et al., 2019).

Frost damages were more frequent and severe in provenances originating from colder sites, which also showed an advanced progression in the timing of budbreak at the time of the frost (Figure 4). Although most trees presented some degree of damage, in most cases, only 5%–15% of buds were damaged. This is in line with results from Charrier et al. (2018), who used modelling approaches to determine that greater frost damages are more related to the intensity of the frost event rather than tree frost hardiness (i.e. tree vulnerability, sensu Charrier et al., 2015). In other words, the main variable influencing frost damage is the minimum temperature reached by the frost event: lower minimum temperatures can overwhelm frost hardiness thresholds and cause more severe damages to the tree. Besides the relatively mild temperatures reached, the overall low percentage of damaged buds may be due to the fact that budbreak was still ongoing at the time of the frost. It is likely that only buds in the most vulnerable phases of budbreak were damaged, since closed buds are more resistant to frost and fully developed shoots are not damaged even at $-3°C$ (Dang et al., 1992). It is also possible that microclimatic variations played a role in determining differences in frost damage, for example lower temperatures near the soil, in higher parts of the canopy or on bud surfaces (Charrier et al., 2015; Peaucelle et al., 2022; Winkel et al., 2009). However, in the present case, the spatial distribution of damaged buds on individual trees appeared homogeneous. This would suggest that phenological phases of the buds (and underlying physiological traits influencing frost hardiness) played an important role in determining bud sensitivity and, therefore, frost damage occurrence. This hypothesis is supported by our field observations, which found healthy and well-developing buds close to browned buds (Figure 5), suggesting that differences in development among buds at the time of frost occurrence determined differences in frost sensitivity and, ultimately, frost damage. Hypothetically, if the frost event studied in this work happened only a few weeks later, buds from northern provenances would have been advanced enough in their cell formation and development to be more frost hardy (Charrier et al., 2015). In this scenario, northern provenances could have been able to better resist the frost. Conversely, southern provenances still in the middle of budbreak would have been more damaged because of their low frost hardiness (Charrier et al., 2013). Further studies quantifying bud frost hardiness levels at different stages of budbreak could validate this hypothesis and shed light on tree sensitivity to frost during this crucial phenological event.

4.2 | Spring phenology in P. mariana provenances

Our results show that provenances originating from colder sites have a lower forcing requirement for spring reactivation and therefore show an earlier budbreak than provenances originating from warmer sites when growing in the same conditions. (Figure 2). The lower threshold for GDD calculation is close to $-3°C$ for all provenances, indicating that there is no difference in sensitivity to warm temperatures (Figure S1). In other words, provenances from colder climates perform an earlier budbreak because they need less heat accumulation, and not because they start accumulating heat at lower temperatures. When growing in the same conditions, that is in the common garden, northern provenances fulfil their forcing requirements faster than southern provenances, resulting in an earlier budbreak.

These findings are consistent with existing knowledge of P. mariana provenances. Earlier field studies in the same common garden (Guo et al., 2021; Usmani et al., 2020), as well as controlled-conditions experiments (Rossi & Bousquet, 2014), observed that provenances from colder places have lower forcing requirements, leading to faster budbreak under the same conditions. Similar findings have been reported for other conifers (Blum, 1988; Worrall, 1983; Zeltiņš et al., 2021) as well as broad-leaved species living in similar environments, such as sugar maple (Acer saccharum Marsh.) (Guo et al., 2020; Ren et al., 2020b). In environments where cold is the main limitation, the timings of budbreak are driven by a trade-off between late frost avoidance and maximisation of growth and reproduction during the short growing season (Chuine, 2010). Late frost avoidance appears to be a major evolutionary constraint driving budbreak timings for several species (Lenz et al., 2016; Marquis et al., 2020). From this perspective, our findings show that northern provenances have lower forcing requirements, allowing them to perform a faster dormancy release and maximise the shorter growing season in cold environments. Future studies should focus on quantifying the risk of late frost damage in northern P. mariana forests. Because of lower forcing requirements, trees in these regions could be more affected by the advance in budbreak induced by warmer spring conditions. This, in turn, could leave the trees exposed to the risk of late frost, which may become more frequent as spring temperatures variability increases (Chamberlain et al., 2021; Marquis et al., 2022).

However, it is not clear how far these results can be generalised to other species or ecosystems. Other studies have found opposite results, that is when growing in the same conditions, northern provenances perform budbreak later than southern. This was observed in common gardens for Pseudotsuga menziesii [(Mirb.) Franco] and Juglans nigra (L.) (Bey et al., 1971; Campbell & Sugano, 1979) and confirmed by experimental treatments in Juglans regia and Juglans regia x nigra (Charrier et al., 2011). This points to factors other than late frost influencing population-specific spring phenology timings. For example, drought-induced growth limitations during the summer can exert selection pressure and drive local provenances to perform an earlier budbreak to maximise growth early in the season (Campbell & Sugano, 1979). Some species may be more sensitive to long photoperiods in the spring, reducing the advancement in budbreak induced by warmer temperatures (Basler & Körner, 2012; Hänninen & Tanino, 2011). These differences highlight the complex interactions between intra-specific traits and environmental factors and the need for more field observations and experimental studies to better understand intra-specific variations in tree phenology.

Photoperiodic control over budbreak phenology could play an important role in mitigating advances in spring phenology (Körner & Basler, 2010). The role of photoperiod is often difficult to predict due to species-specific differences (Basler & Körner, 2014) and the absence of clear patterns among species (Flynn & Wolkovich, 2018; Way & Montgomery, 2015). In the case of *P. mariana*, photoperiod appears to have marginal control over budbreak with respect to temperature (Rossi, 2015). However, photoperiod seems to play a more important role when chilling requirements for budbreak are not met (Malyshev et al., 2018; Ren et al., 2020a). Unfulfilled chilling requirements can also directly delay budbreak (Chuine et al., 2016). Therefore, warmer winters in the future could mitigate or even offset the advances in spring phenology and reduce the risk of late frost damage in these regions. Further studies on the dormancy dynamics could help quantify these diverging drivers and improve predictions of climate change impacts in these regions.

In the context of provenance selection, the higher GDD requirement of southern provenances would delay budbreak under warming conditions. Assisted migration could therefore be a useful tool to decrease the risk of damage from late frost events. The northward movement of provenances has already been suggested, also because southern provenances have a higher potential for growth and timber production (Prud'homme et al., 2018). However, in the present study, we moved provenances southward (Figure 1). This allowed us to simulate an increase in temperatures for the northern provenances but leaves open questions regarding the vulnerability to autumn and winter frosts in southern provenances moved north. Working on the same common garden plantation that we analysed in this work, Silvestro et al. (2019) found that a later budbreak correlates with a later bud set in *P. mariana* provenances. More specifically, bud burst occurred 1.2 days later and was set 1.8 days later for each degree Celsius increase in mean annual temperature at the provenance origin. This suggests a trade-off between reducing the risk of late and early frost. Therefore, southern provenances may be more vulnerable to early frosts in the autumn (Montwé et al., 2018). Moreover, it is possible that southern populations, adapted to milder winters, have lower maximum frost hardiness and may not survive prolonged harsh winter temperatures. There is evidence that different provenances of conifers have different levels of frost hardiness (Repo et al., 2001; Sakai, 1983), although not all species exhibit the same trend (Charrier et al., 2011; Hawkins et al., 1994; Larcher & Mair, 1968; Morin et al., 2007). In boreal environments, where winter temperatures can reach values lower than −40°C, frost tolerance in overwintering organs is an essential aspect to be considered (Sebastian-Azcona et al., 2019).

A relevant aspect that remains to be investigated is the role of physiological regulators of budbreak and their interaction with environmental factors. While temperature is the main environmental cue inducing budbreak (Hänninen, 1997; Junttila, 2007; Sarvas, 1972), biochemical mechanisms are also involved. In particular, bud reactivation in the spring must be sustained by carbohydrates previously stored in other organs (Rinne et al., 1994; Tixier et al., 2017). During winter dormancy, these carbohydrates have a key function in

increasing the tree's frost hardiness (Kasuga et al., 2007). For this reason, carbohydrates ultimately exert a strong regulation over deacclimation dynamics leading to budbreak (Baffoin et al., 2021; Deslauriers et al., 2021). This suggests a positive correlation between maximum frost hardiness in the winter and the quantity of carbohydrates available in the spring to promote a fast reactivation (Delpierre et al., 2019). In this perspective, higher maximum frost hardiness in northern *P. mariana* provenances driven by harsher local winter conditions could provide a mechanistic explanation for faster budbreak. Investigating the link between differences in frost hardiness, carbohydrate content and rates of growth resumption could provide valuable insight into the drivers of phenotypic differences in *P. mariana* populations.

5 | CONCLUSIONS

Our results confirm the hypothesis that provenances originating from colder climates have a higher risk of exposure to late frost because of an earlier budbreak. In a scenario where climate warming advances budbreak and increases variability in spring temperatures, northern provenances can be expected to be more sensitive to local increases in late frost risk (Chamberlain et al., 2019; Gu et al., 2008). Our study highlights the importance of investigating intra-specific differences when studying the ecophysiological traits of trees, especially in the face of climate change. Diverging responses to spring temperatures entail different sensitivity to late frost in tree provenances, with important implications for studying ecological impacts of climate change and implementing adaptive management actions.

Our results support the idea of northward assisted migration of *P. mariana* provenances to minimise the risk of late frost damage. However, more research is necessary to address unanswered questions and fill in the gaps in knowledge. Further studies should measure frost hardiness in *P. mariana* provenances throughout the dormant period to clarify whether southern provenances can survive northern winters. Understanding species-specific dynamics of frost avoidance and frost resistance can improve predictions of climate change impacts and allow for informed choices in assisted migration and provenance selection.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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