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Inland populations of sugar maple manifest higher phenological plasticity than coastal populations

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Plasticity is vital for plants to rapidly acclimate to environmental changes, especially under the climate change. Global warming could advance bud break and extend the growing season, but it also increases the risk of frost damage to developing leaves. In this study, we explored the phenological plasticity of bud burst of half-sib family sugar maple (*Acer saccharum* Marsh.) seedlings from 11 seed origins in two common gardens at the center and the northern edge of the species distribution in Quebec, Canada. Results showed that the phenological plasticity of sugar maple originating from inland was significantly higher than those from coastal areas at the beginning of leaf development. This discrepancy may result from the long-term frost change frequency of seed origins. Our study suggests that in the context of climate warming, the higher plasticity observed in sugar maple originating from inland areas may benefit from the phenological adaptation of sugar maple and the survival of local populations. It also suggests that inland populations may have a higher potential regarding to assisted migration, but this needs to be confirmed for other functional traits than phenology.

KEYWORDS

Acer saccharum, bud burst, common garden, climate change, temperature

1 Introduction

Global climate change has affected tree growth significantly, and trees have to adapt to the environmental changes *in-situ* or migrate to new growth conditions to survive (Aitken et al., 2008). Phenotypic plasticity, determined as the ability to alter phenotype quickly in response to environmental changes (Nicotra et al., 2010; Matesanz and Valladares, 2014; Merilä and Hendry, 2014), is faster than genotypic adaptation and plays a crucial role in

survival in various environments (Chevin et al., 2013; Franks et al., 2014). However, to achieve high phenotypic plasticity, plants need to invest resources to perceive environmental information and produce a series of allocational, anatomical, or morphological traits adjustments to adapt to changing conditions (DeWitt, 1998; Van Kleunen and Fischer, 2005; Auld et al., 2010). Multiple phenotypes exhibit a wide range of variability, which increase the chance to adapt to weather events and gain a high competitive ability (Gomulkiewicz and Kirkpatrick, 1992; Hufford and Gomulkiewicz, 1999; Holloway, 2002), while others may inevitably mismatch the environmental conditions, leading to maladaptation (Ghalambor et al., 2007). Thus, plants with higher plasticity could develop a better competitive ability under climate change. However, the environmental conditions vary within the species range, which create the potential for local adaptation and a variety of amplitudes in the expression of plasticity due to species origins (Vitasse et al., 2013; Valladares et al., 2014).

Phenotypic plasticity could enable genotypes to develop specific reaction norms under environmental changes, thus buffering the rapid growth condition changes and facilitating future genetic variation (Holloway, 2002; Sultan, 2004; Nicotra et al., 2010). The degree of plasticity depends on the variability of environmental conditions (Churkina et al., 2005; Vitasse et al., 2009a; Vitasse et al., 2009b). Wide inter-annual variability in environmental conditions may promote higher plasticity at the individual level to cope with the unstable conditions and produce higher intra-specific trait variations at the population level (Rubio de Casas et al., 2008; Kumordzi et al., 2019; Cardou et al., 2022). However, under stable conditions, there is a tendency for populations to exhibit reduced plasticity (Chevin et al., 2010; Matesanz et al., 2010; Valladares et al., 2014). Compared to the center of the distribution, marginal populations are generally more isolated and show higher plasticity (Valladares et al., 2014). This divergent plasticity shows a deviating sensitivity to environmental factors, indicating a higher ability of marginal populations to cope with changing environmental conditions.

Plant phenology is the study of periodically recurring patterns of growth and development during the year, such as the start (leaf unfolding) and end (leaf coloring) dates of growing seasons (Lieth, 2013; Piao et al., 2019; Inouye, 2022). Numerous efforts have been made to incorporate phenology into climate change models to better understand the response of trees (Chuine and Beaubien, 2001; Badeck et al., 2004; Cleland et al., 2007; Rosbakh et al., 2021). For example, climate warming leads to earlier sprouting and longer growing season, potentially increases net carbon uptake of the ecosystem (Keenan et al., 2014). Also, the temperature has been demonstrated to be a driving factor of ecotypic variation (Silvestro et al., 2019). The developmental phase from dormancy to activity period is one of the most critical transitions in the bud tissues (Jewaria et al., 2021). The breaking of endodormancy in spring requires efficient accumulation of cold temperature in autumn and winter (chilling) (Singh et al., 2016). After that, heat in spring (forcing) and photoperiod could strongly affect the further reactivation of bud break and growth (Chen et al., 2018; Huang et al., 2020). Understanding the adaptive capacity of phenological responses to climate fluctuations, particularly changes in chilling and forcing factors, is crucial for predicting the prospects of species in the context of climate change.

As an important economic species in eastern North America, sugar maple (*Acer saccharum* Marsh.) has been studied to predict the response to climate change (Putnam and Reich, 2017). A previous study showed that phenotypic plasticity plays a dominant role in regulating the bud phenology of sugar maple populations (Guo et al., 2023). However, the geographical pattern of plasticity and the possible climatic drivers are less known. In this study, we examined the intra-specific climatic variation and phenological plasticity of sugar maple seedlings from 11 Canadian origins, which were planted in two common gardens at the central and northern edges of their distribution range. We expect that sugar maple originating from the inland have higher phenotypic plasticity for bud break than those from coastal areas because of higher frost change frequency.

2 Materials and methods

2.1 Seed origins, seed collections, and common garden tests

This study examined open-pollinated progenies of sugar maple from 11 seed origins across the species' range in Canada (Figure 1; one half-sib family per seed origin). This area is included in the bioclimatic domains of deciduous and mixed forests of the northern temperate zone, which is dominated by both broadleaves and conifers (mainly *Acer saccharum* Marsh., *Acer rubrum* L., *Betula alleghaniensis* Britt., *Abies balsamea* (L.) Mill.).

The mean annual temperature among the seed origins ranged between 3.1 and 5.7°C, with the lowest recorded at seed origin 1 and the highest at seed origin 8 (Supplementary Table 1). Seed origin 1 represented the coldest location, with a minimum mean annual temperature of -10.9°C. Conversely, seed origin 6 exhibited the warmest conditions, with a minimum mean annual temperature of -9.0°C and a maximum mean annual temperature of 20.0°C (Supplementary Table 1). The range of mean annual temperature across the seed origins was 2.2°C. Additionally, it is worth noting that the mean annual temperature in Ripon was 4.5°C, and 3.2°C in Chicoutimi. Annual precipitation ranged from 1144 to 3385 mm, increasing from west towards the east.

2.2 Plant material

In April 2018, we used seed material from sugar maple populations to cultivate one-year-old seedlings in greenhouses. Subsequently, in the spring of 2019, these seedlings were transplanted into two common gardens located in Chicoutimi and Ripon (Quebec, Canada, Figure 1). Chicoutimi and Ripon are located at the central and northern edge of the natural distribution of sugar maple, respectively. The different growing conditions of two common gardens provided an experimental design that helped to study the effects of genetic variations and phenological plasticity in bud phenology. The trials were set up using a single-tree plot layout with a spacing of 3 m × 3.5 m. On average, between 6 and 10 seedlings from each seed origin were planted, resulting in a total of 145 and 173 seedlings in Chicoutimi and Ripon, respectively.

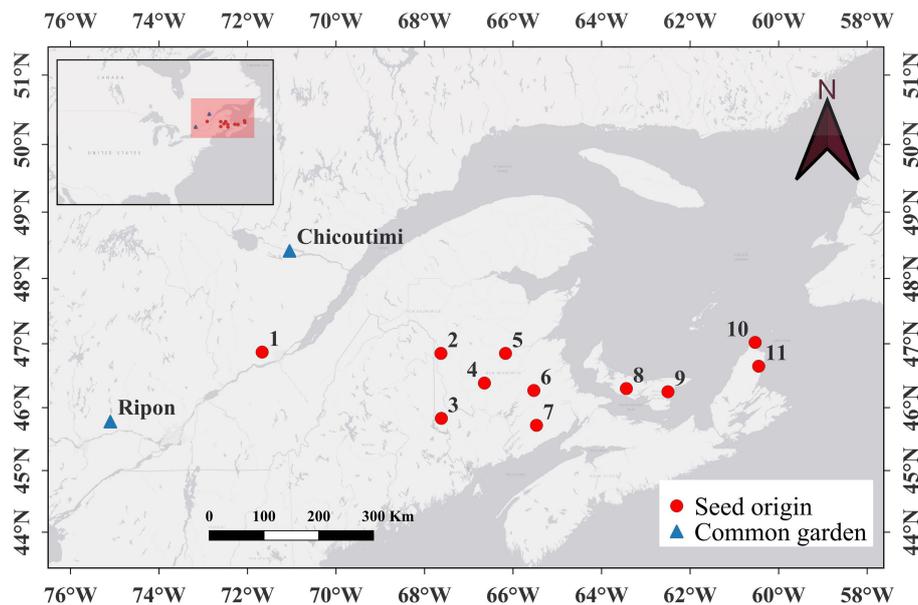


FIGURE 1

Locations of the 11 seed origins (represented by circles) of sugar maple. The triangles mark the locations of the two common gardens in Chicoutimi and Ripon.

2.3 Phenological observations

During mid-April to mid-June in 2020, we meticulously monitored bud and leaf phenology for all seedlings twice a week. Generally, the observed two-year-old seedlings had five buds. To ensure methodological consistency and reduce the influence of confounding factors in subsequent analyses, we deliberately selected and closely observed the apical bud, which is widely accepted and established practice in the field (Rosique-Esplugas et al., 2021). We recorded the progression of bud and leaf development, divided them into eight distinct phases, following the methodology outlined by Skinner and Parker (1994): (1) bud swell, characterized by reddish scales and an enlarging bud; (2) bud elongation, displaying a yellowish hue between the scales; (3) green tip stage, with light green tips and the area between the scales but the bud still closed; (4) bud break, featuring loosened scales but barely visible expanding leaf tips; (5) extended bud break, where the leaf bundle expanded beyond the scales but without separated leaves; (6) initial leaf emergence, marked by leaves starting to expand perpendicularly to the base of the bud; (7) initial leaf expansion, showcasing light green, small, and wrinkled leaves; and (8) full leaf expansion, with entirely flattened and expanded leaves. The onset of each phenological phase was determined as the first day (DOY, day of the year) when that specific phase was observed in each individual.

2.4 Statistical analyses

The daily minimum, maximum, and mean temperature for the year 2020 were obtained by extracting data based on the coordinates

of the common gardens from the ERA5 dataset using Google Earth Engine (Gorelick et al., 2017). Climatologies at high resolution for the earth's land surface areas (CHELSA) climate data include monthly temperature, precipitation, and derived parameter estimates at a spatial resolution of 30 arcsec from 1979–2013 (Karger et al., 2017). Four climatic variables, including frost change frequency (the number of events in which the minimum temperature or maximum temperature goes above or below 0°C), growing degree days (the annual cumulative sum of temperatures exceeding 0°C), growing season length (the number of days with temperatures exceeding 5°C, without snow cover and soil water available), and number of frost days (the annual count of days when the daily minimum temperature is less than 0°C) were downloaded from CHELSA to describe the annual trend and extreme conditions across seed origins and between common gardens. A Principal Component Analysis (PCA) was then performed to determine the contribution of each climatic variable to the total variance. All seed origins were classified into different groups using four climatic variables (frost change frequency, growing degree days, growing season length, and number of frost days) according to the results of the Partitioning Around Medoids clustering algorithm, the extension of the k-means clustering algorithm (Kaufman and Rousseeuw, 1987).

For each common garden, we calculated the average bud phenology for all individuals of the same seed origin, and we used the difference in leaf development between the two common gardens to illustrate population-level plasticity. The analysis of variance (ANOVA) was used to test the difference in plasticity among groups of seed origins based on the abovementioned cluster results. All statistical analyses were performed using R software (R Core Team, 2021).

3 Results

3.1 PCA and cluster results of the climate of the study sites

The average frost change frequency among the seed origins was 67 occurrences, ranging from the highest of 79 occurrences in seed origin 7 to the lowest of 50 occurrences in seed origin 10. The average growing season length was 176 days, with the longest and shortest also recorded in seed origin 7 and 10 (186 and 161 days, respectively). The mean growing degree days were 1570 days, with the longest days recorded in seed origin 7 at 1772 days and the shortest recorded in seed origin 11 at 1330 days. The average number of frost days was 154 days, ranging from a maximum of 171 days in seed origin 2 to a minimum of 135 days in seed origin 10 (Supplementary Table 2). PCA extracted two main principal components (PC), explaining 77.2% and 14.5% of the variability in climatic parameters for seed origins for PC1 and PC2, respectively. Frost change frequency was most strongly correlated with PC1 (-0.94) and had the highest contribution at 68.33%, indicating that frost change frequency was the primary influencing factor (Figure 2; Supplementary Table 3).

According to the K-medoids clustering results (Figure 2; Supplementary Figure 1), the seed origins 1-7 were classified as group 1, and the seed origins 8-11 were classified as group 2. Seed origins in group 1 had longer growing season length, higher number of frost days, and higher frost change frequency than those in group 2 close to the Gulf of Saint Lawrence River.

3.2 Bud and leaf phenology difference between two common gardens

Bud and leaf phenology occurred earlier in Ripon compared to Chicoutimi (Figure 3). Phases 1-3 occurred on DOY 121, 124, and 127 in Ripon, 10 days before Chicoutimi (DOY 131, 134, and 137). The differences between sites for the phases 4-6 were 9, 6, and 3 days, respectively. Phases 7 and 8 differed by 1-4 days between the two common gardens. The differences in bud phenology between the two sites gradually diminished as the phases progressed. Overall, the leafing period in Ripon spanned 30 days, whereas it covered 23 days in Chicoutimi.

3.3 Phenological plasticity on the population level

The seed origins with the highest or lowest phenological plasticity varied across the eight developmental phases. Seed origin 3 exhibited the highest variation for phases 1 and 2, with an 11-day difference between the two common gardens (Supplementary Table 4). In phases 3-5, seed origin 1 showed the most significant difference of 8-13 days between the two common gardens, while seed origin 7 showed the most significant difference in phases 6-8, with a 6-9-day gap. Additionally, seed origin 10 demonstrated the lowest variation in phase 1, with a 9-day difference between the common gardens.

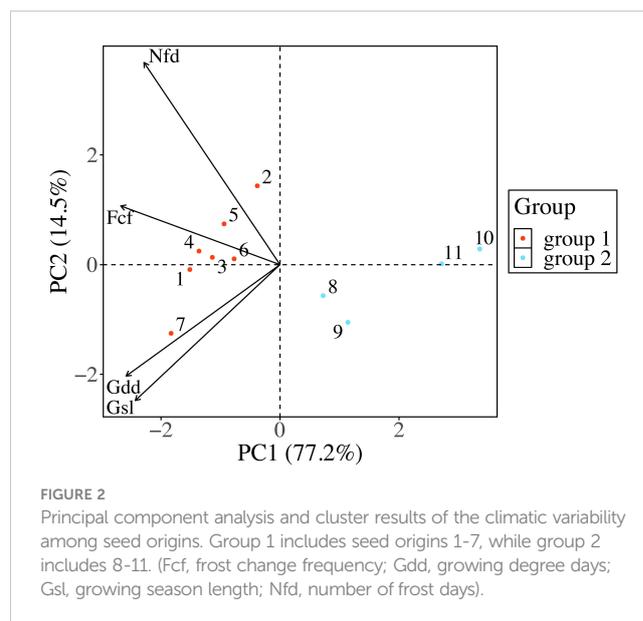


FIGURE 2

Principal component analysis and cluster results of the climatic variability among seed origins. Group 1 includes seed origins 1-7, while group 2 includes 8-11. (Fcf, frost change frequency; Gdd, growing degree days; Gsl, growing season length; Nfd, number of frost days).

For phases 2-4, seed origin 8 exhibited the least variation, with a 7-8-day difference between the gardens. In phases 5-7, seed origin 9 had the smallest difference, ranging from 0-4 days. Seed origin 3 showed the lowest variation in phase 8, with no difference between the common gardens. Almost for all phases, the phenological variation of seed origins in group 1 was higher than that in group 2 (Figure 4). However, the difference was significant only for phases 1-3 ($p < 0.05$; Figure 4; Supplementary Table 5).

4 Discussion

4.1 Comparison of bud phenology in two common gardens

Buds of sugar maple occurred earlier in the southern common garden (Ripon). In our study, the mean spring temperature (April-May) in 2020 in Ripon was 4.6 °C, higher than that in Chicoutimi (2.4 °C). Under warmer spring conditions, sugar maple may be more effective in accumulating heat to achieve the threshold of forcing condition, leading to an advanced break of dormancy (Myking and Heide, 1995; Fu et al., 2013). Our results are consistent with previous studies conducted in temperate and boreal ecosystems (Fu et al., 2014; Zani et al., 2020; Vitasse et al., 2022). For example, the timings of leaf unfolding of *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. advanced by 5.7 days for each additional degree Celsius, as observed across five common gardens (Vitasse et al., 2010). Similarly, the buds of *Populus fremontii* in Arizona flushed earlier when the trees grow in the common gardens located in warmer regions (Cooper et al., 2019; Gao et al., 2023).

The variability of DOY between Ripon and Chicoutimi decreased for the later leafing stages (7 and 8). The difference in photoperiod is an essential factor for spring phenology. Day length during bud burst (phase 1) was 15.0 h in Chicoutimi, which was longer than that recorded in Ripon (14.1 h) due to the different latitudes and timings of growth reactivation between common gardens (Guo et al., 2022). A

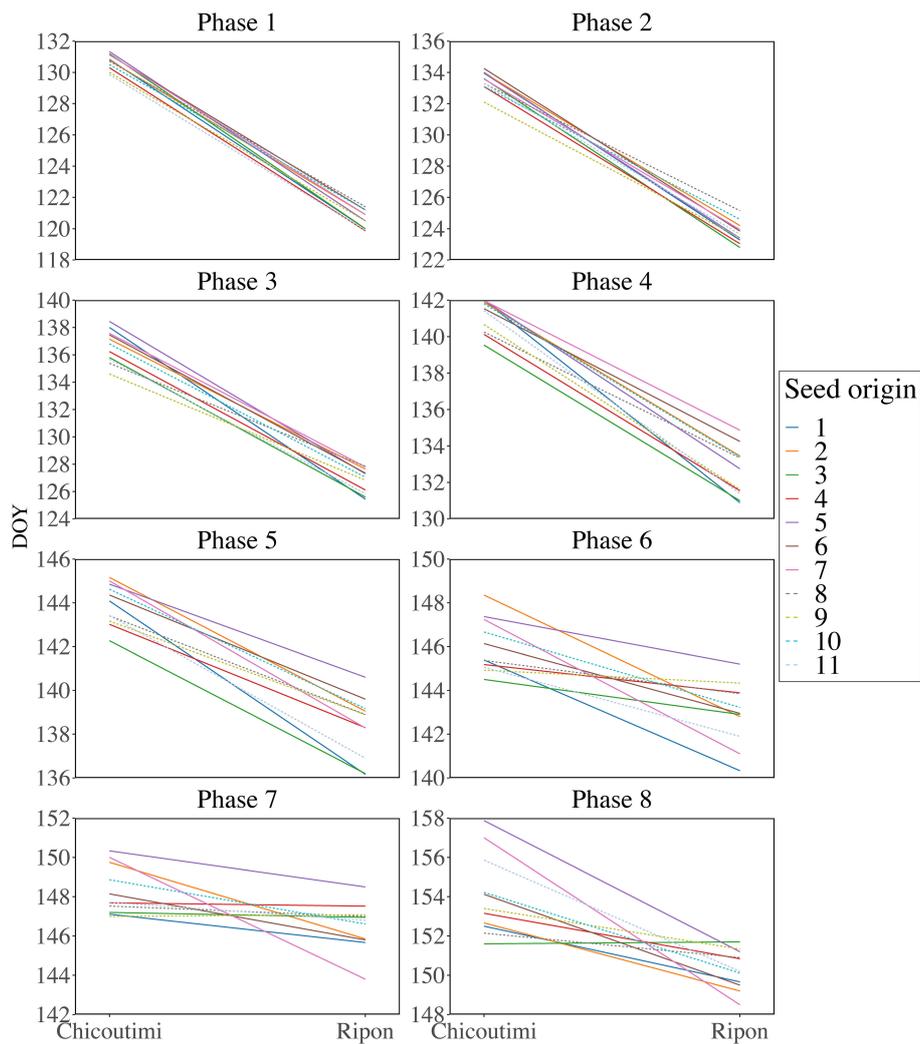


FIGURE 3 Reaction norm of phenological plasticity of sugar maple in the two common gardens. The solid line represents group 1 (seed origins 1-7), while the dashed line represents group 2 (seed origins 8-11).

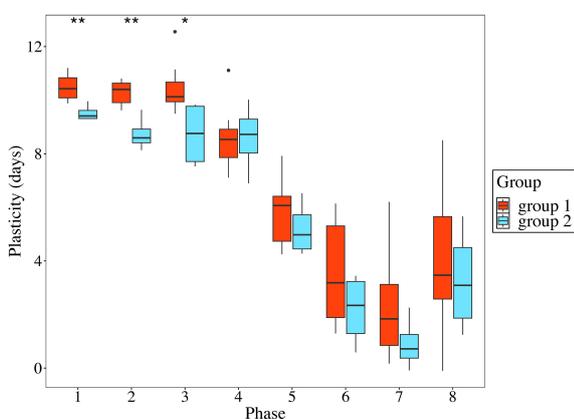


FIGURE 4 The phenological variations of sugar maple seed origins between two groups. Significance levels are * < 0.05 , and ** < 0.01 .

more extended photoperiod could have facilitated bud development (Way and Montgomery, 2014), thus resulting in similar timings of full leaf expansion. A previous study demonstrated that sugar maple leafing benefits from a longer day length, and photoperiod can outweigh the delaying effects of colder springs (Ren et al., 2020). However, the similar ending of leaf expansion in the two common gardens remains partially unexplained and could result from the heat damage events occurring during the studied year. Thus, a better understanding of the impact of current weather on leaf development is needed and requires long-term monitoring of bud phenology in the two common gardens.

4.2 The different degrees of plasticity between inland and coastal areas

We found that inland sugar maple showed a higher plasticity at the beginning of leaf development compared to those in coastal regions.

In our study conducted under continental climatic conditions, sugar maples were exposed to a wide inter-annual weather variability, mainly for temperature. This temperature variation is a critical limiting factor influencing bud phenology during the spring season (Guo et al., 2020). Also, with a higher number of frost days and frost change frequency, sugar maple originating from inland areas may face an increasing risk of frost damage. In order to mitigate the risk of frost damage, enhancing phenological plasticity becomes crucial. This adaptation allows for a rapid response to weather fluctuations and extends the leafing period, thereby improving the available carbon fixation period. (Körner and Basler, 2010; Vitasse et al., 2014). Previous studies have demonstrated that plasticity correlates with climatic variability, and species experiencing a wider climatic fluctuation also exhibit higher plasticity (Van Buskirk, 2008). For example, plasticity for plant performance strongly correlates with inter-annual precipitation variability of original sites (Pratt and Mooney, 2013). Also, phenotypic plasticity in final shoot height and maximum biomass per shoot increases towards the higher latitudes due to the range of climatic variability increases with latitude (Ren et al., 2020). Our study demonstrated that plants from the inland areas exhibit a higher plasticity, which may help them to respond suitably to rapid changes in climate.

Climate might affect the phenology of different seed origins to varying degrees. It was proved that under climate change, instead of the assumption of homogeneously plasticity across a species' range, the model given the factor of population differentiation could increase the forecasts of species range shifts (Valladares et al., 2014). In our study, the higher plasticity was observed in inland areas, which showed a higher variability in a given environmental condition. Compared with coastal areas, sugar maple originating from inland areas may have more advantages to cope with the changing climate. Therefore, future studies on the effects of simulated climate change on species phenology should consider specifically the different degrees of phenological plasticity within the same species.

5 Conclusion

Phenotypic plasticity plays a vital role in the response of plants to the environment, whose changes are critical for the survival of individuals and local populations. In this study, we demonstrated that due to the higher frost change frequency, sugar maple originating from inland areas showed higher plasticity of bud burst than those from coastal areas at the beginning of leaf development. We predict that in an assisted migration context, sugar maple originating from inland may rapidly acclimate its phenology to the local environment. Thus, quantifying the climatic conditions especially the frost change frequency experienced by specific population, may increase the predictive accuracy of its acclimation potential, and help to define its potential in assisted migration efforts.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

YZ: Formal analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. CB: Writing – review & editing. XG: Conceptualization, Data curation, Investigation, Methodology, Supervision, Validation, Writing – review & editing. VM: Formal analysis, Validation, Writing – review & editing. MK: Formal analysis, Validation, Visualization, Writing – review & editing. SD: Data curation, Investigation, Writing – review & editing. SR: Conceptualization, Data curation, Investigation, Methodology, Validation, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1320745/full#supplementary-material>

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