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Advancing frost dates have reduced frost risk among most North American angiosperms since 1980

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Abstract

In recent decades, the final frost dates of winter have advanced throughout North America, and many angiosperm taxa have simultaneously advanced their flowering times as the climate has warmed. Phenological advancement may reduce plant fitness, as flowering prior to the final frost date of the winter/spring transition may damage flower buds or open flowers, limiting fruit and seed production. The risk of floral exposure to frost in the recent past and in the future, however, also depends on whether the last day of winter frost is advancing more rapidly, or less rapidly, than the date of onset of flowering in response to climate warming. This study presents the first continental-scale assessment of recent changes in frost risk to floral tissues, using digital records of 475,694 herbarium specimens representing 1,653 angiosperm species collected across North America from 1920 to 2015. For most species, among sites from which they have been collected, dates of last frost have advanced much more rapidly than flowering dates. As a result, frost risk has declined in 66% of sampled species. Moreover, exotic species consistently exhibit lower frost risk than native species, primarily because the former occupy warmer habitats where the annual frost-free period begins earlier. While reducing the probability of exposure to frost has clear benefits for the survival of flower buds and flowers, such phenological advancement may disrupt other ecological processes across North America, including pollination, herbivory, and disease transmission.

KEYWORDS
climate change, flowering phenology, frost risk, herbarium specimens, plant ecology

1 | INTRODUCTION

In recent decades, advances in the final frost dates of winter or early spring have been observed throughout North America while advances in the timing of flowering have been documented in many angiosperm taxa (Abu-Asab et al., 2001; Inouye, 2008). In response to recent climate warming, the flowering times of many species have changed, which may alter the risk of reproductive structures being exposed to spring frosts (Inouye, 2000). Exposure of reproductive tissues to frost is hazardous for many plant species, as floral tissues are often the most vulnerable to frost damage, and the exposure of

floral tissues to frost or freeze events can reduce pollen and seed production or result in reproductive failure (Gezon et al., 2016; Inouye, 2008; Pardee et al., 2018; Sakai et al., 1981). Over multiple generations, reductions in reproductive success due to increases in frost exposure may lead to progressive declines in local abundance, potentially resulting in local extirpation (Inouye, 2000). Accordingly, the ability to initiate and to complete flowering and fruiting without exposure to frost or freeze events plays a major role in determining the geographic range of many species (Chuine & Beaubien, 2001).

Previous studies have predicted that progressive warming could increase the risk of frost damage to floral tissues for many species if,

in response to warming, flowering times advance more rapidly than the date of last frost, defined as the date that marks the beginning of that portion of each year during which daily minimum temperatures remain above 0°C (Gim et al., 2018; Kimmins & Lavendar, 1992; Ma et al., 2019; Vitasse et al., 2018; Figure 1). This pattern has been particularly well documented among shrub and forb species whose flowering time is primarily driven by snowmelt (Inouye & McGuire, 1991; Pardee et al., 2019; Sherwood et al., 2018; Wheeler et al., 2014), resulting in reductions to annual flower and seed production (Inouye, 2008; Inouye et al., 2002). Conversely, warming climates may advance the date of last frost more rapidly than plant species advance their flowering times, thereby reducing their risk of frost exposure (Long & Hutchin, 1991; Sherwood et al., 2018); this pattern has been detected among 14 European angiosperm species (Bennie et al., 2010; Scheifinger et al., 2003). Warming conditions may also delay bud break and flowering of those taxa that require an extended period of winter chilling (vernalization) to break dormancy, protecting them from flowering prior to the onset of the frost-free period (Asse et al., 2018; Guo et al., 2019).

While the phenological responses of flowering time to climate warming have been measured in thousands of species (Bertin, 2015; Park & Mazer, 2018), and broad-scale temporal reductions in frost risk to developing leaves have been detected among North American trees (Zohner et al., 2020), no large-scale examinations of shifts in frost risk have yet been conducted on a sufficient array of taxa to detect or to characterize general trends in a continental flora. As a result, the general effects of recent climate change on the risk of frost exposure to floral tissues remain largely unknown. Additionally, flowering phenology has previously been documented to be evolutionarily conserved among co-occurring taxa that are closely related (Davies et al., 2013). Given that exposure to frost depends on a species' phenology at a given location, it is also possible that frost risk is phylogenetically conserved. However, no systematic examination of the degree to which frost risk is phylogenetically conserved among closely related taxa has yet been conducted.

To address these gaps, we conducted the first continent-wide assessment of frost risk by evaluating the flowering times (relative to the date of the last frost in the year and site of collection) of 1,653 species collected in flower from 1920 to 2015 and represented by 475,694 digital records of herbarium specimens collected throughout North America, with specimens primarily concentrated in the Western and Eastern United States. By comparing rates of temporal changes in dates of last frost experienced by each species among the sites where it was sampled to rates of temporal changes in flowering date from 1920 to 2015, we determined that, for most species, the advancement of the last frost date has outpaced the advancement of flowering date, resulting in a reduction in the risk of floral exposure to frost. Furthermore, this pattern persisted across regions that historically experienced both early and late dates of last frost. We also conducted a phylogenetically informed analysis to determine whether,
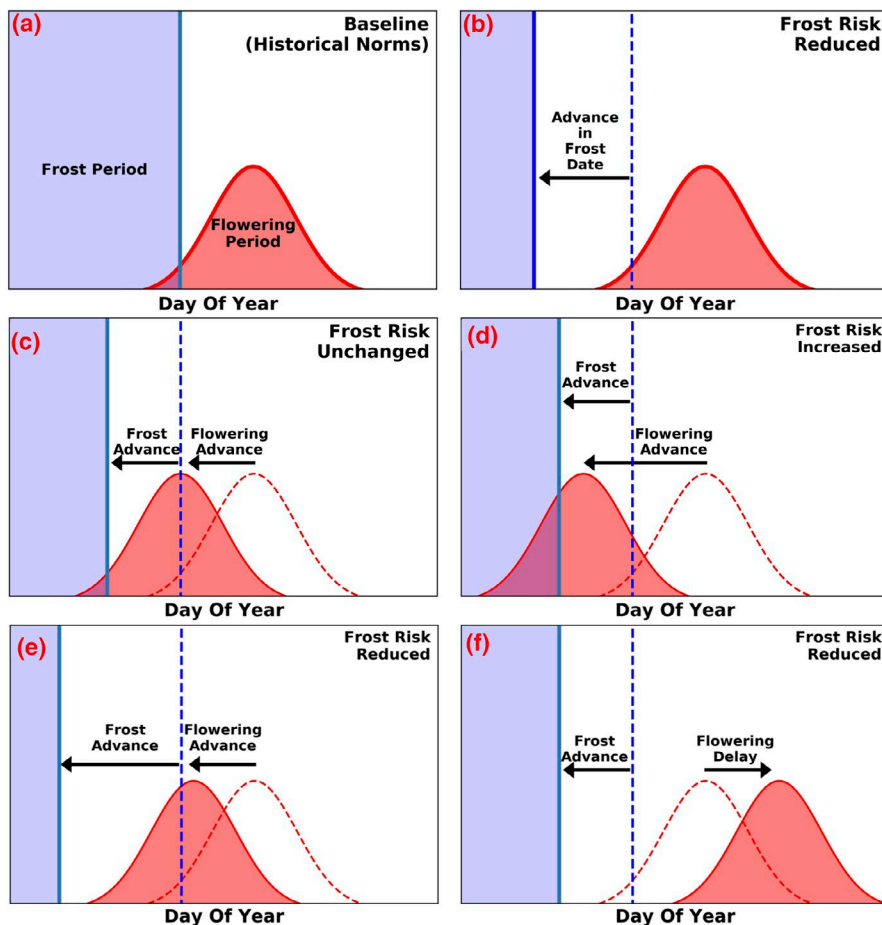
FIGURE 1 Alternative scenarios by which the historical relationship between flowering time and the date of last frost for a given species may become disrupted. A hypothetical relationship between the period of frost versus the distribution of flowering times among individuals of a given species at a given location is illustrated in (a). In (b), advances in the date of last frost occur without corresponding advances in flowering time, reducing frost risk; in (c), advances in the date of last frost are matched by advances in flowering time, maintaining a constant frost risk; in (d), advances in flowering time exceed advances in the date of last frost, leading to increased frost risk; in (e), advances in the date of last frost exceed advances in flowering time, leading to reduced frost risk; in (f), advances in the date of last frost co-occur with delays in flowering time, leading to reduced frost risk. Scenario (e) corresponds to the pattern observed in most species analyzed here [Colour figure can be viewed at wileyonlinelibrary.com]

as has been found for flowering time itself (Davies et al., 2013), the risk of exposure to frost exhibits a phylogenetic signal. Finally, we compared the degree of frost risk experienced by native versus exotic species, and evaluated whether the relatively low risk exhibited by the latter is due to differences in the mean climate conditions they occupy or to differences between natives and exotics in the degree of phenological change that they exhibited.

2 | MATERIALS AND METHODS

2.1 | Phenological data

Phenological data pertaining to flowering times in this study consisted of 475,694 specimen records of angiosperm species collected in flower. These data were derived through filtering of a larger dataset consisting of 894,392 specimen records accessed from the digital archives of 72 herbaria (see Data S1 for full listing), and cleaned using several criteria described below. Estimates of mean flowering date from herbarium specimens have been reported to provide accurate estimates of species' flowering times (Primack et al., 2004) and have yielded estimates of phenological change similar to those derived from in situ observations of living plants across both temporal (Bertin, 2015; Lavoie & Lachance, 2006; Primack et al., 2004) and spatial climate gradients (Bowers, 2007; Houle, 2007).

To ensure the quality of the data used in this study, specimens were included in the dataset analyzed here only if, at the time of digitization, herbarium personnel had: verified that the specimens were collected when in flower; recorded GPS coordinates of the location from which the specimen was collected; and provided the precise date of collection (including month, date, and year). Only those specimens that were explicitly recorded as being in flower within either the DarwinCore "reproductivecondition" or "lifestage" fields of their source's database were included in this study. Specimens that were listed only as "buds present" or "fruiting" were not considered to be in flower for purposes of this analysis, as some perennial species collected during the winter may be described as "buds present" when buds are completely dormant, or may retain aborted or unripe fruits that cannot be distinguished from recently matured fruits preserved on herbarium specimens. The taxonomic nomenclature used to identify all specimens, which sometimes changed over time or differed among collectors, was standardized according to The Plant List (www.theplantlist.org) and TROPICOS (www.tropicos.org) using the Taxonomic Name Resolution Service iPlant Collaborative, Version 4.0 (Boyle et al., 2013, Accessed: 4 April 2017; http://tnrs.iplantcollaborative.org) and subsequently filtered to eliminate all taxa not identified to species level within the megaphylogeny used by the PhyloMaker package in R (Zanne et al., 2014), which similarly used a standardized taxonomy derived from TPL and TROPICOS (Jin & Qia, 2019; Smith & Brown, 2018; Zohner et al., 2020). To avoid pseudoreplication, duplicate specimens (i.e., specimens of a given species collected on the same date and from identical locations) were also removed. Each species was then classified as native or exotic based on its characterization in the USDA Plants Database (USDA, 2006).

The resulting dataset included 475,694 specimens representing 1,653 species distributed throughout North America (Figure 2a). The date of last frost (i.e., the date that marks the beginning of the portion of each year during which temperatures remain above 0°C) at the site and year of each collection event, as well as each collection site's long-term mean date of last frost (based on 1901–1990 climate averages), were estimated using the ClimateNA v5.51 software package, available at http://tinyurl.com/ClimateNA (Hamann et al., 2013).

2.2 | Estimating frost risk

In this study, we calculated the frost risk of each sampled species using annual estimates of the date of last frost at each collection site obtained from ClimateNA version 5.5.1. Frost risk of each species was defined as the proportion of its specimens collected in flower before the date of last frost in the years and locations in which they were collected. Frost risk in this context does not invariably predict the risk of reproductive damage, which depends not only on species- and population-specific cold tolerances, which are undocumented for most taxa (Tryon & True, 1964), but also on microclimate conditions that cannot be easily incorporated into continental-scale datasets, such as humidity, wind speed, and recent precipitation (Augspurger, 2011; Smith, 2019). Nevertheless, temperatures of 0°C have been documented to damage floral tissues of
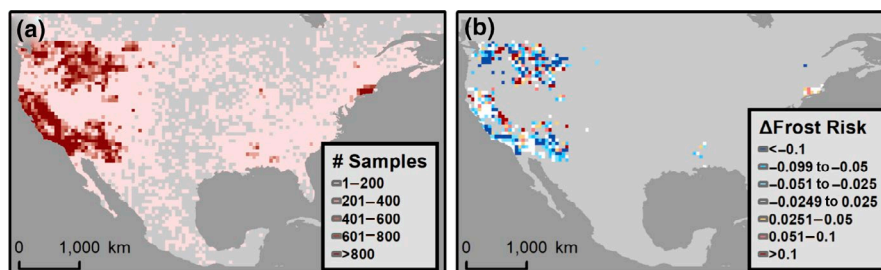
FIGURE 2 (a) Spatial distribution of all herbarium specimens used in this study. (b) Mean differences in frost risk among specimens collected in each 0.5° cell within which >100 specimens were collected in flower both before 1980 and post-1979. Note that within each cell, these differences do not reflect changes in frost risk within any specific set of taxa, but rather the overall observed change in frost risk among all specimens observed within that cell across both time periods [Colour figure can be viewed at wileyonlinelibrary.com]

a wide variety of species (Vitasse et al., 2018), as radiative cooling often results in damage to floral tissues and emerging leaves under nighttime temperatures of 0°C even in species that otherwise remain hardy to subzero temperatures (Ducrey, 1998; Perraudin & Fellay, 1975). Thus, frost risk is used here as a standardized metric indicating the likelihood of exposure of floral tissues to frost or freeze events.

2.3 | Comparing current to historical frost risk

To estimate historical (pre-1980) frost risk for each species, we calculated the proportion of specimens of each species collected from 1920 to 1979 that were collected prior to the date of last frost at the site and year of their collection. To estimate recent (1980–2015) frost risk, we similarly calculated the proportion of specimens of each species collected from 1980 to 2015 that were collected prior to the date of last frost at the site and year of their collection (Table S1).

To ensure that a sufficient number of observations of each species were available to produce meaningful estimates of frost risk within both periods, we eliminated all species that were not represented by at least 50 specimens both (a) prior to the year 1980 and (b) after the year 1979.

The year 1980 was selected as a breakpoint for these data as it has previously been identified by the Intergovernmental Panel on Climate Change as the year after which global land temperatures rose consistently above the 1961–1990 normal (Alley et al., 2007; Hartmann et al., 2013).

We then tested for significant differences in mean estimated frost risk between historical (1920–1979) and recent (1980–2015) time periods across all taxa by conducting a comparison of the pre-1980 and the 1980–2015 frost risk estimated for each species using a Wilcoxon paired rank test. It should be noted that some late-spring and summer-flowering species were not exposed to frost within the duration of this study, or were exposed to frost only rarely. However, to avoid the inherent biases that would result from selectively including only those species that were exposed to frost (some of which may have never experienced frosts prior to 1980), all species were included in this analysis regardless of frost exposure.

The number of specimens of each species that were collected prior to 1980 often differed from the number collected post-1979, as did the mean frost date normals of the locations from which those specimens were collected. This difference in sampling had the potential to bias estimates of the change in frost risk between these two periods. We therefore conducted a multiple regression to test whether significant differences in frost risk between pre-1980 and 1980–2015 samples persisted after controlling for variation in (a) the mean flowering dates among species, (b) the number of specimens of each species that were collected pre-1980 and post-1979, and (c) the mean normal frost dates of the locations from which specimens were collected pre-1980 and post-1979. In this analysis, frost risk was the dependent variable, while species-specific mean flowering dates, species-specific mean frost date normals (both

pre-1980 and post-1979), and the time period of collection (i.e., pre-1980 or post-1979) were treated as independent variables. Pre-1980 values for each species were distinguished from post-1979 values using a categorical variable coded as 0 for pre-1980 values, and 1 for post-1979 values (Table S2).

2.4 | Comparing directional changes over time in phenology and dates of last frost

We complemented our assessment of historical versus current frost risk by comparing the magnitude of directional change over time in phenology among species to the change in dates of last frost (henceforth "DLF") within their ranges. We estimated rates of phenological change over time (Days/Year) using a random-slope mixed-effects model, which includes a random component in the coefficient of one or more covariates whose effects might differ across groups (across species, in this case). We included the day of year of flowering (DOY) of all specimens for each species i in year j and location k as the response (DOY_{ijk}) and year of collection of each specimen ($Year_j$) as a predictor, with random slopes reflecting species-level differences in flowering trends over time ($\beta_1 + v_{1i}$), where v_{1i} is a zero-centered, normally distributed random component of the coefficient for year. To control for potential changes in the spatial distribution of specimen collections within a species' range over time (and possible confounding effects with $Year_{ijk}$), we included the 1961–1990 DLF normal at the site of collection k of each specimen i as a fixed effect (DLF Normal$_k$ with coefficients β_2). We also included species-, genus-, and family-level random intercepts to account for taxonomic differences in mean flowering time (α_{1i}, α_{2m}, and α_{3n}, respectively).

$$DOY_{ijk} \sim \alpha_{0i} + \alpha_{1m} + \alpha_{2n} + (\beta_1 + v_{1i}) \times Year_j + \beta_2 \times DLF\ Normal_k. \quad (1)$$

To quantify directional changes in dates of last frost over time, we first standardized DLF relative to historical DLFs in each site of specimen collection. To do this, we calculated DLF anomalies as the difference between observed dates in the year and site of collection and the 1961–1990 DLF normal for that site. Consequently, positive and negative values of the anomalies, respectively, indicate later-than-average and earlier-than-average dates of last frost for a given year and location. We then calculated directional shifts in DLF within the range of each species using the random-slopes mixed-effects model in Equation (1), but using DLF anomalies in the year and site of specimen collection as a response instead (DLF Anomaly$_{ijk}$; Equation 2).

$$DLF\ Anomaly_{ijk} \sim \alpha_{0i} + \alpha_{1m} + \alpha_{2n} + (\beta_1 + v_{1i}) \times Year_j + \beta_2 \times DLF\ Normal_k. \quad (2)$$

We transformed the units of rates of change in both DOY and DLF to days per decade by multiplying the coefficients for Year$_{ijk}$ from Equations (1) and (2) by a factor of 10. We then tested for differences in mean changes over time in DOY and in the date of last

frost using a non-parametric Mann–Whitney *U* test. All mixed-effects models in this study were implemented using the "lme4" package version 1.1-24 in R (Bates et al., 2015; R Core Team, 2019).

Freezing tolerance differs among species (Thomashow, 1998), and temperatures of 0°C might not constitute damaging frost events for some taxa. To our knowledge, no high-spatial-resolution gridded climate product spanning our study period provides dates of last frost defined using temperature thresholds other than 0°C. Consequently, we were not able to directly quantify changes in frost risk over time when defining frost risk using temperature thresholds other than 0°C. Instead, we assessed whether temporal changes in the date of last occurrence of alternative temperatures below 0°C were similar in direction and magnitude to temporal changes in the date of last occurrence of 0°C temperatures. To do so, we obtained data from 801 weather stations in the World Meteorological Organization network across North America to quantify rates of temporal change in DLFs defined using 0°C, –1°C, –2°C, –3°C, and –4°C. We then assessed whether directional changes over time in DLF defined using 0°C thresholds agreed in magnitude and direction with changes over time in DLF for other temperature thresholds using simple linear regression (see Figure S2 for further methodological detail). Weather station data were obtained using the "rnoaa" package v. 1.1.0 in R (Chamberlain, 2020).

2.5 | Comparing past and present frost risk among native and exotic plants

To determine whether frost risk differs between native versus exotic species, and whether recent climate changes have differentially impacted the frost risk of native (*n* = 1,503) versus exotic (*n* = 137) species, we calculated the mean frost risk for native and exotic species both pre-1980 and from 1980 to 2015. Note that of the 1,653 species evaluated in this study, 13 could be considered as either native or exotic depending on where in North America they were sampled; these species were excluded from this portion of the analysis. As the variances in frost risk were found to be similar among native and exotic species both pre-1980 ($F_{1,1638}$ = 3.119, *p* = .78) and from 1980 to 2015 ($F_{1,1638}$ < 1.234, *p* = .267), differences in frost risk between native and exotic species were then compared one-way ANOVA tests. As Shapiro–Wilk's tests indicated that shifts in frost risk between pre-1981 and post-1980 time periods were not normally distributed (*W* = 0.890, *p* < .001, *df* = 1,651), Wilcoxon paired rank tests were used in preference to classical t-testing to determine whether significant differences in frost risk were observed pre-1980 versus 1980–2015 among either native or exotic species.

To determine whether native and exotic species differed in (a) their mean flowering dates, (b) the mean dates of last frost at the habitats from which they were collected, (c) their mean pre-1980 frost risk, or (d) their post-1979 frost risk, we evaluated whether significant differences existed between native and exotic species with respect to each of these parameters using Mann–Whitney rank tests (Table S3). As exotic species were found to inhabit sites with earlier mean dates of last frost, it was also necessary to determine whether the differences in pre-1980 and post-1979 frost risk that we observed between native and exotic species could be attributed either to differences in mean flowering date between native and exotic species, or to differences in the date of last frost among the sites from which native and exotic species were collected. We therefore conducted multiple linear regressions (using Type III sums of squares for significance testing) to determine whether significant differences in either pre-1980 frost risk (Table S4) or post-1979 (Table S5) frost risk persisted between native and exotic species after controlling for variation in mean flowering date and in mean date of last frost among the locations from which each species was collected.

2.6 | Estimating the degree of phylogenetic conservation in frost risk

To determine whether clades differ with respect to mean frost risk or either the magnitude or direction of the change in their frost risk in response to recent climate change, we estimated Bloomberg's *K*, a metric of phylogenetic conservatism (Blomberg et al., 2003) for both (a) the pre-1980 frost risk for each species and (b) the magnitude and direction of changes in frost risk post-1979. Phylogenetic distances used in this study were calculated using angiosperm nodes aged according to the V.Phylomaker package in R (Jin & Qia, 2019), which was also used to estimate Bloomberg's *K*. Note that all genera used in this study were present in this tree, and that all genera were considered to be polytomies.

2.7 | Relating frost risk to temporal shifts in climate

To evaluate the relationship between frost risk and short-term climate deviations, we first calculated the mean frost risk for all species using a 20-year moving window average calculated at 1-year increments from 1920 through 2015. To eliminate those taxa for which sample density was too low to produce robust estimates of frost risk throughout the entire time series, only those taxa that were represented by a minimum of 40 specimens within all 20-year windows were included in this analysis. A total of 268 species distributed throughout North America met this criterion. Overall frost risk within each 20-year window was then assessed by calculating the mean estimated frost risk across these 268 species within that time period.

For each specimen that fell within a given 20-year window, we also calculated its annual deviation from the local normal date of last frost at the location in which it was collected (i.e., the difference between the last frost date in the year [and location] of specimen collection and the 1961–1990 normal frost date for the location). For each species, we then calculated both the frost risk and the mean annual deviation from normal dates of last frost among all the specimens represented within each 20-year window. Within each

successive 20-year window, we then calculated the mean frost risk and mean annual deviation from normal dates of last frost among all species.

We predicted that, among the 20-year windows, as the mean deviation between current and historical last frost dates increases (e.g., as the last frost dates become increasingly earlier in response to warming), the mean frost risk of the species in each successive 20-year window would also decline. To test for the effects of annual deviations in local dates of last frost on frost risk, we conducted a linear regression of the mean frost risk within each 20-year window on the mean annual deviation in the date of last frost within that 20-year window. To determine whether the relationship between frost risk and short-term climate deviations persisted across regions of North America characterized by both early and late dates of last frost, we separated taxa into two groups: (a) those for which the mean last frost date normal of the collection sites was earlier than the median last frost date normals across the entire dataset and (b) those for which the mean late frost date normal of the collection sites was later than the median last frost date normal. Having separated taxa that were predominantly sampled from locations characterized by early versus late last frost dates, we conducted the above analyses separately on each group of taxa.

3 | RESULTS

3.1 | Temporal change in last frost dates, flowering time, and frost risk

Across all 1,653 species that were well documented both pre-1980 and post-1979, mean frost risk has declined significantly since 1979, from 12.1% to 8.7% (Figures 2b and 3; Table S2), representing a ~28% reduction in frost risk. Moreover, the number of species that experience minimal frost risk (i.e., species for which <0.1% of all sampled specimens were collected in flower prior to the date of last frost) has increased from 234 species pre-1980 to 291 species post-1979 (Figure 3b). Of the 66.1% of species (1,092 of 1,653 species) that exhibited a reduction in frost risk post-1979, the mean frost risk declined from 16.0% to 9.7%. Conversely, of the 24.5% of species (405 of 1,653 species) that exhibited a post-1979 increase in frost risk over this pre-1980 frost risk, mean frost risk increased from 6.3% to 9.3% (Figure 3c), with only 77 species exhibiting a net increase in absolute frost risk greater than 5% (Table S1).

Median rates of directional change in dates of last frost over time were 3.3 times greater than rates of directional changes in flowering time among species (Figure 4). Consistently, while both frost dates and mean flowering dates among most species were found to occur earlier post-1979 than pre-1980, differences in the mean date of last
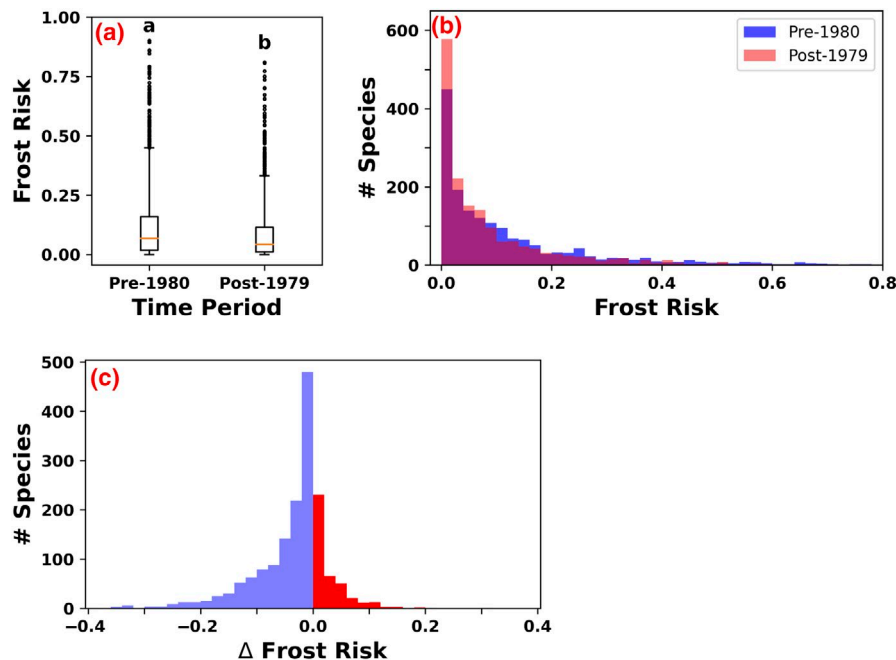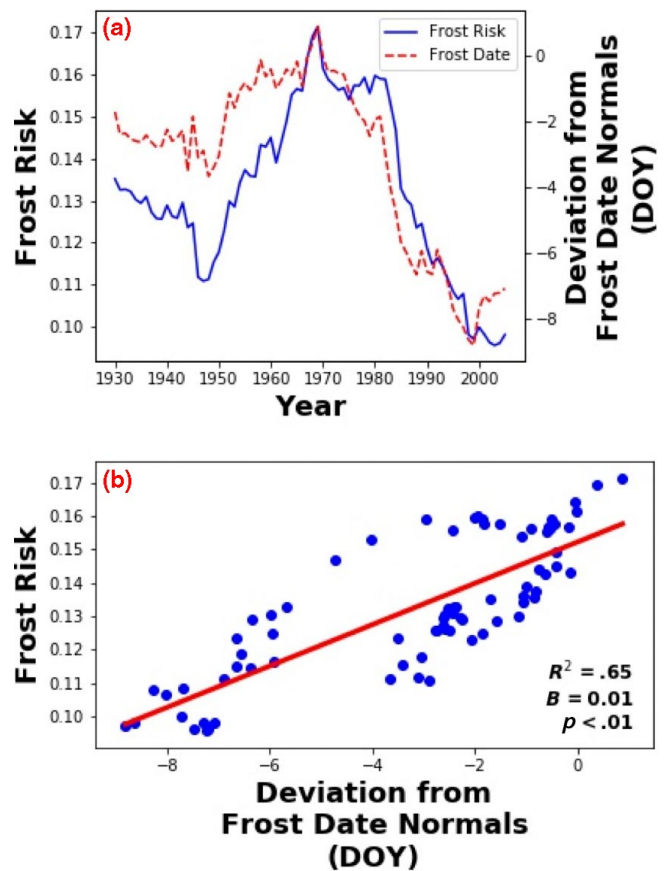

FIGURE 3 The mean and frequency distributions of frost risk among 1,653 species before 1980 and post-1979, and the distribution of the change in frost risk among all 1,653 species. (a) The mean frost risk of 1,653 species during each period; the red horizontal line denotes the median, the boxes represent the 25th–75th percentiles, and the whiskers extend to the 5th and 95th percentiles. Points outside the whiskers represent outliers. Significant reductions in mean frost risk were detected among the 1,653 species evaluated in this study, based on related samples Wilcoxon paired rank tests conducted in SPSS ($p < .001$, $df = 1,650$). This difference remained significant after controlling for variation in the number of specimens collected and in the frost date normals among all sites from which specimens were collected pre-1980 and post-1979 (Table S2). (b) The frequency distributions of frost risk among all species sampled before 1980 and after 1979. Blue bars indicate pre-1980 frost risk, while red bars indicate post-1979 frost risk. Purple indicates overlap between the two histograms. (c) The frequency distribution among species of the change in mean frost risk between samples collected prior to 1980 versus after 1979. Values of Δfrost risk <0 represent species for which the risk of floral exposure to frost declined between sampling periods (in red); values >0 represent species for which the risk of floral exposure to frost increased over time (in blue) [Colour figure can be viewed at wileyonlinelibrary.com]

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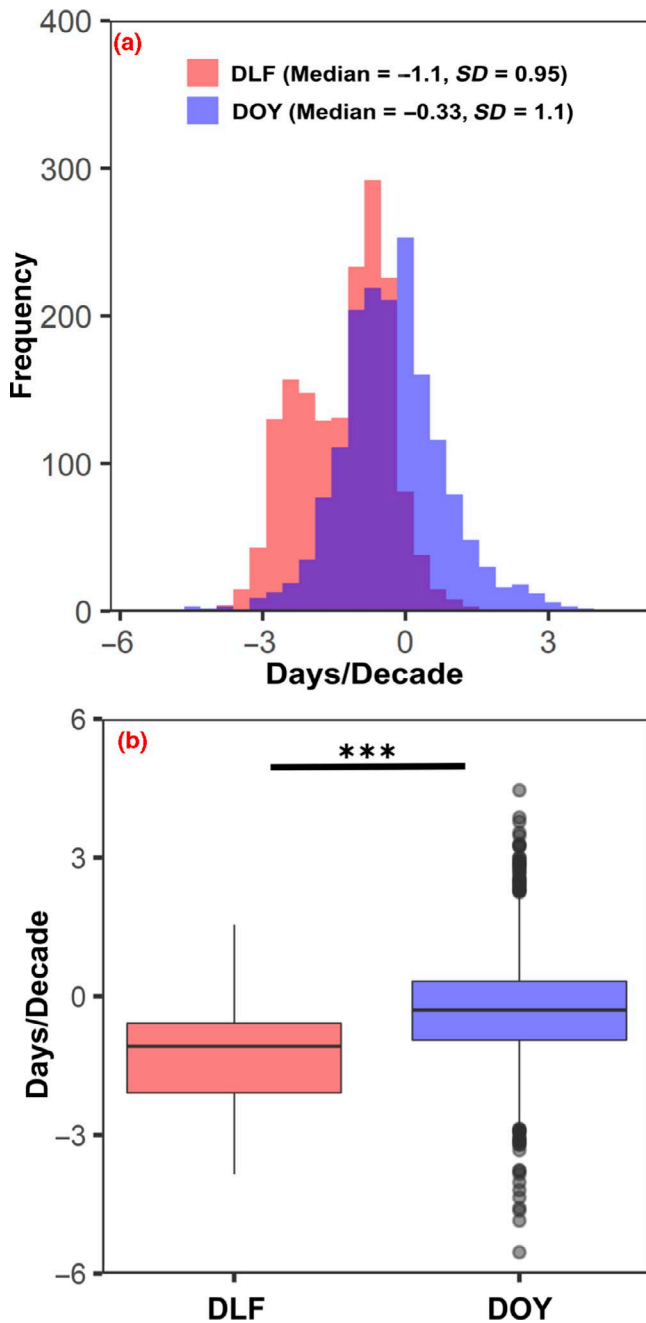
FIGURE 4 (a) Frequency distributions of directional changes in flowering time (DOY) and in date of last frost (DLF, defined as the date of last occurrence of 0°C temperatures in the year and site of specimen collection) within the range of 1,653 species throughout the continental US. (b) Boxplot comparison of the distribution of directional changes over time in DLF and flowering times among species. Significant differences in median directional changes were detected between dates of last frost and flowering time, with changes over three times greater for last frost dates than for flowering time. ***p < .001 [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 (a) Temporal variation in frost risk and in annual deviations from average last frost dates (defined as the mean frost date from 1901 to 1990) among all 20-year moving windows from 1930 to 2005, and (b) the linear relation between the mean frost risk and mean deviation from frost date normals among all 20-year moving windows. The midpoint of each 20-year window is used to represent its placement in time (e.g., the year 1930 indicates data drawn from 1920 through 1939). Negative values of the deviation from frost date normals indicate advances in mean frost date relative to local frost date normals across all specimens collected within each 20-year window. Only those species for which at least 40 specimens were collected in flower within all moving windows were included in this analysis, representing 268 species [Colour figure can be viewed at wileyonlinelibrary.com]

frost between reference periods were of greater magnitude than those in flowering phenology (Figure S1). Temporal changes in frost risk during this period are clearly associated with annual deviations from normal dates of last frost (Figure 5a). From 1970 to 2015, as the annual dates of last frost have generally become progressively earlier than the 1901–1990 mean last frost date, the mean frost risk has declined. Moreover, among 20-year moving windows from 1920 to 2015, advances in the frost-free date explain 65% of the observed variation in mean frost risk (Figure 5b). When examined separately, this pattern remained consistent among taxa occupying regions with late frosts and those occupying regions with early frosts, although late-frost regions experienced slightly greater reductions in frost risk during years experiencing earlier frosts (Figures S3 and S4).

Analysis of 801 weather stations across North America revealed that rates of change over time for the date of last occurrence of 0°C temperatures were highly correlated to changes in last occurrences for −1°C, −2°C, −3°C, and −4°C temperatures (Figure S2). The magnitude of change over time in last 0°C dates closely matched that of changes for last −1°C and −2°C dates of occurrence (Figure S2). In

turn, directional changes in dates of last frost defined using −3°C, and −4°C were of moderately lesser magnitude than changes in 0°C dates of last frost (on average, 69.2 ± 2.4% and 63.1 ± 2.6% of the magnitude of changes in 0°C dates of last frost, respectively; Figure S2).

3.2 | Phylogenetic signal for frost risk

Our statistical test for the degree to which frost risk is conserved (using Blomberg's K, which ranges from a value of 0.0, indicating no phylogenetic conservatism, to 1.0, and tests whether $K > 0$) among the species sampled here indicated that a significant but weak phylogenetic signal exists both in the magnitude of pre-1980 frost risk ($K = 0.04$, $p < .01$), and in the magnitude of change between pre-1980 and post-1979 frost risk ($K = 0.03$, $p = .05$). However, both of these properties exhibited less conservatism than would be predicted under a Brownian motion model of evolutionary change.

3.3 | Native versus exotic species

While frost risk was not found to be highly conserved evolutionarily among our sampled taxa, we detected significant differences in frost risk between exotic species ($n = 137$) and those that are native to
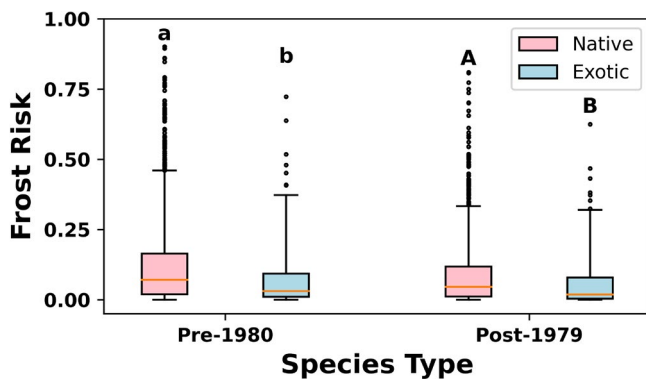
FIGURE 6 Mean frost risk among native and exotic species pre-1980 and post-1979. Red bars indicate the mean frost risk for 1,503 native angiosperm species; blue bars indicate frost risk for 137 exotic species. Center (horizontal) lines denotes the median values, the boxes cover the 25th–75th percentiles, and the whiskers extend to the 5th and 95th percentiles. Points outside the whiskers represent outliers. Related-sample Wilcoxon paired rank tests determined that frost risk among native species was significantly higher than among exotic species both pre-1980 and post-1979 ($p < .001$ in both cases). Although significant reductions between pre-1990 and post-1989 frost risk were detected among both native and exotic species based on related samples Wilcoxon paired rank tests conducted using IBM SPSS statistics software version 24 ($p < .001$ in both cases), a one-way ANOVA test found that native species exhibited greater reductions in mean frost risk than exotic species ($F = 3.09$, $df = 3,1647$, $p = .026$). Within each time period, a significant difference between the mean frost risk of native versus exotic species is indicated by distinct letters (a vs. b or A vs. B) [Colour figure can be viewed at wileyonlinelibrary.com]

North America ($n = 1,503$). Native species exhibited greater frost risk than exotics both pre-1980 and post-1979 (Figure 6; Table S3), although the former exhibit a greater temporal reduction in frost risk. The lower frost risk of exotics appears to be driven primarily by their occupation of habitats with earlier dates of last frost than those of native species ($t = 3.34$, $df = 1,638$, $p < .01$, Table S3). After controlling for variation among species in mean flowering time and in the mean date of last frost of all locations from which each species was collected, no significant differences were detected between native and exotic species in either pre-1980 ($t = −0.45$, $df = 1,636$, $p = .66$, Table S4) or post-1979 ($t = 1.20$, $df = 1,636$, $p = .23$, Table S5) frost risk. Thus, exotic species have historically experienced similar frost risk to native species occupying similar climates, but at the continent-wide scale, exotic species are more likely to occupy warmer climates, in which frost risk is typically lower (Figures S3 and S4).

4 | DISCUSSION

Frost risk throughout North America appears to have declined in response to recent climate change. Furthermore, advances in the date of last frost from 1920 to 2015 have typically outpaced advances in flowering phenology, despite advances in both frost dates and mean flowering dates among most species. We recognize that, for any given species, the frost risk during any particular time period could have been overestimated if the species was disproportionately sampled from sites where phenological advancement exceeded the advancement of the date of last frost, or underestimated if the species was disproportionately sampled from sites where the advancement of the date of last frost exceeded phenological advancement. However, the fact that these results remained consistent across so many taxa, and remained similar even when taxa occupying relatively warm regions (with early dates of last frost) and those occupying relatively cold regions (with late dates of last frost) were examined separately, indicates that such biases did not contribute significantly to the observed temporal changes in frost risk. Moreover, by constructing models in which we controlled statistically for spatial variation in the climate normals of each species' specimens sampled before 1980 versus after 1979, we further minimized this possibility. Thus, although it is well documented that early-flowering species, which flower in closest proximity to the last spring frost, are typically more phenologically sensitive to local temperature and show more rapid advances under warming conditions than late-flowering species (Cook et al., 2012; Dunne et al., 2003; Fitter & Fitter, 2002; Fitter et al., 1995; Mazer et al., 2013; Menzel et al., 2006; Miller-Rushing & Primack, 2008; Park et al., 2019; Scheifinger et al., 2003; Sparks et al., 2000; Wolkovich et al., 2012), this study indicates that early-flowering species do not typically advance more rapidly than the date of last frost throughout North America.

This pattern is relatively consistent among taxa, with less than 25% of sampled taxa exhibiting increases in frost risk post-1980. However, these results also indicate that, while significant phylogenetic signal

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for exposure to frost exists among the taxa sampled here, the degree to which frost risk is conserved among closely related taxa is minimal. Instead, similarities in frost risk among related taxa are more likely to be the result of convergent evolution in traits that are correlated with attributes that lead to exposure to frost rather than to strong phylogenetic conservatism (Blomberg et al., 2003). Thus, it does not appear that there are systematic differences among angiosperm clades with respect to the effect of recent warming on frost risk. Similarly, while a higher proportion of invasive species was observed in relatively warm regions (in which frost risk is typically lower), no systematic differences in frost risk were apparent between native and invasive taxa after controlling for differences in long-term frost dates across their ranges (Table S3). Thus, although previous studies have indicated that invasive species often exhibit more responsive phenologies (Willis et al., 2010; Wolkovich & Cleland, 2010) and weaker chilling requirements (Primack et al., 2015) than their native counterparts, this study indicates that more successful avoidance of frost risk is unlikely to be a systematic factor that determines the invasive ability of most exotics.

Dates of last frost have typically advanced more rapidly than dates of flowering for most of the 1,653 North American species sampled in this study (Figure 4), and temporal advances in the mean date of last frost are closely associated to reductions in frost risk (Figure 5). These results are supported by previous examinations of exposure to frost by growing leaves among North American tree species by Zohner et al. who also found reduced frost exposure in association with recent warming. Collectively, these results demonstrate that the risk of frost exposure and damage to both reproductive and vegetative tissues are systematically decreasing across North America.

The ecological implications of these reductions in frost risk may be complicated by variation among species in their resilience to frost-related damage and in the degree to which frost damage to floral tissues may reduce their reproductive success, both of which remain largely unknown for most species. We were not able to directly quantify changes in frost risk defined using temperature thresholds other than 0°C because, to our knowledge, no gridded products provide dates of last frost defined using a lower temperature threshold at high spatial resolutions and spanning our study period (1920–2015). However, weather station data revealed that rates of temporal change in dates of last frost defined using different temperature thresholds (i.e., 0 to −4°C) were highly correlated and of similar magnitude. Temporal changes in dates of last frost defined using thresholds of −3°C and −4°C were moderately lower in magnitude than rates of change for 0°C dates of last frost (~31% and ~37% lower, respectively). However, given that rates of change over time in dates of last frost at 0°C were more than three times greater than those in flowering time (Figure 4), the moderately slower rate of change of −3°C and −4°C dates of last frost likely outpaced changes in flowering time as well. Therefore, although the identity and exact proportion of taxa experiencing changes in frost risk over time might vary when using freezing temperatures more severe than 0°C to define frost, the general trend toward lower frost risk over time is likely

to be robust to different definitions of the temperatures that is likely to induce tissue damage.

In addition to direct effects of frost damage on vulnerable vegetative or reproductive tissues, the effects of these changes in frost risk on the survival and local abundances of many species will likely be mediated by a variety of factors. Some species may experience reduced herbivore damage as a result of lowered frost exposure (Little et al., 2017). Conversely, warmer temperatures may lead to increased exposure to pathogens and pests (Dantec et al., 2015) or to reduced survival due to intensifying summer droughts (Iler et al., 2019) or extended winter freeze–thaw cycles (Connolly & Orrock, 2015).

It should be noted that any herbarium-based study of this magnitude is susceptible to the criticism that it includes potentially faulty records, either because of differing biases among collectors in the timing and location of collection, or because of limited documentation of the error distances associated with georeferencing of each specimen. Previous examinations of herbarium collections have found, for example, that collection effort is often concentrated at locations that are easily accessed and may also avoid periods of severe inclement weather such as intense storms or blizzards (Daru et al., 2017). However, multiple studies have determined that estimates of phenological change keep pace with estimates of phenological change derived from in situ data sources, indicating that collector preferences in the timing of collection are unlikely to produce systematic bias in the resulting estimates of flowering time or phenological advancement (Bertin, 2015; Davis et al., 2015; Lavoie & Lachance, 2006; Primack et al., 2004). Similarly, while the rarity with which estimates of georeferencing accuracy are recorded in digital specimen data limits our ability to directly analyze the effects of georeferencing errors on this analysis, such errors are more likely to be a source of noise rather than of systematic bias in a study of this scale. To produce systematic biases in the resulting data, locations associated with large error distances would be required to be biased toward locations with frost risks that differed in a specific direction (e.g., toward cooler locations than were actually sampled). Furthermore, such biases would be required to persist across records produced and georeferenced by many different collectors and multiple independent institutions, all of which would be required to exhibit similar directional or climatic biases.

It should also be noted that these results represent broad regional patterns in frost risk among 1,653 taxa across a large portion of the continental US. As this study documents, a significant proportion of taxa (24.5%) have exhibited increased frost risk post-1979. While beyond the scope of the current study, certain regions or floras have likely exhibited lesser reductions (or greater increases) in frost risk than were observed across the broad spatial scales examined in this study. Furthermore, examinations of frost risk to various crop species have indicated that microclimate variations that occur at smaller scales than can be observed in this study may also play significant roles not only in determining local temperature but also in the process of ice nucleation, thereby affecting the resulting risk of frost-related damage to plant reproductive tissues (Augspurger, 2011; Logan et al., 2000;

Smith, 2019). Nevertheless, the results presented here are consistent with broad-scale models of past and present frost risk to vegetative tissues among native tree species (Zohner et al., 2020), indicating that, for the majority of species and in the majority of locations, frost risk to reproductive tissues is likely to be decreasing as a result of progressive climate changes.

While the effects of these changes will likely produce complex impacts on fruit and seed production across taxa and throughout North America, understanding the degree to which broad, systematic shifts in frost risk, phenology, and other ecological processes are occurring among taxa in response to recent climate change remains critical to understanding the broad-scale effects of climate change. Broad generalizations about the phenology of a flora at regional or continental scales, however, require historical data that are both temporally deep and spatially extensive. By leveraging the wealth of data presented by herbarium specimens and other natural history collections data, we may seek and identify broad, climate-driven patterns in reproductive phenology (Park et al., 2018; Park & Mazer, 2018, 2019). By demonstrating that recent warming has produced a systematic reduction in frost risk to floral tissues throughout the North American flora, this study highlights a critical aspect of the effects of future climate change, and the likelihood that future warming will further reduce frost risk across the majority of taxa across North America.

DATA AVAILABILITY STATEMENT

The data used to conduct these analyses are available from the Consortium of California Herbaria, the Consortium of Pacific Northwest Herbaria, and the SEINnet network of participating herbaria. Identification fields required to access those specimens used in this study, as well as python code used to conduct the analyses presented in this study are publicly available at https://github.com/isaacWpark/Frost_Risk.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.