

## PRIMARY RESEARCH ARTICLE

# Siberian plants shift their phenology in response to climate change

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## Abstract

Siberia has undergone dramatic climatic changes due to global warming in recent decades. Yet, the ecological responses to these climatic changes are still poorly understood due to a lack of data. Here, we use a unique data set from the Russian 'Chronicles of Nature' network to analyse the long-term (1976–2018) phenological shifts in leaf out, flowering, fruiting and senescence of 67 common Siberian plant species. We find that Siberian boreal forest plants advanced their early season (leaf out and flowering) and mid-season (fruiting) phenology by  $-2.2$ ,  $-0.7$  and  $-1.6$  days/decade, and delayed the onset of senescence by 1.6 days/decade during this period. These mean values, however, are subject to substantial intraspecific variability, which is partly explained by the plants' growth forms. Trees and shrubs advanced leaf out and flowering ( $-3.1$  and  $-3.3$  days/decade) faster than herbs ( $-1$  day/decade), presumably due to the more direct exposure of leaf and flower buds to ambient air for the woody vegetation. For senescence, we detected a reverse pattern: stronger delays in herbs (2.1 days/decade) than in woody plants (1.0–1.2 days/decade), presumably due to the stronger effects of autumn frosts on the leaves of herbs. Interestingly, the timing of fruiting in all four growth forms advanced at similar paces, from 1.4 days/decade in shrubs to 1.7 days/decade in trees and herbs. Our findings point to a strong, yet heterogeneous, response of Siberian plant phenology to recent global warming. Furthermore, the results highlight that species- and growth form-specific differences among study species could be used to identify plants particularly at risk of decline due to their low adaptive capacity or a loss of synchronization with important interaction partners.

## KEYWORDS

climate change, flower, fruit, leaf out, long-term observation, phenology, senescence, Siberia

## 1 | INTRODUCTION

Siberia has undergone dramatic climatic changes due to global warming in recent decades (Groisman et al., 2013; Romanovsky et al., 2007). Since 1850, the mean annual temperature in Siberia

has increased by  $1\text{--}2^\circ\text{C}$ , while the global terrestrial average has increased only by  $0.5\text{--}1^\circ\text{C}$ ; and warming has accelerated since 1990 (Balzter et al., 2007; Lugina et al., 2006; Tchebakova et al., 2010). The regional consequences of this warming trend include decreased duration of sea ice cover (Stocker et al., 2014), accelerated glacier

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shrinkage (Surazakov et al., 2007; Takahashi et al., 2011), altered hydrological regimes (Yang et al., 2002), activation of thermokarst processes (Kirpotin et al., 2009; Ulrich et al., 2019) and initiation of permafrost degradation, which results in increased greenhouse gas emissions (Schoor et al., 2015; Walter et al., 2006). These changes are likely to have strong effects on ecosystems in this region, which spans a range of biomes from tundra to temperate steppe covering a vast territory of 13.1 million km<sup>2</sup> and plays a large role in global ecology.

The ecological responses to these climatic changes, however, are still poorly understood. Phenology, the study of the timing of organisms' life cycle events (e.g. when plants leaf out or flower), is arguably one of the most compelling and responsive metrics for documenting the effect of climate change on ecosystems (Burrows et al., 2011; Post et al., 2001) since temperature is one of the main drivers of plant phenology (Flynn & Wolkovich, 2018). Plant phenology has responded to climate change with shifts in timing (Augspurger & Zaya, 2020; König et al., 2018; Liu et al., 2016; Menzel et al., 2020) that impact sexual reproduction (Pardee et al., 2019), plant–plant and plant–animal interactions (Kharouba et al., 2018), coexistence in diverse plant communities (Rafferty et al., 2020) and carbon and nutrient dynamics, resulting in increased growth and ecosystem productivity in many ecosystems (Gallinat et al., 2015; Wolkovich et al., 2012). However, most phenology studies on this topic concentrate on the temperate zone, with some studies as well in the boreal zone in Europe and America. Other regions of the world are less well studied. To our knowledge, there are no studies of plant phenology based on ground observations in Siberia; the few existing studies of phenology in this vast area are based primarily on remote sensing data (e.g. Morozumi et al., 2020). These few published studies have reported phenological shifts broadly in line with reports from other ecosystems—including range shifts of forest, tundra, steppe and wetland zones (Meyer et al., 2008; Tchebakova et al., 2010), an extension of the growing season (Shulgina et al., 2011) and increased forest productivity (Berner et al., 2013; Callaghan et al., 2013; Esper & Schweingruber, 2004). While these observations are useful, it is notoriously difficult to get exact phenological observations from space, and detailed ground-based analysis of phenological data in Siberia and other cold environments, such as the Arctic and the alpine ecosystems (e.g. Richardson et al., 2013), is urgently needed.

Our current understanding of how phenology is responding to climate change is based nearly exclusively on data from temperate Europe and North America, where most phenological studies have been conducted (Augspurger & Zaya, 2020; König et al., 2018; Menzel et al., 2020). The few existing regional studies in other biomes (Bjorkman et al., 2015; Mo et al., 2017; Park & Schwartz, 2015) suggest that the magnitude and, in some cases, even the direction of phenological shifts may depend on plant adaptations to regional and local climatic parameters. For example, Bjorkman et al. (2015) report that despite the Arctic having one of the highest warming rates, flowering in some places has been delayed in recent years, due to increased winter precipitation and deeper snow cover. In

another example, Park and Schwartz (2015) report that spring plant phenology has not shifted earlier in the subtropical, southeastern USA. Consequently, more regional studies are needed to form a comprehensive, global picture about phenological shifts across various ecosystems.

Here, we report the results of phenological shifts from a long-term, exceptionally detailed, recently digitized data set of phenological records from the Russian boreal forest, also known as taiga, collected at the Barguzin Nature Reserve in Siberia. The data consist of >15,000 phenological records of four phenological events—leaf out, flowering, fruiting and senescence (seasonal dieback in herbaceous plants and leaf fall in woody species)—systematically collected at one location over four decades (1976–2018) for more than 60 plant species representing different growth forms. These data contribute important, new phenological information about plant responses to climate change at the species and community levels in this unique, remote region. Specifically, we address the following questions:

1. Are the direction and magnitude of phenological shifts in Siberian plants different from those observed in other regions? Based on previous research on cold-adapted plants, we predicted that leaf out, flowering and fruiting similarly advanced as a response to warming spring and summer temperatures, due to the high temperature responsiveness of these stages. Furthermore, we expected warmer autumns to delay senescence in Siberian plants, due to temperature's effect on late seasonal plant physiology (e.g. Fracheboud et al., 2009; Shi et al., 2014).
2. Are the direction and magnitude of phenological shifts in Siberian plants over time species specific? We expect that the majority of species will follow the trends established in the phenological literature (e.g. advance in leaf out and delay in senescence), with some species showing divergent patterns, because mechanisms underlying phenological timing (e.g. responsiveness to climate; Badeck et al., 2004; Basler & Körner, 2012; Rathcke & Lacey, 1985) are likely to differ from species to species (Augspurger & Zaya, 2020; Ovaskainen et al., 2013; Panchen & Gorelick, 2017; Sherry et al., 2007). For the same reason, we also expect the species with advanced leaf out, flowering and fruiting, and delayed senescence to differ in the magnitude of shifts over time, among these events.
3. Are these species-specific phenological responses related to plant growth forms (i.e. trees, shrubs, dwarf shrubs, herbs)? Growth form can alter the effects of environmental change on plant phenology, because it expresses evolved morphological and physiological adaptations to predominant growth conditions, such as temperature, precipitation and photoperiod (Du et al., 2020; Heberling et al., 2019; König et al., 2018). Leaf and flower buds, ripening fruits and leaves in trees, shrubs, dwarf shrubs and herbs are positioned at different heights from the ground (Raunkiaer, 1934) and are therefore exposed to different thermal conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

Our study site is Barguzin Nature Reserve (Russian: 'zapovednik'), the oldest protected area in Siberia, Russia (54°48', 109°61'; Figure 1) and including the north-eastern region of Lake Baikal. The reserve has a total area of 2482 km<sup>2</sup> and was established in 1916 to preserve and foster the population of endangered sable (*Martes zibellina* L.). The Barguzin Reserve is located in the Baikal Rift Zone and has topography typical of this region, including mountain summits in the Barguzin Range up to 2650 m a.s.l. and intermountain depression valleys. The climate is continental with a mean annual air temperature of -3.9°C and low precipitation (300–650 mm average per year near Lake Baikal shoreline and more than 1000 mm in the uplands; mean air temperature and precipitation from 1961 to 2011; Lunina & Gladkov, 2007). The short growing season (120–140 days

is characterized by rapid temperature rise and drop in spring and autumn respectively; maximum air temperatures are reached in July, and the first snowfall typically occurs in the middle of September (Suzuki et al., 2001; Ye & Cohen, 2013).

The vegetation of the Barguzin Reserve has an altitudinal zonation due to complex relief and influence of the Baikal Rift. The study site was near Lake Baikal's shoreline, where the ecosystem is a boreal coniferous forest dominated by Siberian larch (*Larix sibirica*) with patches of Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*). Soils are represented by Entic Podzols according to the World Reference Base for Soil resources classification ([www.isric.org](http://www.isric.org)).

### 2.2 | Phenological observations and weather data

Phenological observations have been collected by the permanent research staff of Barguzin Reserve since 1976 as part of the

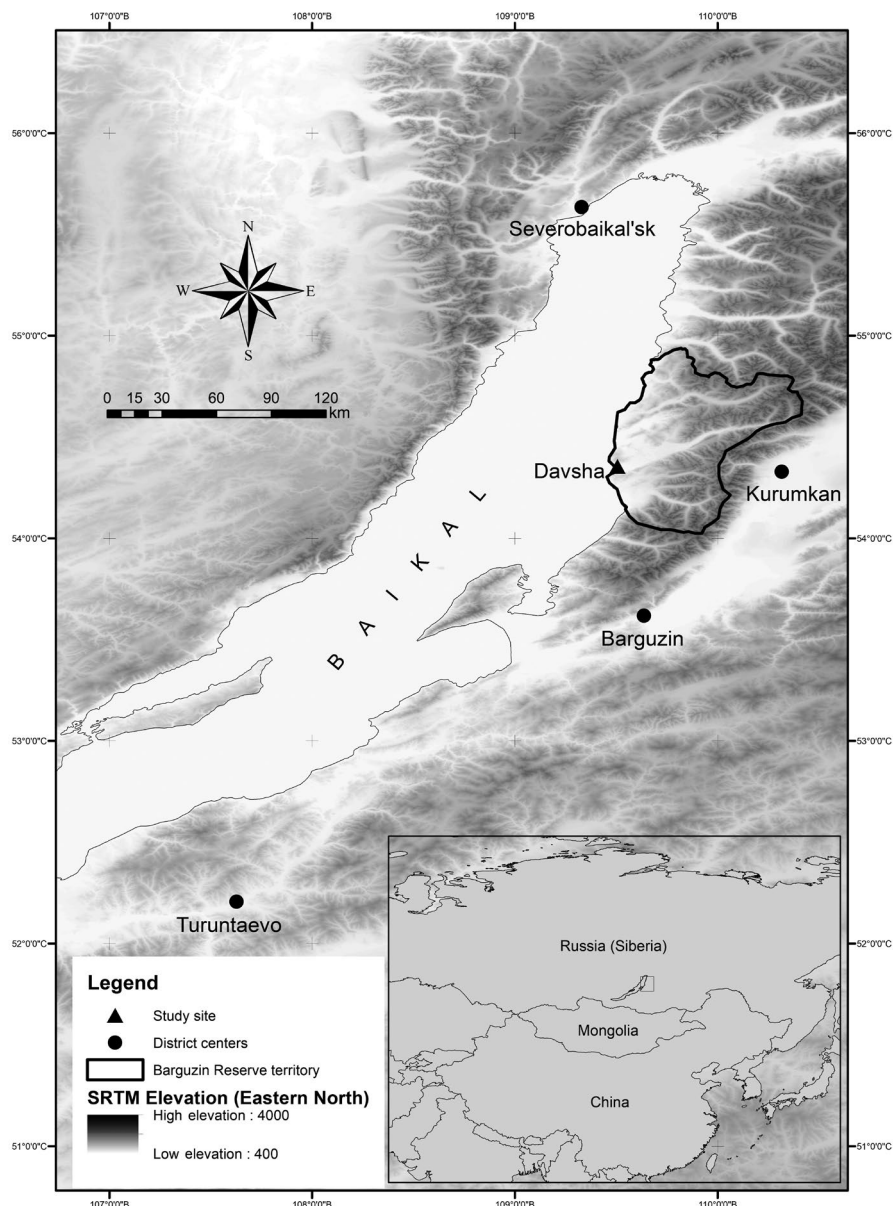


FIGURE 1 Location of the study site

'Chronicles of Nature', a monitoring program of Russia's network of nature reserves and national parks (Ovaskainen et al., 2020). These long-term phenological observations were initiated for monitoring multiple taxa on permanent plots and undisturbed natural habitats, and for revealing the influence of environmental change on different components of ecosystems. The phenological data were acquired year-round either along established routes and/or in permanent plots.

Phenological events were recorded on a weekly basis for the 67 most common Siberian species naturally occurring in five permanent plots, each 400 m<sup>2</sup> and located 400–500 m apart from each other. Common species (e.g. *B. pendula*, *Empetrum sibiricum*) were observed in more than one plot, while many rare species were only found in one plot (Appendix S1). The phenological plots represent a boreal mixed forest made up by *L. sibirica*, *P. sylvestris* and *B. pendula* in different proportions with a canopy height of 10–20 m and canopy cover between 60% and 80%. The shrub layer (1–4 m in height, with a canopy cover between 5% and 40%) is represented mainly by *Ledum palustre*, *Rosa acicularis* and *Spiraea media*. The understorey layer is dominated by dwarf shrubs (up to 80 cm height) including *Linnaea borealis*, *Pyrola rotundifolia* and three *Vaccinium* species (*V. myrtillus*, *V. uliginosum* and *V. vitis-idea*). Various herbs typical for boreal forests (e.g. *Bergenia crassifolia*, *Lilium pilosiusculum* and *Veratrum lobelianum*) are also an important component of the plant communities in these phenological plots.

In the present study, the following four key stages of plant phenological cycles were observed and analysed: first leaf out, first flower, first fruit and start of senescence. These stages reflect the observation of when the first young leaves, first open flowers, first ripe fruits and first senescent leaves were observed respectively. The onset of a phenological stage was recorded when at least 10% of all individuals of a species were in a corresponding stage (visual estimation). Leaf senescence was not observed in evergreen plants. Data on first flower in *Arctostaphylos uva-ursi* covered a comparatively short period of time and thus were omitted from further analysis. All dates are expressed as the day of year (DOY; 1 = 1st January, etc.) and account for leap years. Other phenological stages were recorded, such as different stages of flowering, but these stages are not presented in this current analysis.

All species were classified into trees, shrubs, dwarf shrubs or herbs based on the Raunkiaer plant growth form classification (Raunkiaer, 1934). Trees and shrubs are long-lived woody perennials with resting buds located more than 50 cm above the soil surface with trees being at least 5 m tall (e.g. *Larix czekanowskii* Szaf., *Pinus sibirica* Du Tour) and shrubs (e.g. *Betula nana* L., *Dasiphora fruticosa* (L.) Rydb.) not exceeding 5 m. Dwarf shrubs are plants with resting buds on persistent (in some cases woody) shoots near the soil surface, but are not taller than 25 cm (e.g. *L. borealis* L., *V. myrtillus* L.). Herbs include plant species with resting buds always located below-ground (e.g. *B. crassifolia* (L.) Fritsch., *Lupinaster pentaphyllus* Moench). The data set included nine trees, nine shrubs, 10 dwarf shrubs and 39 herbs (Appendix S2).

Data on air temperature, precipitation and snow cover depth were collected on a daily basis at a weather station 'Davsha' located

100–500 m from the phenology plots. The weather station has been in operation since 1955 and records minimal, mean and maximal air and soil temperature, atmospheric pressure, precipitation and snow cover. Temperature is measured by thermograph; precipitation is measured by a rain gauge. Data on air temperature and snow cover are available for the same period as phenological observations (1976–2018), whereas precipitation data are available from 1985 onwards. Daily weather records have not yet been digitized, so the analysis of frost events is not yet possible.

## 2.3 | Statistical analysis

### 2.3.1 | Climate change at the study site

To assess the patterns of climate change at the study site, we calculated mean annual air temperature and precipitation, snow cover duration (from the first to the last day of stable snow cover) and snow cover formation (the first day with stable snow cover) from 1976 to 2018 (1985–2018 for precipitation). Additionally, we calculated mean air temperature and precipitation for 'phenological spring' (April, May and June), 'phenological summer' (May, June and July) and 'phenological autumn' (August, September and October), three seasonal periods in which the majority of plants leaf out, flower, fruit and senesce respectively (Moloznikov, 1970). The overlap between the first two phenological seasons is due to the growth form-specific phenological schedules (Figure 3) and is a short part of the overall growing period. Winter is defined as a dormant period between the end of leaf senescence in November and the onset of leaf out in March. We fitted ordinary least squares regressions to test for temporal trends in each of these three seasonal temperature variables.

### 2.3.2 | Phenological responsiveness to climatic variables

We used linear mixed-effects models to determine the phenological response to year-to-year climatic variability ('phenological responsiveness'). Five models were calculated for all species and for each of the four growth forms. In all models, we used mean temperature of the corresponding phenological season (described above) as a predictor. Temperatures during flowering, which mainly occurs in April–June ('phenological spring'), were included as a predictor of fruiting phenology, because temperatures during this phase can also significantly affect fruiting patterns (Rosbakh et al., 2018). We opted for mean temperatures rather than other temperature metrics due to their clear correlation with phenology in temperate and northern climates and the ability to allow direct comparisons to previous phenological seasons (Assmann et al., 2019; Augspurger & Zaya, 2020; Heberling et al., 2019). Previous studies have suggested that alternative temperature-based predictors, such as degree-day models, typically produce similar results but are often less intuitively interpretable (Basler & Körner, 2012).

Precipitation can be another important driver of plant phenology (König et al., 2018), especially in the comparatively dry (ultra) continental climate of Siberia, so we included mean precipitation in the models for first fruit and start of senescence modes as explanatory variables for phenology. Mean precipitation during fruiting, which occurs in May–July ('phenological summer') was also included in the models for start of senescence. Precipitation was not included into the first leaf and first flower models because melting snow is the main source of soil water in the spring in boreal forests (Pederson et al., 2011) and is not a limiting factor to spring growth. The effects of snow cover, another important driver of early and late plant phenophases in cold climates (Assmann et al., 2019; Bjorkman et al., 2015; Gallinat et al., 2015), were also estimated by including snow cover duration and snow cover formation in the models for first leaf and start of senescence respectively. We also included the year of phenological observations into the model to test changes over time not strictly related to changes in environmental variables included in the models. To account for variation in phenological responsiveness among species, and microclimatic variation among the observational plots, all models included species and sites as random effects.

### 2.3.3 | Phenological shifts over four decades

To estimate the changes in phenology over the last four decades, we regressed the onset of each phenological phase for each species

separately against the year of observation. The calculated regression slopes represent phenological shifts (days/year), which were transformed to days/decade for clarity.

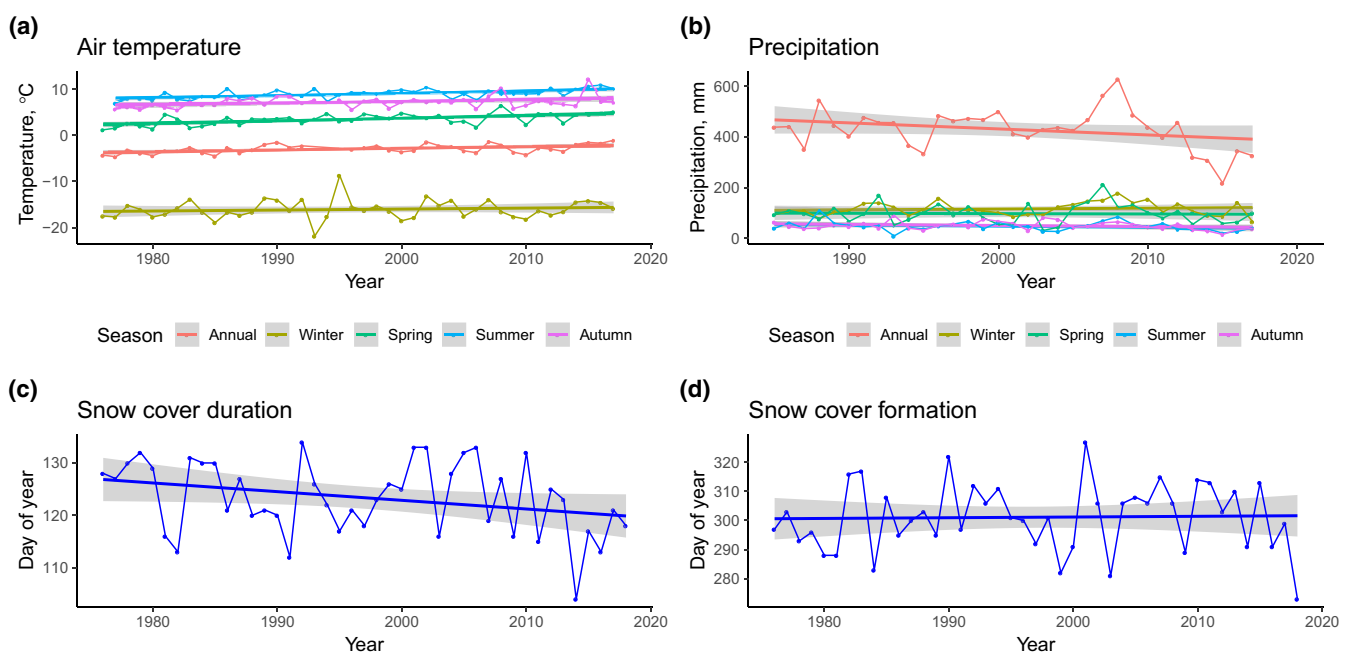
We then used weighted linear models to compare the estimated shifts between the growth forms. Weighted means included the standard errors of the calculated shifts for each single species as weights in the regression, thereby accounting for the different uncertainties of the individual species estimates. Within this framework, we calculated several statistical indicators. First, we calculated mean phenological shifts and associated confidence intervals per growth form, and tested whether those shifts were significantly different from zero. Second, we used an ANOVA to test for an overall difference between the growth forms, followed by post hoc tests (Tukey) for specific tests between all the group levels.

All statistical calculations were done with R software (R Core Development Team, 2021).

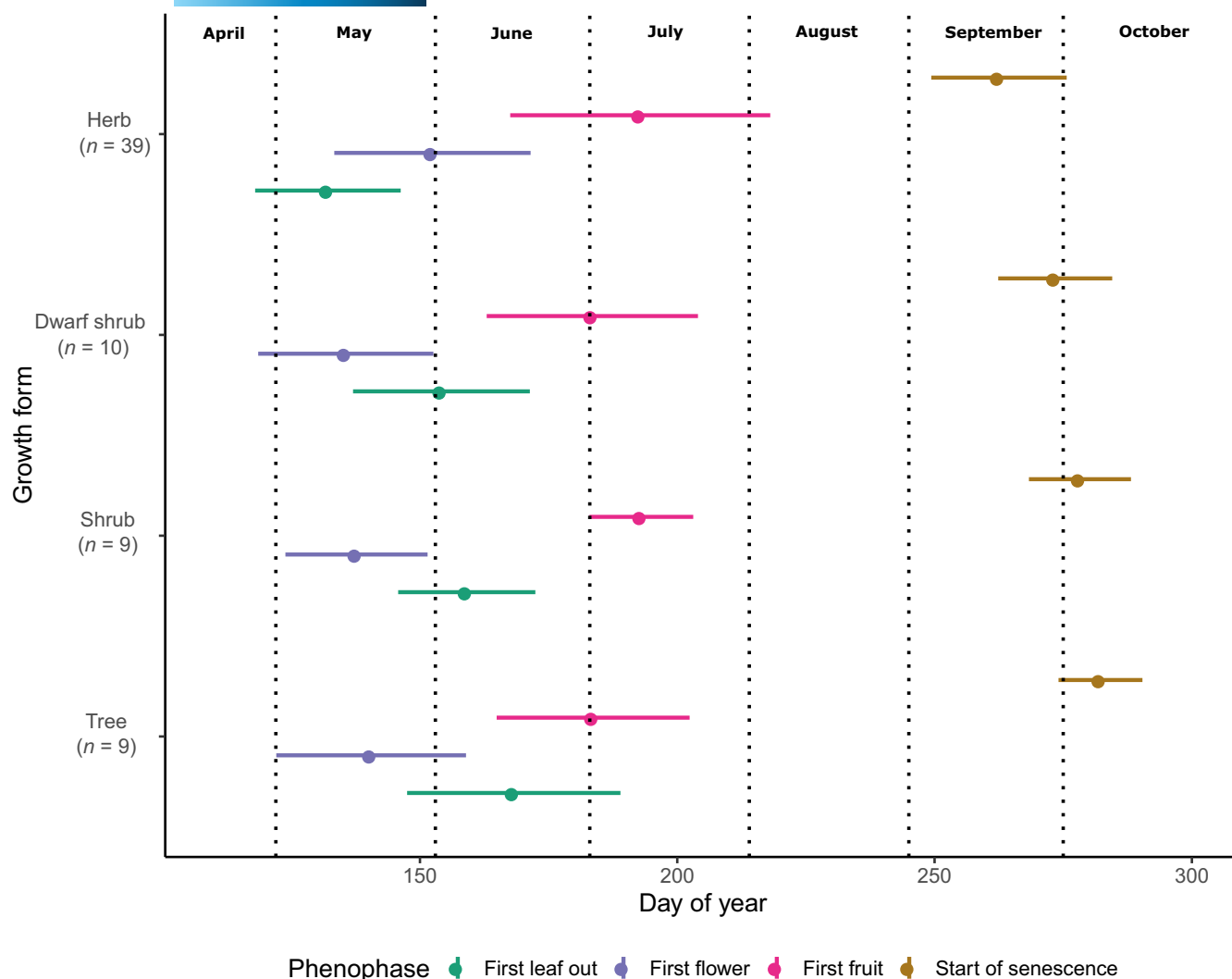
## 3 | RESULTS

### 3.1 | Climate change at Barguzin Reserve

The analysis of our climate data revealed a significant increase in mean annual temperature (on average,  $0.4 \pm 0.1^\circ\text{C}/\text{decade}$ ;  $\pm$  here and elsewhere refers to the standard error of the estimate; Figure 2a). The strongest seasonal temperature rise was observed



**FIGURE 2** Patterns of climatic change in the Barguzin State Reserve, Siberia. (a) Air temperature by season; (b) precipitation by season; (c) annual snow cover duration date; (d) Annual snow cover formation date. Spring, summer and autumn are defined as periods in which the majority of plants leaf out, flower, fruit and senesce respectively. Winter is the dormant period between the end senescence and the onset of leaf out. Regression lines show climatic trends during the study period; only air temperature shows statistically significant increases—for annual, spring, summer and autumn but not winter temperatures ( $p < 0.05$ ). Shaded areas denote the 95% CI for the regression lines



**FIGURE 3** Comparative phenology of four plant growth forms. Average dates (1976–2018) for first leaf out, flowering, fruit ripening and senescence days are shown with their standard deviations. The dotted lines indicate month ranges

in spring ( $0.6 \pm 0.2^\circ\text{C}/\text{decade}$ ), followed by summer ( $0.5 \pm 0.2^\circ\text{C}/\text{decade}$ ) and autumn ( $0.4 \pm 0.2^\circ\text{C}/\text{decade}$ ). Precipitation, which was highly variable from year to year, did not change significantly over the last three decades (Figure 2b). Similar to precipitation, snow cover duration and formation displayed considerable year-to-year variation (Figure 2c,d), and neither changed significantly over the course of the study period.

### 3.2 | Phenological responsiveness to climate

The timing of all four phenophases (first leaf out, first flower, first fruit and start of senescence) showed substantial variation over time for all species (Appendix S3). In the following paragraphs, we describe the effect of air temperature and precipitation as well as snow pack duration and formation on this variation. Statistical details can be found in Appendix S4.

#### 3.2.1 | First leaf out date

The first leaves were observed from 27 April to 9 July with an average of 30 May (trees—14 June, shrubs—4 June, dwarf shrubs—31 May and herbs—10 May; Figure 3). Variation in the first leaf out date was significantly positively affected by air temperatures with mean effects for all species combined of 1.6 days/ $^\circ\text{C}$  advance in phenology, whereas snow cover duration had a negative significant effect on this phenophase with a mean effect of 0.3 days delay in leaf out per day with stable snow cover (Appendix S4). Plants of different growth forms differed in their sensitivity to air temperatures with mean effects for trees, shrubs, dwarf shrubs and herbs of 1.7, 2.6, 1.9 and 1.1 days/ $^\circ\text{C}$  earlier leaf out respectively. Similarly, snow cover duration had a negative significant effect on this phenophase in trees, dwarf shrubs and herbs, with mean effects of 0.1, 0.2 and 0.4 days delay in phenology per day with stable snow cover. This climatic parameter had no significant effect on the first leaf out in shrubs (Appendix S4).

### 3.2.2 | Flowering

On average, observed species began to flower on 27 May, ranging from 27 April to 3 July (mean date for trees—20 May, shrubs—18 May, dwarf shrubs—19 May and herbs—2 June; Figure 3). Warmer springs advanced flowering by 1.8 days/°C, whereas springs with long-lasting snow cover delayed it (0.3 days/1 day of stable snow cover; Appendix S4). These environmental predictors had similar effects on the first flower date as on the first leaf out date in different growth forms: flowering was advanced in warmer springs (2.0, 3.0, 1.4 and 1.6 days/°C in trees, shrubs, dwarf shrubs and herbs respectively) and delayed in springs with long-lasting snow cover (0.2, 0.5, 0.6 and 0.2 days/1 day of stable snow cover; Appendix S4).

### 3.2.3 | Fruiting

Similar to the previous two phenophases, fruiting phenology displayed high variability, ranging from 27 May to 22 August with a mean date of 8 July for the first fruit observations (mean date for trees—5 July, shrubs—8 July, dwarf shrubs—5 July and herbs—13 July; Figure 3). The first fruit date was driven by mean air temperatures prior to the onset of flowering and fruiting as well as precipitation conditions preceding the onset of this phenological phase (Appendix S4). On average, fruiting advanced in years with warmer springs and summers by 2.2 and 1.2 days/°C, respectively, as well as in summers with higher amounts of precipitation (0.05 days advance per 1 mm of precipitation). Plants of different growth forms displayed a similar response of fruiting phenology to higher air temperatures in spring and summer with an average advance across all growth forms of 2.1 days/°C for the former and 1.3 days/°C for the latter. This phenological stage in trees, shrubs and herbs was found to be responsive to higher summer precipitation, with advances 0.11, 0.05 and 0.05 days/mm of precipitation respectively. Year explained additional variation in fruiting phenology in herbs only (Appendix S4).

### 3.2.4 | Senescence

The variation in the start of senescence was considerably less than in the previous three phases; on average, senescence began on 30 September (earliest 6 September, latest 15 October). On average, senescence in trees, shrubs, dwarf shrubs and herbs began on 7 October, 3 October, 29 September and 19 September respectively (Figure 3). Averaged over all species, temperature had a complex effect on the onset of senescence: warmer mean temperatures during fruiting (summer) were associated with earlier senescence (−1.5 days/°C), whereas warmer autumns delayed senescence (0.44 days/°C; Appendix S4). The temperature effects on the late-season phenology of Siberian plants differed considerably among the four growth forms. Mean temperatures during fruiting significantly advanced the start of senescence in shrubs and herbs only (−1.6 days/°C in both cases; Appendix

S4), whereas the timing of this phenophase was not affected by autumn temperatures in any of the growth forms. Averaged over all species, summer and autumn precipitation and snow cover formation had a small but significant effect on the onset of senescence, with delays of 0.03 days/mm of precipitation (both summer and autumn) and 0.04 days/snow cover formation day respectively (Appendix S4). Summer precipitation had a positive effect on the onset of senescence (delay) in herbs only, suggesting a delay in senescence in years with wetter summers (0.04 days/mm of precipitation; Appendix S4). Autumn precipitation and snow cover formation had no significant effect on the timing of senescence in the four growth forms studied (Appendix S4). Year had a significant effect on the first leaf out (all species and all growth forms), first flower (all species and all growth forms except for dwarf shrubs) and start of senescence (all growth forms), suggesting that the environmental variables in our model were not the sole drivers of these three phenophases (Appendix S4).

## 3.3 | Mean shifts in phenology

Analysing the temporal trends in phenology, we see that Siberian plant phenology has shifted significantly since the 1970s. On average, the study species begin to leaf out, flower and fruit  $8.8 \pm 0.2$ ,  $2.8 \pm 0.2$  and  $6.4 \pm 0.2$  days, respectively, earlier in 2018 than in 1976. Similarly, the start of senescence now begins  $6.0 \pm 0.2$  days later than at the beginning of the phenological observations (Table 1).

## 3.4 | Species-specific shifts in phenology

Individual species displayed a high degree of variability among species, both in direction and magnitude (Figure 4; Appendix S3). Thirty-four species (51%) demonstrated significant advances in leaf out between 6.7 (*Sambucus sibirica* Nakai) and 1.6 days/decade (*L. pilosiusculum* (Freuen) Mischz.), while only three species (4%) delayed the onset of leaf out with increasing temperature (*Aegopodium alpestre* Ledeb. 5.4 days/decade; *Caltha crenata* Belaeva et Sipl. 3.5 days/decade; and *Chamerion angustifolium* (L.) Holub. 2.5 days/decade).

Flowering of 20 of 66 species (30%) responded significantly to climate warming, among which 17 (26%) species flower earlier and three (5%) later than in 1976. Similar to first leaf date, the rate of flowering advance varied considerably between 7 days/decade in *Pinus pumila* (Pall.) Regel and 1.5 days/decade in *Viola canina* L. Four species, *Fragaria vesca* L. (7.1 days/decade), *Aquilegia sibirica* Lam. (2.8 days/decade), *C. crenata* Belaeva et Sipl. (2.0 days/decade) and *Vaccinium vitis-idaea* L. (1.2 days/decade) are the only species displaying significantly delayed onset of flowering in response to climate warming.

The first fruit date for 29 (43%) of 67 species significantly advanced over the study period, while the onset of fruit was delayed in only one species (1.5%; *Juniperus sibirica* Burgsd., 2.4 days/decade). Again, the shift rates among species with significantly advanced fruiting dates varied strongly between 6 days/decade in *Euphrasia pectinata* Ten. and 1.4 days/decade in *E. sibiricum* V. Vassil.

Phenological phase	Growth form	Shift, days/decade			Pairwise comparison
		Mean	SE±	p-value	
Leaf out	All species	-2.2	0.2	<0.001	-
	Tree	-3.1	0.5	<0.001	a
	Shrub	-3.3	0.5	<0.001	a
	Dwarf shrub	-2.7	0.4	<0.001	a
	Herb	-1.0	0.3	0.003	b
	ANOVA	F-value: 7.3, df = 67, p < 0.001			
First flower	All species	-0.7	0.2	0.003	-
	Tree	-1.9	0.6	0.001	a
	Shrub	-1.5	0.7	0.03	a
	Dwarf shrub	-0.3	0.5	0.50	a
	Herb	-0.3	0.3	0.5	a
	ANOVA	F-value: 2.8, df = 66, p = 0.049			
First fruit	All species	-1.6	0.2	<0.001	-
	Tree	-1.7	0.5	<0.001	a
	Shrub	-1.4	0.4	<0.001	a
	Dwarf shrub	-1.6	0.4	<0.001	a
	Herb	-1.7	0.3	<0.001	a
	ANOVA	F-value: 0.08, df = 67, p = 0.96			
Start of senescence	All species	1.5	0.2	<0.001	-
	Tree	1.2	0.4	0.009	a
	Shrub	1.0	0.4	0.01	a
	Dwarf shrub	1.1	0.5	0.03	a
	Herb	2.1	0.3	<0.001	a
	ANOVA	F-value: 2.3, df = 56, p = 0.09			

**TABLE 1** Direction and magnitude of phenological shifts over time in 67 Siberian species averaged over all species ('All species') and grouped into trees, shrubs, dwarf shrubs and herbs. Bold entries indicate a significant ( $p < 0.05$ ) estimate difference from zero. SE ± indicate standard errors. ANOVAs with post hoc tests (Tukey) were performed to test for differences in phenological shifts among four growth forms

For the onset of senescence, 23 out of 55 species (42%) delayed, while only two species (4%; *P. rotundifolia* L., 13.0 days/decade and *Duschekia fruticosa* (Rupr.) Pouzar 2.1 days/decade) advanced. Among species with significantly delayed onset of senescence, the shift rates varied from 1.0 to 8.8 days/decade in *V. uliginosum* L. and *Taraxacum officinale* Wigg. respectively.

### 3.5 | Growth form-specific shifts in phenology

Plant growth form could partially explain high species-specific differences in temporal shifts (Table 1; Figure 5).

The first leaf out date advanced significantly in all four growth forms. The strongest phenological shift in first leaf out was in trees, shrubs and dwarf shrubs—species of these three groups leaf out  $12.4 \pm 0.5$ ,  $13.2 \pm 0.5$  and  $10.8 \pm 0.5$  days earlier in 2018 than in 1976. The shifts in this phenophase in herbs was significantly smaller ( $4.0 \pm 0.3$  days), and an ANOVA supports overall differences among growth forms ( $p < 0.001$ ).

The onset of flowering shifted significantly in trees ( $-7.6 \pm 0.6$  days earlier,  $p = 0.001$ ) and shrubs ( $-6 \pm 0.7$  days earlier,  $p = 0.03$ ), but not significantly in dwarf shrubs ( $p = 0.5$ ) and herbs ( $p = 0.5$ ) during the observation period. These differences among growth forms were

overall significant (ANOVA,  $p = 0.049$ ), but results of the post hoc test among groups were non-significant.

The onset of fruit ripening has significantly advanced in all growth forms, with the strongest shift in trees ( $6.9 \pm 0.5$  days earlier in 2018 than in 1976), followed by herbs ( $6.7 \pm 0.5$  days), dwarf shrubs ( $6.5 \pm 0.4$  days) and shrubs ( $5.8 \pm 0.4$  days). We found no significant differences among growth forms (ANOVA  $p = 0.96$ , post hoc tests not significant).

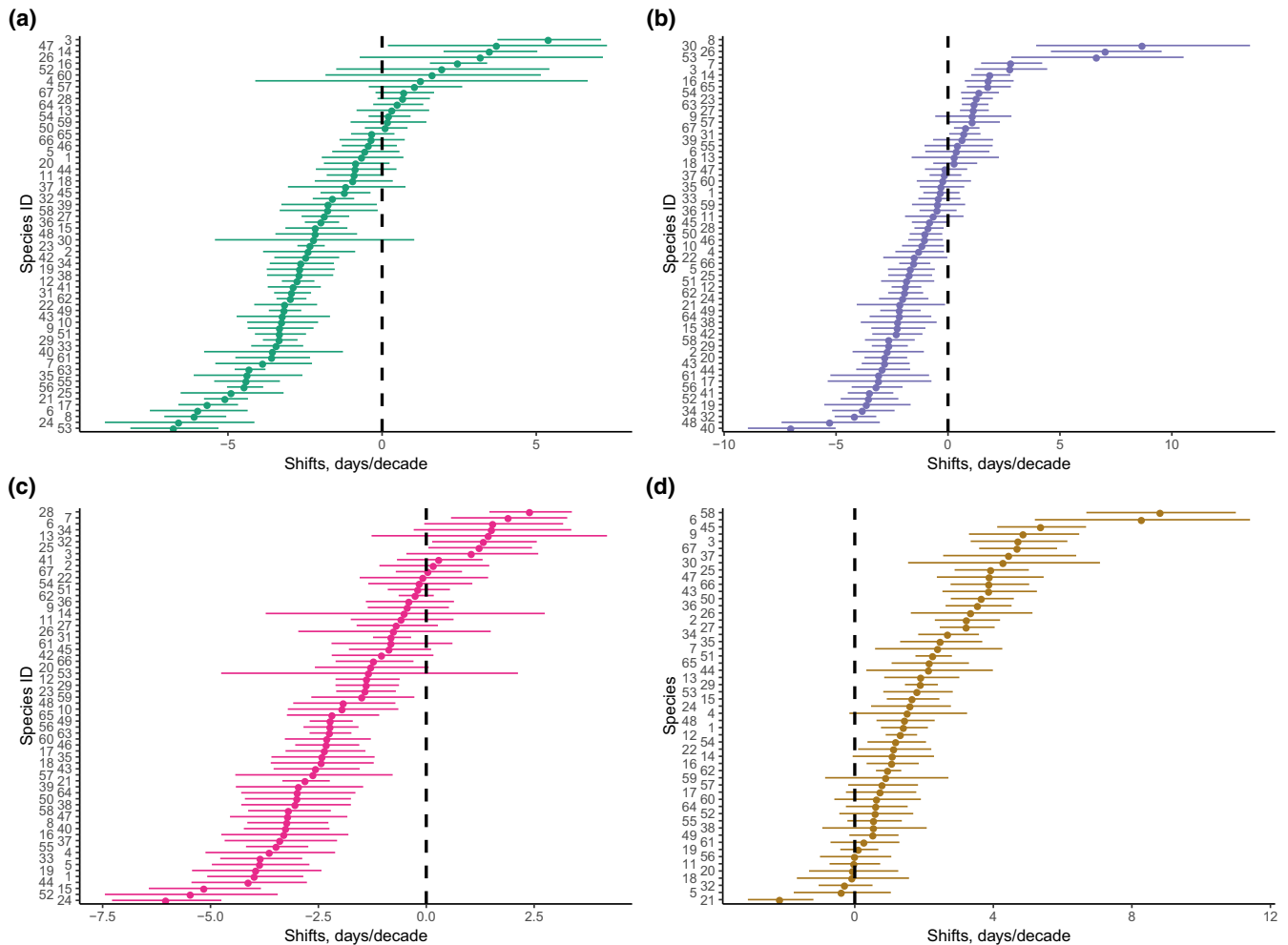
The start of senescence was delayed significantly in all four growth forms during the last four decades with the strongest shifts in herbs ( $8.4 \pm 0.3$  days later than in 1976) followed by comparatively similar shifts in trees, shrubs and dwarf shrubs ( $4.7 \pm 0.4$ ,  $4.2 \pm 0.4$  and  $4.5 \pm 0.5$  days respectively). Differences among growth forms were not significant (ANOVA  $p = 0.09$ , post hoc tests not significant).

## 4 | DISCUSSION

### 4.1 | Siberian plant phenology shifts in response to climate warming

Our results suggest that the climate warming during the last four decades caused an advance of early season phenology and delayed timing of late-season phenology. Similar to previous research in





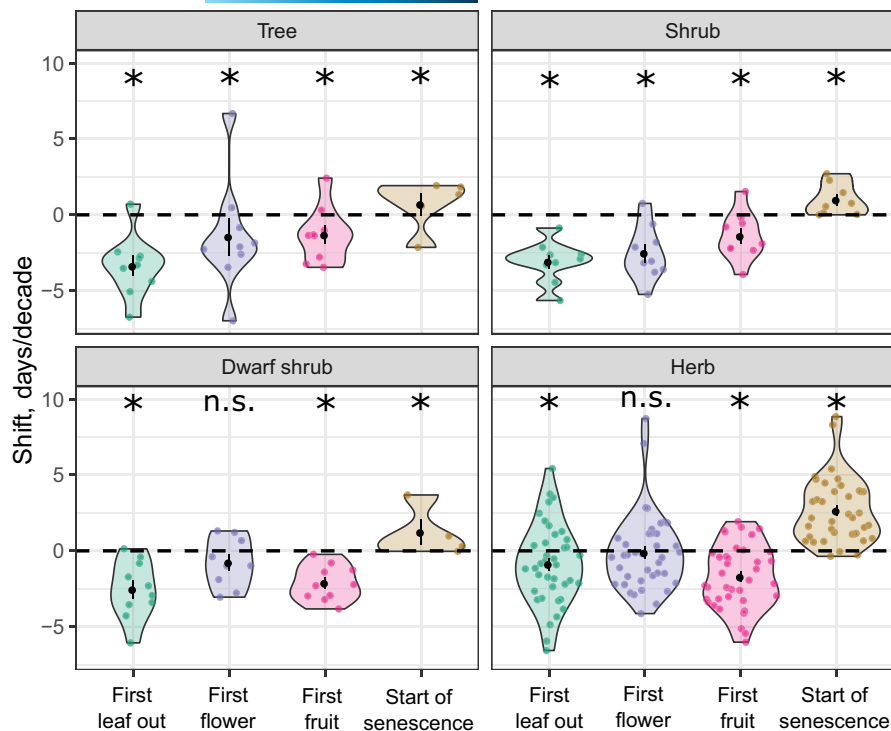
**FIGURE 4** Species-specific phenological shifts of 67 Siberian plants from 1976 to 2018. Dots indicate mean values, horizontal lines are 95% confidence intervals. (a) first leaf out, (b) first flower, (c) first fruit and (d) start of senescence. See Appendix 2 for detailed information on species IDs and estimated shifts (mean value, standard error and significance values). See Appendix S5 for the interactive version of this figure

boreal and temperate Europe, North America and Asia (Augspurger & Zaya, 2020; Ge et al., 2015; König et al., 2018; Liu et al., 2016; Menzel et al., 2020), warming spring and summer temperatures at Barguzin Reserve were associated with advanced leaf out, flowering and fruiting of the study species, presumably due to the sensitivity of these phenological processes to ambient temperature. Remarkably, leaf out advanced at twice the rate of flowering and fruiting times, suggesting a higher responsiveness of early leaf phenology to the rising temperatures at the study site. The advanced rates in these three phases are comparable to the responses of cold-adapted plants to climate warming in the mid latitudes (e.g. 2.4, 2.5 and 2.2 days/decade advance in leaf out, flowering and fruiting in European or Chinese plants; Ge et al., 2015; Menzel et al., 2020).

Our observation of delayed senescence in Siberian plants (on average 1.5 days/decade) is similar to other phenological studies in strongly seasonal cold climates (between 0.36 and 3.7 days/decade, e.g. Ge et al., 2015; Gill et al., 2015; Menzel et al., 2020). The explanation for the delayed start of senescence in our case is less straightforward than the advance of leaf out, flowering and fruiting

as the environmental controls of this phenological stage remain significantly understudied in contrast to spring and summer phenology (Gallinat et al., 2015; Gill et al., 2015). One possibility is that warmer autumns in recent years resulted in an increased activity of photosynthetic enzymes and slower chlorophyll degradation, both of which lead to delayed senescence (Fracheboud et al., 2009; Shi et al., 2014). However, these changes cannot be an exclusive explanation for delayed senescence, as advance in senescence was associated with warmer summers that is in line with the recent findings by Zani et al. (2020). One possible explanation is that the higher temperatures in autumn affected the frequency and intensity of weather stressors triggering senescence in plants. For example, warmer autumns might have reduced the potential for frost damage due to the reduced number of freezing days (Hartmann et al., 2013) and later occurrence of first frost day in autumn (Gill et al., 2015; Schwartz, 2003), two environmental factors, which were unaccounted for in our model of phenology responsiveness.

It is worth mentioning that the sites of phenological monitoring are located close to Lake Baikal, which, due to its vast size



**FIGURE 5** Phenological shifts in four growth forms from 1976 to 2018. Black dots and vertical lines are model estimates and standard errors for each phenological phase (for details, see Table 1). Coloured dots are model estimates for each species. Asterisks indicate statistically significant shifts ( $p < 0.05$ ); n.s., non-significant

(650 × 40 km), has a pronounced cooling effect on the surrounding area. Specifically, the many phenological phases at the lake's shore are delayed by approximately 3 weeks compared to areas further away (Moloznikov, 1970). Thus, we presume that the reported magnitude of the phenological changes for all four stages in other mid-latitude Siberian regions affected by warming could be even stronger (Callaghan et al., 2013).

#### 4.2 | Species-specific phenological responses to warmer climate

Although most individual species followed general phenological trends (advance in early and mid-season and delay in late season phenology), there were species that consistently responded in different ways (see also Augspurger & Zaya, 2020). Interspecific variability of flowering and leafing phenology was substantial and a few species even delayed first leaf and flower during the last four decades, despite an overall mean advance. The more remarkable pattern is, however, that, except for leaf out, the majority of the species did not significantly change the timing of their flowering, fruiting or senescence over the study period. This suggests that for many of these species, a factor other than temperature, such as photoperiod, might be important in controlling phenology. Finally, species with significantly altered phenology also displayed high variability in the magnitude of their phenological shifts (e.g. advance in leaf out, flowering and fruiting varied between approximately 1 and 7 days per decade).

Finding substantial species-specific differences in direction or magnitude of plant phenological shifts over time largely suggests that the timing and length of phenological events are driven by

species-specific cues, including, for example, photoperiod (Basler & Körner, 2012), temperature (Augspurger & Zaya, 2020), precipitation (König et al., 2018), snow-melt patterns (Assmann et al., 2019) and combinations thereof. Future investigations could expand on this study to include a larger number of species in order to reveal physiological and/or anatomical specializations behind the phenological responsiveness of Siberian species to climate change (e.g. Heberling et al., 2019; König et al., 2018). Additionally, it would also be interesting to look at intraspecific variation and plasticity in phenological responses, which may have an important effect species-level climate change impacts (Moran et al., 2016).

It is also possible that some of the species-specific phenological patterns described here might be due to changes in population sizes (Miller-Rushing et al., 2008; Ovaskainen et al., 2013). Species' changes over time in phenology might be due in part to changing abundance due to sampling issues. Moreover, other studies have shown that species that do not shift their phenology in response to climate change are also often declining due to mistimed ecological relationships (Kharouba et al., 2018; Willis et al., 2008). Finally, the lack of phenological response of leaf out and flowering in many species may reflect the rapid onset of spring after snowmelt and fixed developmental schedules (Miller-Rushing et al., 2008).

#### 4.3 | Contrasting responses of different growth forms to warming

We found significant differences between growth forms in the magnitude of phenological shifts for the early phenophases (leaf out, flowering). The advance in leaf out was about three times stronger in trees, shrubs and dwarf shrubs (−3.1, −3.3, −2.7 days/

decade respectively) than in herbs ( $-1$  day/decade). We attribute this pattern to the more direct exposure of leaf buds to ambient air (Heberling et al., 2019) for woody plants, while the effects of warming spring temperatures on herbs may be buffered by snow cover, soil and surrounding vegetation (Geiger et al., 2009). The lower sensitivity of herbs to spring temperatures (Appendix S4) as compared to other growth forms supports this assumption. This suggests that over time, trees may be shading out wildflowers and reducing their period of full sunlight early in the spring (Heberling et al., 2019).

The timing of first flowering was advanced in trees and shrubs at comparable rates (1.9 and 1.5 days/decade), and was greater than for dwarf shrubs and herbs. The differences between growth forms were overall significant, even though post hoc tests were not able to identify specific groups, presumably due to data limitations, which resulted in low power when accounting for multiple comparisons. Nevertheless, a stronger advance in flowering in the taller woody plants (trees and shrubs) would be plausible given their higher phenological responsiveness to spring temperature (Appendix S4; Heberling et al., 2019). First, the flower buds of trees and shrubs are directly exposed to the ambient air and, thus, can better track changing air temperature, both year-to-year variation and long-term warming trends. Second, such species can quickly activate reproductive tissues once ambient temperatures approach their optimal physiological range without the need to produce sustaining photosynthetic tissues first, which occurs in many herbs (Du et al., 2020). Dwarf shrubs also possess the former adaptation, but due to their short stature, their responsiveness to warming trends is limited by the buffering effects of near-ground climatic conditions on the warming trends (Geiger et al., 2009) and altered light quality and quantity, due to the warming-induced earlier leaf out in trees and shrubs (Figure 3; Heberling et al., 2019).

The timing of fruiting advanced significantly for all growth forms, albeit at slightly different rates, from 1.4 days/decade in shrubs to 1.7 days/decade in trees and herbs. These differences among growth form, however, were not significant. There are two possible explanations for the observed advance of fruiting across growth forms. First, the advance of first fruit in trees can be related to the close link between flowering and fruiting; plants produce fruits earlier because they flower earlier as response to warmer temperatures (Gallinat et al., 2018). This assumption is supported by our data indicating comparable paces of shifts in flowering and fruiting in trees and shrubs (Table 1; Figure 5) and high temperature sensitivity of mid-season fruiting to spring temperature (Appendix S4). The second explanation is based on seed dispersal pressure; the plants of all four growth forms might be under strong evolutionary pressure to maintain fruiting in a specific phenological window, in order to maximize seed dispersal (by animals) during the comparatively short Siberian growing season (Gallinat et al., 2018).

Senescence was significantly delayed for all growth forms, with the strongest shift for herbs (2.1 days/decade) and somewhat weaker shifts for trees, shrubs and dwarf shrubs (1.2, 1.0 and 1.1 days/decade respectively). These differences between the growth forms were, however, not significant. It is possible that woody plants might

show a differing senescence response to a changing climate due to their higher susceptibility to frost events, which is one senescence trigger (Gallinat et al., 2015, 2018). In a highly seasonal Siberian climate, there is typically a rapid temperature drop at the end of the growing season characterized by high probability of frosts (Suzuki et al., 2001; Ye & Cohen, 2013), especially radiation frosts during still nights with a clear sky (Sakai & Larcher, 1987). Frosts at the end of the growing season may be most significant for trees as the coldest temperatures are at the top of the vegetation. On the other hand, the effects of frost on senescence in herbs may be buffered and delayed by the soil, which moderates the local surface temperature (Geiger et al., 2009). Alternatively, photoperiod responses might have different importance as a senescence trigger in trees, shrubs, dwarf shrubs and herbs. This suggestion remains to be tested, as comparative research into this topic is largely unavailable (Gallinat et al., 2015).

## 5 | CONCLUSIONS

This study reports results of long-term (1976–2018), multi-species and multi-phenophase phenological observations at the Barguzin Nature Reserve in Siberia. We find that the Siberian boreal forest plants are advancing their early (leaf out and flowering) and mid-season (fruiting) phenology and delaying the onset of senescence, at comparable rates to other cold climates with high seasonality. These results suggest a strong response of the Siberian boreal ecosystem to recent global warming, a pattern which has not been previously reported for this remote region and which plays an important role in global ecology. The results further indicate that during the last four decades, the growing season in the Siberian boreal forests has extended by approximately 15 days. The longer growing season might have led to increased productivity (higher biomass production, but see Zani et al., 2020) and higher fecundity (e.g. Sletvold & Ågren, 2015) in this temperature-limited ecosystem. Globally, the extended growing season might also imply the higher carbon sequestration potential of Siberian boreal forests under climatic warming (Keenan et al., 2014; Leinonen & Kramer, 2002).

Furthermore, our study also revealed considerable variability among individual species and plant growth forms in their response to a warming climate. Parts of these species-specific differences were explained by their traits (growth form), but a significant amount of interspecific variation in phenological sensitivity remained unexplained. Future work should both aim at a better understanding of the ecophysiological mechanisms behind these differences in direction and/or magnitudes, and also at their possible implications for Siberian plants. For example, species that did not shift their phenology during the last four decades of warming might be less well adapted to climate change and may eventually become outcompeted by more flexible species (Willis et al., 2008).

Further work is also needed on how climate change at Siberian sites is affecting animals, including the arrival and departure of migratory birds, and the spring emergence of insects. It would be particularly valuable to know if different phenological responses among

ecologically linked species of plants and animals have the potential to create phenological mismatches. For example, how does the earlier maturation of fruits impact the ecology of fruit-eating birds, and affect their autumn migration times?

More generally, the contrasting phenological responsiveness of individual species and plant growth forms to temperature shifts suggests that climate change may considerably alter the functioning of Siberian boreal forest communities, due to phenological mismatches within and among different trophic levels (e.g. plant–plant and plant–insect interactions; Heberling et al., 2019; Ovaskainen et al., 2013; Panchen & Gorelick, 2017). Possible changes in these interactions are unknown in Siberia, and we still need detailed studies in different biomes and climate zones to explain synchrony or asynchrony across trophic levels to assess future possible consequences.

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## AUTHOR CONTRIBUTION

Denis V. Sandanov and Sergey Rosbakh conceived the paper. Evgenya V. Bukharova and Denis V. Sandanov collected the data. Sergey Rosbakh and Florian Hartig performed the statistical analysis. Sergey Rosbakh, Tara K. Miller and Richard B. Primack wrote the first version of the manuscript. All the authors contributed substantially to the paper and gave approval for publication.

## DATA AVAILABILITY STATEMENT

The data used for the analysis are available on Zenodo (<https://zenodo.org/record/3607556%23.YGMLqVVzTIU>).

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## SUPPORTING INFORMATION

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

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