



Characterizing spring phenology in a temperate deciduous urban woodland fragment: trees and shrubs

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Abstract

Phenological research in temperate-deciduous forests typically focuses on upper canopy trees, due to their overwhelming influence on ecosystem productivity and function. However, considering that shrubs leaf out earlier and remain green longer than trees, they play a pivotal role in ecosystem productivity, particularly at growing season extremes. Furthermore, an extended growing season of non-native shrubs provides a competitive advantage over natives. Here, we report spring phenology, budburst, leaf-out, and full-leaf unfolded (2017–2021) of a range of co-occurring species of tree (ash, American basswood, red oak, white oak, and boxelder) and shrub (native species: chokecherry, pagoda dogwood, nannyberry, American wild currant and Eastern wahoo, and non-native species: buckthorn, honeysuckle, European privet, and European highbush cranberry) in an urban woodland fragment in Wisconsin, USA, to determine how phenology differed between plant groups. Our findings show that all three spring phenophases of shrubs were 3 weeks earlier ($p < 0.05$) than trees. However, differences between shrubs groups were only significant for the later phenophase; full-leaf unfolded, which was 6 days earlier ($p < 0.05$) for native shrubs. The duration of the spring phenological season was 2 weeks longer ($p < 0.05$) for shrubs than trees. These preliminary findings demonstrate that native shrubs, at this site, start full-leaf development earlier than non-native species suggesting that species composition must be considered when generalizing whether phenologies differ between vegetation groups. A longer time series would be necessary to determine future implications on ecosystem phenology and productivity and how this might impact forests in the future, in terms of species composition, carbon sequestration, and overall ecosystem dynamics.

Keywords Spring phenology · Timing and duration · Temperate deciduous trees · Native shrubs · Non-native shrubs

Introduction

The complex phenology inherent in temperate deciduous forest ecosystems has implications for a range of ecological processes such as determining the active photosynthetic and carbon uptake periods, regulating the hydrological cycle, and influencing synchrony across trophic levels. Regulation of these processes is determined by the timing and duration

of phenological events across species, populations, and communities. For example, the timing of the start of budburst defines a transition in ecosystem processes from dormancy to photosynthetic activity (e.g., Peñuelas et al. 2009), nutrient cycling (Ehrensfield 2003), and food availability (e.g., Pettoirelli et al. 2007). Therefore, any disruption to the timing of phenological events by changes in species composition, for example, could have consequences for overall ecosystem dynamics. Furthermore, as temperatures rise due to climate change, the timing of spring phenophases such as budburst in many temperate deciduous trees occurs earlier in the season (e.g., Menzel et al. 2006; Piao et al. 2007) and may be accompanied by accelerated leaf development (Richardson and O'Keefe 2009; Klosterman et al. 2018) giving rise to greater net primary production and increased food availability for herbivores. Despite the role of leaf development in determining the magnitude and pace of carbon uptake, surprisingly few studies report the duration of phenophases

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(Klosterman et al. 2018) or the implications of changing phenophase duration on ecosystem function. A small number of studies have shown that a later start to spring tends to result in a faster leaf development rate in some temperate deciduous trees (Richardson and O'Keefe 2009; Klosterman et al. 2018), but not all (Donnelly et al. 2017). Therefore, reporting both the timing and duration of phenophases is important for accurately estimating future changes in carbon budgets and food availability.

Given that trees are the dominant plant functional type in forest ecosystems, in terms of abundance and biomass, it is not surprising that their phenology has tended to be more widely reported than other plant groups (Gill et al. 1998; Donnelly and Yu 2017, 2021; Huff et al. 2018). However, in recent years, the need to quantify the contribution of the shrub community to the overall phenological profile of temperate deciduous forests has gained recognition due to their role in ecosystem processes such as gas exchange, nutrient cycling, and as a food source (Donnelly and Yu 2021; Schuster et al. 2021; O'Connell and Savage 2020; Maynard-Bean et al. 2020). Since shrubs tend to leaf out prior to trees in spring, in order to take advantage of high light levels, and often senesce after trees become leafless in autumn (Schuster et al. 2021), they contribute to an extension of the growing season in temperate deciduous forest ecosystems (Panchen et al. 2014; 2015; Schuster et al. 2021). The extended growing season of shrubs can influence factors such as response to climate change, biodiversity within an ecosystem, species composition, and the carbon balance (reviewed in Donnelly and Yu 2021). In addition, shrubs play a pivotal role in temperate deciduous forest ecology by providing food and habitat for a range of organisms as well as contributing to nutrient and carbon cycling (Fridley 2012). Even though shrubs have a longer growing season than trees, the difference is rarely quantified, and few studies have focused specifically on shrub phenology. Therefore, characterizing shrub phenology will improve our understanding of the role shrubs play in ecosystem processes especially in early spring and provide insights into the future response of temperate forest ecosystems to climate change.

The challenge of shrub invasion in forested ecosystems is not new, and the role of phenology in the invasion process has gained attention in recent years (Polgar and Primack 2011; Fridley 2012; Donnelly and Yu 2017, 2021; Schuster et al. 2021; O'Connell and Savage 2020; Maynard-Bean et al. 2020; Maynard-Bean and Kaye 2020; Schuster et al. 2021). Therefore, it is necessary to characterize the phenology of non-native compared to native shrubs in order to determine any potential competitive advantage. In a 3-year common garden experiment, Fridley (2012) observed the timing of leaf-out [and leaf fall] of a suite of 43 native and 30 non-native shrubs common to deciduous forests in eastern USA. He reported that native shrubs tended to

leaf out earlier than non-native species in spring. However, other field studies in northeastern (Polgar et al. 2014) and Midwestern (Harrington et al. 1989) USA indicated that non-native shrubs leafed out earlier in spring than natives, thus giving them a competitive advantage. Earlier leafing in spring has been shown to reduce niche overlap through shade avoidance, thus enhancing competitive advantage for non-native species (Wolkovich and Cleland 2011). Furthermore, Schuster et al. (2021) reported comparable spring phenology between the non-native buckthorn and four native shrubs in a common garden experiment in Minnesota. These somewhat contrasting results highlight the need for further research to quantify the phenology of co-occurring shrubs (native and non-native) and trees growing in the wild. Since, in the medium term (20–50 years), the species composition of shrubs is more likely to change due to invasion than longer-lived trees, it is important to understand the phenology of native and non-native shrub species competing in the same forest and how they may respond to future warming and what the implications may be for shrub species composition over time.

While a small number of studies (Fridley 2012; Knight et al. 2007; O'Connell and Savage 2020; Schuster et al. 2021) compared the phenology of temperate deciduous native and non-native shrubs, most were from common gardens or other controlled systems over very few years (1–3). These studies provide valuable insights into how native and non-native shrub phenology differ but may not be reflective of what happens in the wild. The objective of the current work was to characterize the timing and duration of spring phenophases of a small number of temperate deciduous shrubs and trees growing in a natural habitat, in an urban woodland fragment in Wisconsin, USA. Our aims were to (i) quantify differences in phenology between shrubs and trees and (ii) investigate whether consistent differences in phenology existed between native and non-native invasive shrub species in spring.

Materials and methods

In situ phenological observations: data collection and preprocessing

This study was conducted, over a 4-year period (2017, 2018, 2020, and 2021), in Downer Woods (43°4'52"N, 87°52'51"W), a small (4.5 ha) urban woodland fragment on the University of Wisconsin-Milwaukee campus (southeastern Wisconsin, USA). The tree and shrub community is typical of that found in temperate deciduous forests throughout Midwestern USA (further site information in Yu et al. 2016). All trees observed were native species, while the shrubs were categorized into native and non-native (Table 1). The

Table 1 List of temperate deciduous tree and shrub species monitored at Downer Woods, Wisconsin, USA (2017–2021). The number (*N*) of individual plants for some species varied across years due to insect damage, disease, and death

Plant group	Species	<i>N</i>	
Tree species	<i>Fraxinus</i> spp. (ash)	3–8	
	<i>Tilia americana</i> (American basswood)	11	
	<i>Quercus rubra</i> (red oak)	3	
	<i>Quercus alba</i> (white oak)	4	
	<i>Acer negundo</i> (boxelder)	3	
Shrub species	Native	<i>Prunus virginiana</i> (chokecherry)	4–5
		<i>Cornus alternifolia</i> (pagoda dogwood) added in 2018	2–3
		<i>Viburnum lentago</i> (nannyberry)	5
		<i>Ribes americanum</i> (American wild currant)	5
		<i>Euonymus atropurpureus</i> (Eastern wahoo) added in 2018	2
	Non-native	<i>Rhamnus cathartica</i> (buckthorn). Introduced from Europe as an ornamental	5
		<i>Lonicera morrowii</i> (honeysuckle). Introduced from Asia as an ornamental	1–3
		<i>Ligustrum vulgare</i> (European privet). Introduced from Europe as an ornamental	3
		<i>Viburnum opulus</i> (European highbush cranberry). Introduced from Europe as an ornamental	7–9

selected trees were a subset of an ongoing phenology monitoring campaign (Yu et al. 2016) and were chosen due to their proximity to the shrubs which were centrally located within the woodland fragment under closed canopy to avoid edge effects. In general, the individual trees being monitored remained healthy throughout the study period apart from the *Fraxinus* spp. which became infested by the emerald ash borer (*Agrilus planipennis*) resulting in a number of trees being unsuitable for monitoring. Our aim was to monitor 3–5 randomly chosen individual plants of each species each year, but this was not always possible. The shrubs were susceptible to attack from pests and pathogens and accidental death. For example, individuals of *V. opulus* were practically totally defoliated due to attack by the viburnum leaf beetle (*Pyrrhalta viburni*). In addition, *V. lentago* became progressively infected by powdery mildew during the growing season, and, finally, two of the *Ribes americanum* individuals were knocked over when a dead tree fell on them. Due to these natural occurrences, it was not possible to monitor the same individuals throughout the time period of the study. Therefore, in order to maintain a continuous time series of shrub phenology at the study site, we selected nearby healthy individuals, of similar size and canopy structure, to replace the diseased or dead ones. Furthermore, some species were added to the campaign after monitoring began. Even though we did not monitor the same individuals or the same number of individuals of each species each year, we are confident that the data collected remains representative of the overall shrub phenology at the site. Tree data for spring 2019 showed a number of inconsistencies due to observer error. For example, a number of individual trees progressed from dormant buds to full-leaf unfolded in 2–3 days which was

considered unlikely to be accurate. Therefore, the quality of the data was considered too questionable to include in the analyses, and we omitted all observations (trees and shrubs) for spring 2019.

Technical note

One of the dominant shrubs present at our study site was *Viburnum opulus* L. (known as European highbush cranberry in North America and Guelder rose in the UK). As the common name suggests, *V. opulus* was introduced to North America from Europe and has a closely related native congener, *V. trilobum* Marshall (American highbush cranberry). The two species are easily confused but can be distinguished by the size and shape of the petiolar glands on the leaf stalk just below the leaf blade (Voss and Reznicek 2012). The taxonomy of *V. opulus* and *V. trilobum* is not resolved. While they are sometimes treated as separate species (Voss and Reznicek 2012; Flora of Wisconsin—<https://wisflora.herbarium.wisc.edu/taxa/index.php?taxon=13468>), *V. trilobum* can also be treated as a variety or subspecies of *V. opulus*. Under this classification, *V. opulus* var. *opulus* is the introduced European variety, and the native variety is referred to as *V. opulus* var. *americanum* Aiton or *V. opulus* subsp. *trilobum* (Marshall) R.T. Clausen (Voss and Reznicek 2012). For example, the USDA PLANTS Database treats these taxa as varieties and lists both the European *V. opulus* var. *opulus* and the native *V. opulus* var. *americanum* for Milwaukee County, Wisconsin. Chadde (2000) also treats the two taxa as varieties rather than full species.

Because of the similarities between the two varieties, European cranberry is often sold in garden centers as

the native highbush cranberry and widely planted as an ornamental shrub. It readily escapes cultivation and hybridizes with the native variety (<https://www.minnesotawildflowers.info/shrub/american-highbush-cranberry>). However, after much scrutiny, we are confident that the *V. opulus* in Downer Woods is the non-native species and therefore included in the non-native shrub group.

In situ phenological observations were recorded for the co-occurring tree and shrub species (Table 1) 3–4 times per week throughout the spring seasons. We used data for three spring phenophase categories: budburst (bud scales parted and tiny amount of leaf tip visible), leaf-out (obvious leaf tips emerging from bud), and full-leaf unfolded (leaf emerged and petiole clearly visible). Note: full-leaf unfolded does not mean the leaves had reached their fully mature size. On each occasion, each individual plant was observed, and the percentage of buds or leaves

at the most advanced phenophase was recorded. Each category was subdivided into 10 percentage classes (<10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80%, 80–90%, and >90%) representing progressively more advanced stages of development. The duration of the spring phenological season was determined by the number of days between phenophase categories <10% budburst and >90% full-leaf unfolded. Linear interpolation (see Sect. 2.3 below for details) was used to determine the day of year (DOY) for pheno-categories that were not directly observed in the field.

Statistical analyses

Four interpolation methods (linear, pchip, spline, and makima) were compared to determine which was best suited to the phenological data (Fig. 1). In contrast to linear interpolation, pchip, spline, and makima

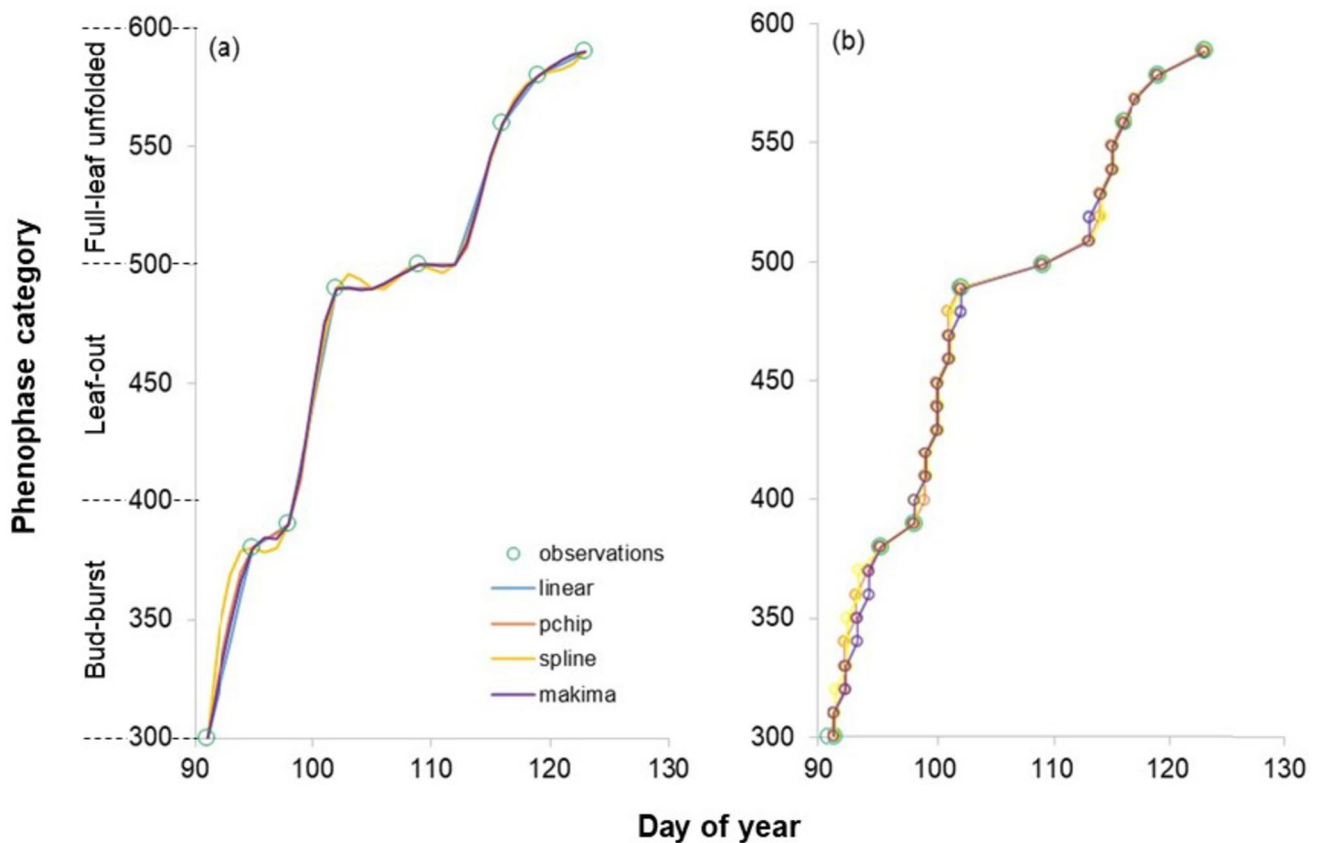


Fig. 1 Day of year (DOY) for spring phenophase categories 300 to 590 (300: budburst; 400: leaf-out; 500: full-leaf unfolded). Each category was subdivided into 10 percentage classes (<10%, 10–20%, 20–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80%, 80–90%, and >90%). For example, phenophase value of 350 meant that between 50 and 60% of the buds were open, whereas a value of 500 indicated that <10% of the leaves on the shrub were fully unfolded. Comparison of in situ spring phenological observations (2021) and

a range of data interpolation methods (linear, pchip, spline, and makima) for a native shrub species (*Prunus virginiana* chokecherry) at Downer Woods, University of Wisconsin-Milwaukee, USA. **a** Phenophase category interpolated based on observed DOY (green circles) and **b** DOY of each phenophase category based on observations (green circles). Color scheme for interpolation methods same for each graph

perform different forms of piecewise cubic Hermite interpolation which attempts to smooth the data fit. Visual inspection of the different methods suggested that all perform reasonably well, so we decided to use the simplest method, i.e., linear interpolation for all further data analyses.

ANOVA was used to test differences in the mean timing and duration of spring phenophases across years, between trees and the shrub community (combined native and non-native). Nested ANOVA with Tukey's post hoc test was used to identify significant differences in the mean timing and duration of phenophases between three vegetation groups: native shrubs, non-native shrubs, and trees across years. Vegetation category (native shrubs, non-native shrubs, and trees), species, and year were included as the main effects in the model with species being nested under vegetation category. The interaction term examined was vegetation category*year. All statistical tests were carried out using IBM SPSS version 20.0.

Results

Comparison of the timing and duration of spring phenophases of trees and shrubs in an urban woodland community

Across years and species, the start of budburst, leaf out, and full-leaf unfolded occurred on DOY 96, 108, and 120, respectively, in the shrub community (native and non-native species combined), which was significantly ($p < 0.001$) consistently earlier than the trees (DOY 121, 129, and 137, respectively) (Fig. 2a; Table 2). The difference in timing decreased from budburst (25 days) to full-leaf unfolded (17 days), indicating that tree development progressed at a faster rate than the shrub community. Out of three spring phenophases, full-leaf unfolded was the only spring phenophase to occur statistically significantly ($p < 0.05$) earlier (6 days) in native compared to non-native shrubs (Fig. 2a, Tables S8–S10). The timing of budburst did not differ significantly across native shrub species (Fig. 3a:

Fig. 2 Boxplots showing the distribution (2017, 2018, 2020, 2021) of start time (DOY) of three spring phenophases **a** budburst (< 10% bud-scales parted), leaf out (< 10% leaf-tip visible), and full-leaf unfolded (< 10% leaves fully unfolded), and **b** duration (days between start (< 10%) and end (> 90%)) of budburst, leaf out, full-leaf unfolded and the spring phenological season (days between start of budburst and end of full-leaf unfolded) for average of five native (chokecherry, dogwood, Eastern wahoo, nannyberry, and wild currant) and four non-native (buckthorn, highbush cranberry, honeysuckle, and privet) temperate deciduous shrubs, and five native tree species (ash, basswood, boxelder, red oak, and white oak) at Downer Woods, Wisconsin, USA. Horizontal lines represent the minimum, first quartile, median, third quartile, and maximum values in the distribution. "X" represents distribution mean, and dots are outliers. Means with different letters denote statistical differences within phenophases. Statistical analyses are available in supplemental material Tables S7–S10; S20–S23

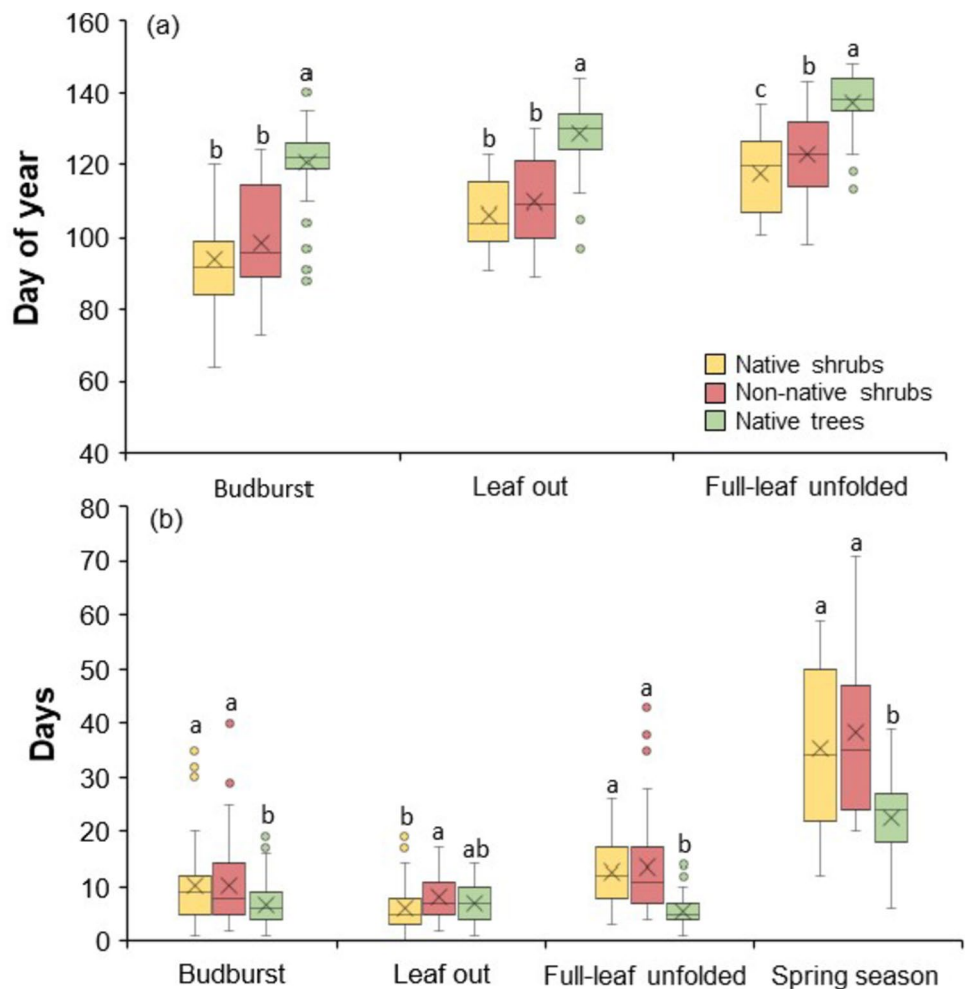


Table 2 Results of an ANOVA test comparing differences between trees and shrubs (native and non-native combined) for the start (average DOY \pm SE) and duration (average number of days \pm SE) of spring

Average	Budburst (DOY)	Leaf-out (DOY)	Full-leaf unfolded (DOY)	Duration of phenophases (days)			
				Budburst	Leaf-out	Full-leaf unfolded	Spring phenological season
Trees	121 ^a \pm 0.91	129 ^a \pm 0.88	137 ^a \pm 0.74	6.8 ^b \pm 0.40	7.1 ^a \pm 0.34	5.5 ^b \pm 0.25	22.6 ^b \pm 0.65
Shrubs	96 ^b \pm 1.29	108 ^b \pm 0.95	120 ^b \pm 0.95	10.2 ^a \pm 0.66	7.2 ^a \pm 0.35	13.1 ^a \pm 0.64	36.8 ^a \pm 1.36

phenophases. Means with different letters denote statistical differences at $p \leq 0.05$. Statistical tests are available in supplemental materials Tables S1–S7

Table S11). However, significant differences emerged in later spring phenophases. For example, Dogwood leafed out later ($p < 0.05$; 21 days) than Eastern wahoo (Fig. 3b; Table S12) and reached full-leaf unfolded later ($p < 0.05$; 16 days) than wild currant (Fig. 3c) (Table S13). Within the non-native grouping, honeysuckle exhibited an earlier ($p < 0.05$; 10 to 20 days) start to all three spring phenophases (Tables S14–S16) and boxelder was the first of the trees to start ($p < 0.05$; 17 to 30 days) each phenophase (Fig. 3a–c) (Tables S17–S19).

In general, the duration of each phenophase was longer for shrubs compared to trees (Fig. 2b; Table 2). Budburst and full-leaf unfolded lasted, on average, 10 and 13 days, respectively, for shrubs which was significantly ($p < 0.05$) longer compared to 7 and 6 days for trees. Overall, the spring phenological season lasted 14 days longer ($p < 0.05$) for shrubs (37 days) than trees (23 days) (Fig. 2b; Table 2). Leaf-out was the only spring phenophase to exhibit a statistically significantly ($p < 0.05$) shorter (2 days) duration for native compared to non-native shrubs (Fig. 2b, Tables S20–S23). Furthermore, no consistent pattern was observed within the native shrub grouping as regards individual species, across spring phenophase durations (Fig. 3d–g; Tables S24–S27). However, within the non-native shrubs, only honeysuckle exhibited a significantly ($p < 0.05$) longer (12–13 days) duration of full-leaf unfolded compared to other non-native species (Fig. 3d–f; Tables S28–S31). The duration of leaf-out was 4 days longer ($p < 0.05$) for white oak than both ash and basswood (Table S33), whereas boxelder exhibited a 3-day longer ($p < 0.05$) full-leaf unfolded duration than basswood and white oak (Fig. 3d–f; Table S34) which contributed to a 1–2 week longer ($p < 0.05$) spring duration than for other trees (Table S35).

Interannual variation in the timing and duration of spring phenophases of trees and shrubs in an urban woodland community

Differences in the timing of budburst, leaf-out, and full-leaf unfolded between vegetation groups exhibited a statistically significant ($p < 0.001$) interaction with year indicating

that differences were greater in some years than other (Table S36–S38). In particular, differences in the timing of the spring phenophases between shrubs (native and non-native) and trees were much smaller in 2018 compared to other years, and the difference increased for native full-leaf unfolded in shrubs (Tables S39–S41; Fig. 4a–c). In 2018, the timing of budburst was 8 days ($p < 0.05$) and 4 days ($p < 0.002$) earlier in native and non-native shrubs compared to trees (Table S39). In other years, the difference ($p < 0.01$) between shrubs (native and non-native) and trees was much greater and varied from 22 to 39 days (Fig. 4a). Even though the difference in timing of leaf-out and full-leaf unfolded between trees and shrubs (native and non-native) was statistically significant, the difference was smaller in 2018 (Fig. 4a–c; Tables S39–S41).

A statistically significant ($p < 0.001$) interannual pattern emerged for the duration of each spring phenophase and the spring phenological season, whereby differences in phenophase duration between trees and shrubs (native and non-native) were smaller, for most phenophases, in 2018 compared to other years (Fig. 4d–f; Tables S42–S49). The duration of full-leaf unfolded was between 1 and 18 days shorter ($p < 0.001$) in trees than shrubs (native and non-native) across years, but the difference was smallest in 2018 (1–2 days) (Fig. 4e; Table S48). Differences in the duration of the spring phenological season followed a similar pattern being shorter (9–30 days; $p < 0.001$) in trees than shrubs in all years apart from 2018 (Fig. 4g; Table S49).

Discussion

Interest in temperate deciduous shrub phenology has increased in recent years due to their earlier leafing, compared to trees (Kato and Komiyama 2002; Jolly et al. 2004; Schuster et al. 2021), which extends the photosynthetically active period of these ecosystems particularly at the extremes of the seasons (Fridley 2012; Panchen et al. 2014, 2015; Polgar et al. 2014; Donnelly et al. 2019, 2020). In addition, the phenological characteristics of non-native shrub species has been cited as a potential contributing factor to

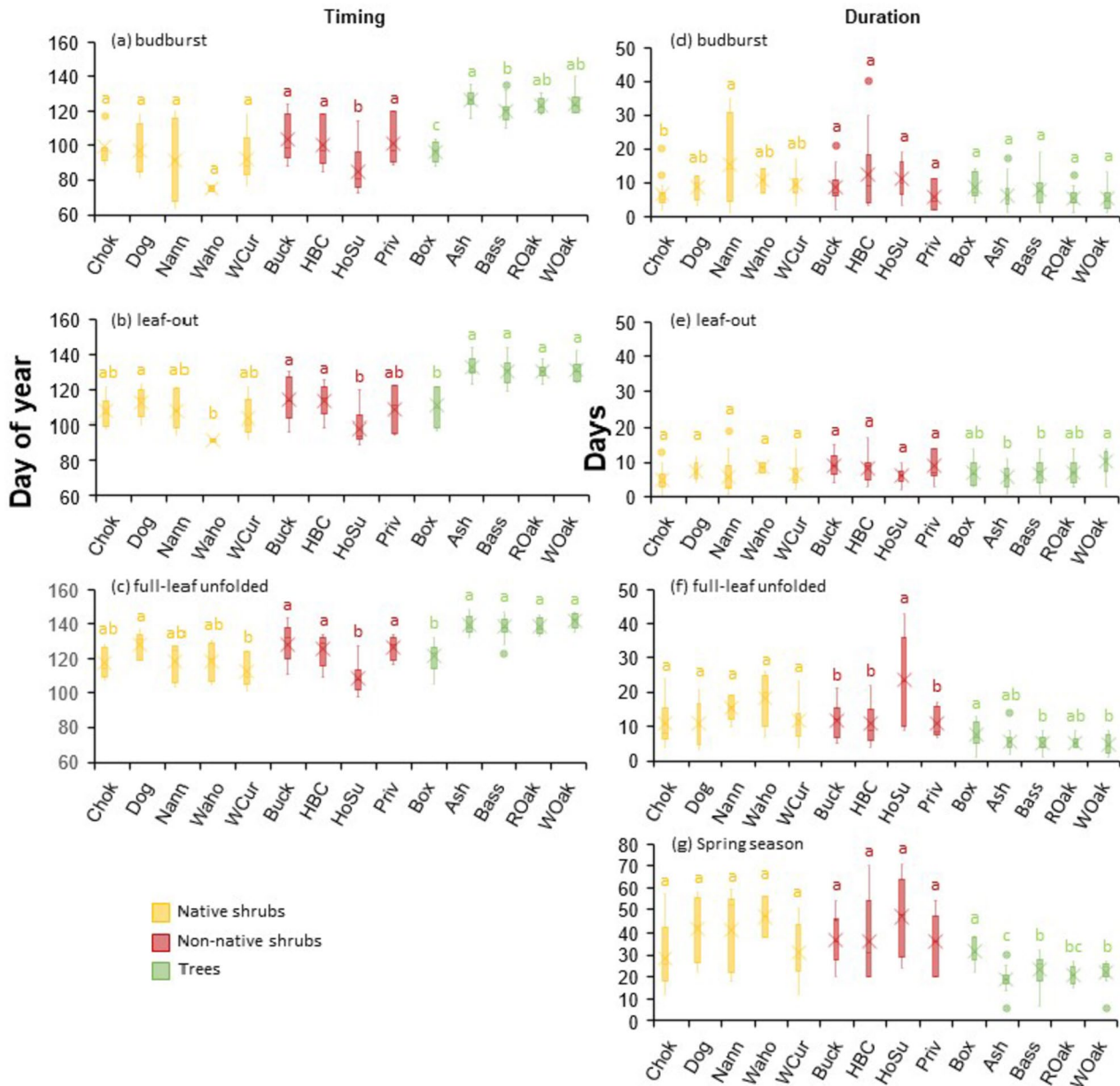


Fig. 3 Boxplots showing the distribution (2017, 2018, 2020, 2021) of the start time (day of year) of three spring phenophases **a** budburst (<10% bud-scales parted), **b** leaf out (<10% leaf-tip visible), and **c** full-leaf unfolded (<10% leaves fully unfolded), and duration (days between start (<10%) and end (>90%)) of **d** budburst, **e** leaf out, **f** full-leaf unfolded, and **g** the spring phenological season (days between start of budburst and end of full-leaf unfolded) for five native (chokecherry (Chok), dogwood (Dog), Eastern wahoo (Waho), nannyberry (Nann) and wild currant (WCur)) and four non-native (buck-

thorn (Buck), highbush cranberry (HBC), honeysuckle (HoSu), and privet (Priv)) temperate deciduous shrubs, and five native tree species (ash (Ash), basswood (Bass), boxelder (Box), red oak (ROak), and white oak (WOak)) at Downer Woods, Wisconsin, USA. Horizontal lines represent the minimum, first quartile, median, third quartile, and maximum values in the distribution. “X” represents distribution mean, and dots are outliers. Means with different letters denote statistical differences within plant groups. Statistical analyses are available in supplemental material (Tables S11–S19; S24–S35)

their competitive advantage over native shrubs. Many of these studies have focused on one non-native shrub species growing among native species in a natural habitat (e.g., Harrington et al. 1989; Chen and Matter 2017; O’Connell and Savage 2020; Schuster et al. 2021), or many species of native and non-native shrubs growing together in a common

garden (Fridley 2012). Our unique study both complements and advances previous research by characterizing the timing and duration of spring phenology of co-occurring temperate deciduous trees and a suite of native and non-native shrubs growing in a fragment of natural woodland located in an urban setting in Milwaukee, WI, USA.

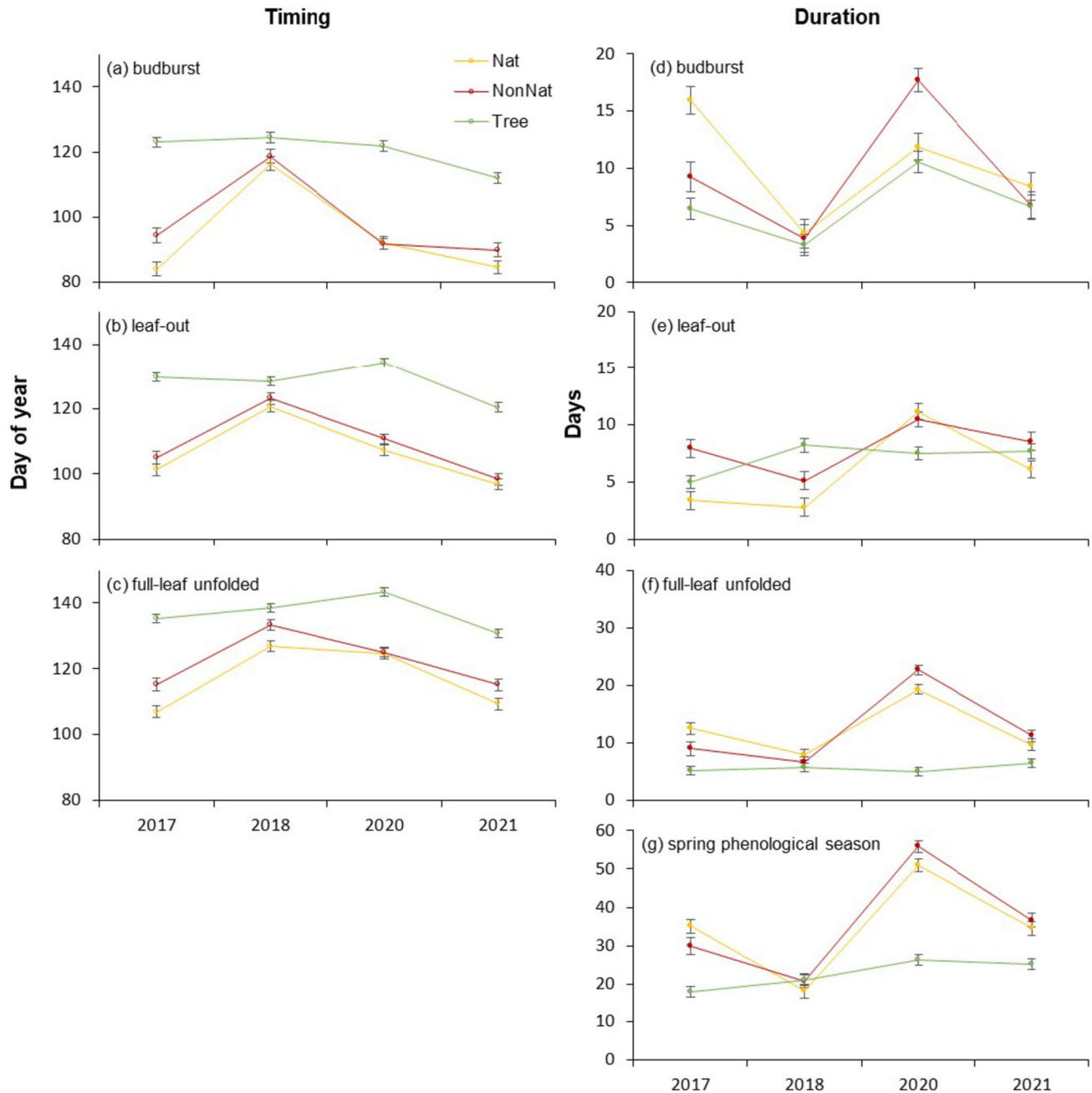


Fig. 4 Mean and standard error (vertical bars) (2017, 2018, 2020, 2021) start time (day of year) of three spring phenophases **a** budburst (<10% bud-scales parted), **b** leaf out (<10% leaf-tip visible), and **c** full-leaf unfolded (<10% leaves fully unfolded), and duration (days between start (<10%) and end (>90%)) of **d** budburst, **e** leaf

out, **f** full-leaf unfolded, and **g** the spring phenological season (days between start of budburst and end of full-leaf unfolded) for native shrubs (Nat), non-native shrubs (NonNat), and trees (Tree) across years. Note scales differ, and data for 2019 are missing. Differences are generally smaller in 2018 than other years

Timing and duration of spring phenophases of trees and shrubs in an urban woodland community

As was expected, on average, the timing of the three spring phenophases, budburst, leaf out, and full-leaf unfolded, occurred significantly earlier in the shrub community (early (DOY 96), mid (DOY 108), and late (DOY 120) April,

respectively) compared to the trees. The time interval between the two groups became progressively shorter as the spring season progressed, i.e., budburst occurred 25 days earlier in shrubs than trees, but full-leaf unfolded was only 17 days earlier. The shrubs reached full-leaf unfolded just as the trees began to budburst which is consistent with results reported by Schuster et al. (2021) in a forested ecosystem in

northern Minnesota. This pattern is typical of a deciduous forest ecosystem whereby understory shrubs exhibit earlier development in order to benefit from high light levels prior to the gradual shading imposed as the canopy closes over.

Three of four non-native shrubs (buckthorn, honeysuckle, and privet) present in Downer Woods have all been identified as major woody invaders of Eastern US forests (Webster et al. 2006). Even though the timing of the start of the three spring phenophases tended to be earlier for native compared to non-native shrubs, the difference was only significant for the latest phenophase, i.e., full-leaf unfolded. To some extent, this contrasts with results reported by Fridley (2012), O'Connell and Savage (2020), and Schuster et al. (2021) in which no difference in the timing of spring phenology between native and non-native shrubs across years was observed. Furthermore, Fridley (2012) reported a slightly later timing for full-leaf emergence in native compared to non-native species, for two out of 3 years, which contrasts with our findings of earlier (overall 2017–2021) timing of full-leaf unfolded for native shrubs. A number of contributing factors may explain some of the differences between these studies including different locations, very short time series and time periods being reported, slight differences in the phenophases being monitored, and differences in study sites. Fridley (2012) reported results from a range of 43 native and 30 non-native shrub and liana species, common to eastern US forests, grown in a common garden in New York, whereas our results are from a smaller number of co-occurring species growing naturally in an urban woodland fragment in Wisconsin. O'Connell and Savage (2020) compared four native and four non-native shrubs in a nature reserve in Minnesota, whereas Schuster et al. (2021) conducted a comparison of one non-native shrub and four native woody species in a common garden. Together, these studies suggest that making generalizations about whether native or non-native shrubs have earlier or later spring phenology than the other is problematic, as experimental conditions and, in particular, species composition vary across sites.

In the current study, there were no consistent patterns in the timing of early spring phenophases among species within the groupings (native and non-native shrubs). Eastern wahoo tended to budburst and leaf out earlier than most other native shrubs but did not differ from other shrubs in the timing of full-leaf unfolded. However, within the non-native group, honeysuckle exhibited consistently earlier timing of all three early spring phenophases. Therefore, even though the number of individual species within each group was small (5 native and 4 non-native), there tended to be greater consistency among native than non-native shrubs in early spring. There was a clear difference in the timing of early spring phenophases between boxelder and the other trees where budburst, leaf-out, and full-leaf unfolded were 17 to 30 days earlier. This result was not unexpected as boxelder

is a small under canopy tree in the study site and behaves opportunistically taking advantage of high light levels early in the season. This result is consistent with previous experimental observations whereby early successional species, such as Birch and Willow, were shown to budburst earlier than late successional species, such as small-leaf Lime and Beech (Caffarra and Donnelly 2011). Interestingly, as the spring season progressed, the difference in timing of the phenophases between boxelder and the other trees decreased, suggesting that the upper canopy trees progressed through spring phenophases at a faster rate.

The phenology of buckthorn has been reported to be unique or distinctive from native shrub species, thus contributing to its success as an invader (Knight et al. 2007); however, in recent years, its distinctiveness from other species has been challenged (Schuster et al. 2021). Earlier leafing of buckthorn compared to co-occurring native shrubs (*Cornus racemosa* and *Prunus serotina*) growing in the wild has been reported previously for one growing season (Harrington et al. 1989); however, more recently, in a common garden experiment in Minnesota, budburst was earlier for buckthorn but still comparable to five native woody (tree and shrub) species (*Sambucus canadensis*, *Sambucus racemosa*, *Corylus americana*, *Cornus racemosa*, and *Acer saccharum*) (Schuster et al. 2021). In addition, O'Connell and Savage (2020) reported that native (*Cornus sericea*, *Corylus cornuta*, *Rubus idaeus*, *Viburnum lentago*) and non-native shrubs (*Berberis thunbergii*, *Frangula alnus*, *Lonicera X bella*, *Rhamnus cathartica*) leafed out simultaneously over a 2-year period in a forest ecosystem also in Minnesota, USA. Interannual differences in spring phenology for native and non-native shrubs reported by O'Connell and Savage (2020) whereby spring occurred later and progressed faster in 2018 than in 2017 were similar to our findings for 2018. Even though Minnesota is further north and the species were different from our site, the pattern was similar albeit spring started earlier in Wisconsin. Interestingly, our findings showed that early spring phenophases for honeysuckle were consistently earlier than other non-native shrubs, suggesting that early and late phenology is relative, making species comparison key in determining if natives are earlier or later than non-natives. Therefore, whether native shrubs exhibit earlier or later phenology than non-native shrubs will be site-specific and dependent more on species composition than origin.

Few studies report the duration of phenophases; however, we found the duration of budburst and full-leaf unfolded was consistently longer in the shrub community (3 and 7 days, respectively) compared to the trees and resulted in a significantly longer spring phenological season. The difference in the duration of the phenophases increased as the leaves developed with a 3-day difference in the duration of budburst between the shrub and tree communities and a 7-day

difference in the duration of full-leaf unfolded. Overall, leaf development started later and progressed at a faster rate in trees compared to the understory shrub community which reflects the conservative nature of late growth and development in trees to avoid excess damage from potential late frost. There were very few differences in the duration of spring phenophases between native and non-native shrubs with leaf-out being the only phenophase to exhibit a small but significant difference lasting 2 days longer in the non-native (9 days) group. The lack of consistent differences in the duration of spring phenophases among individual native and non-native shrubs suggested a high level of consistency across groups. However, given the opportunistic behavior of boxelder (*Acer negundo*), the duration of the spring phenological season was 1–2 weeks longer than later successional trees which was primarily driven by a longer full-leaf unfolded than the earlier phenophases. Opportunistic species, such as *Betula pubescens* and *Salix simthiana*, have previously been demonstrated experimentally to respond to high light levels and warming temperatures earlier in the season compared to the long-lived late successional species *Tilia cordata* and *Fagus sylvatica* (Caffarra and Donnelly 2011).

Interannual variation in the timing and duration of spring phenophases

Interannual variation in the timing and duration of both spring and autumn phenophases is to be expected due to differences in growing conditions across years. In the current study, the timing of spring phenophases across plant groups was fairly consistent across years whereby native shrubs were earliest and trees latest. However, the number of days difference in timing between the plant groups was not consistent with differences being smaller in some years. Of particular note was 2018, whereby the timing of spring phenophases was significantly later in shrubs (native and non-native) compared to other years. This resulted in shrub budburst occurring just 2 days (non-native) and 4 days (native) earlier than trees compared to roughly a month in other years. Interestingly, leaf-out and full-leaf unfolded were also later in shrubs in 2018 but to a lesser extent compared to budburst. Overall, the later start to spring phenophases in 2018 resulted in a shorter duration for the phenophases and for the spring season as a whole.

Even though shrub phenology was significantly delayed by nearly 1 month in 2018, the average spring temperature was relatively high (9.4 °C data not shown), but April (DOY 91–120) temperature, which coincides with the time when budburst usually begins, was significantly 1–5 °C lower than in other years. This suggests that shrubs respond well to early season temperature to avoid potential damage by frost. However, it also indicates that the average spring

temperature may be too coarse to predict the timing of early season shrub phenology. Early stage tree phenology was also later in 2018 than other years, but the delay was much less (1–12 days) than for shrubs, presumably, as budburst occurs later in trees and the temperature in early April would be expected to have less of an influence. These results suggest that when phenophases start late in spring, progression of leaf development is faster, which confirms Klosterman et al. (2018) findings that later spring tends to drive faster green-up.

Future phenology of trees and shrubs in an urban woodland community

It will be important to understand how leaf phenology of trees and shrubs will respond to rising temperatures to determine if the current relationship will change in the future (Kato and Komiyama 2002; Jolly et al. 2004). For example, if the timing of leaf-out of trees and shrubs does not advance at the same rate, then light conditions at the shrub level may be sufficiently altered to either reduce or increase shrub productivity and reproductive success (Maeno and Hiura 2000) with potential consequences for herbaceous species, recruitment, and organisms dependent on shrubs for food and habitat. In a warming experiment, Rollinson and Kaye (2012) reported a 14–18-day advance in the timing of tree leaf-out in response to a 2 °C increase in temperature, but shrub phenology did not respond. However, Zohner and Renner (2019) reported the opposite, whereby understory species (mainly shrubs) showed greater response than canopy species to a 4 °C increase in temperature. Species that have early spring phenology are generally more responsive to warming than later developing species due, at least in part, to a lower chilling requirement (Beaubien and Hamann 2011). In addition, early development can provide a competitive advantage through early resource gain (Polgar et al. 2014). Predicting whether native or non-native shrubs will benefit most from projected warming could help inform management plans and accurate carbon budgeting. Therefore, continued phenological monitoring of co-occurring shrubs and trees is of critical importance to understand how both groups will respond to a changing environment and how this will impact temperate deciduous forest dynamics in the future.

Conclusions

Many studies on non-native shrub species in temperate deciduous forests tend to focus on one species, often honeysuckle (*Lonicera spp.*), or in the case of Fridley (2012) a large number of native and non-native shrubs grown together in a common garden. Both approaches have contributed to our understanding of how seasonal phenological profiles may

differ between native and non-native shrubs. However, our unique study which examined a suite of co-occurring native and non-native shrubs growing in the wild highlights the complexities associated with making generalizations based on one species or from experimentally grown shrubs. The species composition of the shrub community in any given forest will determine which group (native or non-native) will leaf out first. We have observed spring phenology to be earlier in some native shrubs than non-native species; therefore, growing a large number of native and non-native shrubs, each with their own range of early and late phenology, in the same location may mask the subtleties of what may occur in a natural ecosystem where only a sub-set of these groups are growing together. In order to reliably predict shrub phenology, and hence potential carbon flux implications, in temperate deciduous forest ecosystems, it will be necessary to accurately determine shrub species composition. The sequence of phenological development in the ecosystem will be determined by the ecological position of the individuals making up the community, whether they are native or non-native shrubs or opportunistic or late successional trees. Given the strong interaction between the timing and duration of phenophases and year and the tendency for delayed timing in spring to result in faster leaf development care must be taken when making generalizations about phenology from 1 year to the next. These results illustrate the importance of considering shrub species composition in determining forest carbon balance and other ecosystem functions and highlight the complexities of interannual variations in shrub and tree phenology, factors which need to be taken into account when making future predictions of the implications for forest phenology. Even though this study was based at one site, with data on a small number of trees and shrubs spanning only a few years, there was clear evidence that native and non-native shrubs behave differently in terms of spring phenology. Therefore, in order to make meaningful predictions of how temperate deciduous ecosystems will respond to future changes in climate, we encourage researchers to collect phenological observations on co-occurring trees and shrubs, across more species, locations, and over longer time periods.

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Author contribution Alison Donnelly conceived and designed the research project, established the monitoring campaign, analyzed the data, and wrote the MS. Rong Yu helped with data analysis. Chloe Rehberg collected some of the data. Mark D. Schwartz provided some data.

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Data Availability All phenological data are in the process of being assessed for inclusion in the data repository PANGAEA (www.pangaea.de).

Declarations

Competing interests The authors declare no competing interests.

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