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Flowering Phenology of Native and Exotic Plants in Species-Rich *Themeda triandra* Grasslands, Western Victoria: Implications for Fire Management

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ABSTRACT

Frequent fire in temperate native grasslands in south-east Australia has maintained high plant diversity. The timing of fire implemented by fire agencies over the last several decades has been in summer and autumn. This coincides with the dormant season for many grassland plants. Recent trends in agency burning, partly driven by earlier curing and the need to protect high-asset crops in the wider landscape, have seen a shift to earlier season burning, often coinciding with when grassland plants may be growing or flowering. The potential implications of this shift in burning season have not been documented. We sought to understand how earlier fires may impact grassland species by studying their phenology (i.e., the timing of flowering). We demonstrate that flowering was strongly seasonal; native species flowered predominately in spring, while exotics peaked in early spring and declined thereafter. Four types of species-level phenology were identified. For native species, phenological patterns included (i) early-season (strictly spring-flowering only), (ii) late-season (strictly summer-flowering only), (iii) long-flowering, and (iv) spring–summer overlap flowering. Exotic species were predominantly early-season flowering, or spring–summer overlapping. Differences in phenology can be explained by life form. Exotic species were predominantly C3 therophytes (annuals), whereas native species include a mix of C3 geophytes and hemicryptophytes. Hence, the greatest proportion of native and exotic species are reproductive at the time of spring burning, with consequent effects likely for their flowering and seed set. Strategic use of spring burns may suppress annual exotic species populations by preventing seed set, a potentially useful management tool; efforts to control exotics must be carefully balanced against risks to native flora that also flower in spring. Understanding species phenology can help frame hypotheses about how fire season may affect grassland communities, but direct studies of fire impacts are needed to guide management.

1 | Introduction

Plant phenology studies offer valuable insights into the timing and seasonal patterns of plant growth, reproduction, and dormancy, all of which are crucial for understanding the dynamics of ecosystems (Fay et al. 2015; Pereyra Almena et al. 2024). This knowledge helps land managers predict how plant species respond to environmental changes (e.g., temperature, precipitation) and disturbances such as fire (Cleland et al. 2007). In the context of fire management, understanding plant phenology allows for burns that are timed to minimise negative impacts on sexual reproduction while promoting the regeneration of fire-adapted plants.

Fire is a fundamental disturbance that shapes plant communities at varying spatial and temporal scales (Bond 1995; He et al. 2019). Many species have evolved adaptations to fire, but their persistence depends on the characteristics of the fire

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Implications for Managers

- The timing of flowering of plants in temperate native grasslands was quantified over one season, and species variation explained by origin (native, exotic) and life form.
- Exotics typically flower earlier than native species, mostly because they are annuals. Native species exhibit a range of flowering strategies linked to their broader range of life forms.
- Shifts to earlier burning by land managers—when some grassland species are flowering—could pose a threat to their reproductive success. Studies of fire impacts early in the growing season on individual species responses are needed to accurately quantify this.

regime (i.e., the frequency, severity, intensity, and timing of fires; Bond 1995; Gill 1975; Keeley 2009; Hammill et al. 2016). Shifts in these key components can lead to significant changes in species composition, function, and ecosystem dynamics (Bowman et al. 2014; Doherty et al. 2024). Research on fire regimes has often emphasised fire frequency, where the recurrence of fire events has been a focal point for understanding their ecological impacts (e.g., Bradstock 2010; Bowman et al. 2014; Morgan et al. 2021). By comparison, the seasonality of fire remains a relatively underexplored area, despite its potential to profoundly influence vegetation dynamics (Bradstock et al. 1995; Miller et al. 2021; Tangney et al. 2022).

The influence of summer fire season burning (January–March) on temperate native grasslands in south-east Australia is well-known (Lunt and Morgan 2002; Lunt et al. 2012). Summer burning, when most native species have completed their seeding phase and have died back to underground storage organs (due to summer drought), has little direct impact on plants (Morgan 1999; Walker and Morgan 2022) and can enhance seedling recruitment in the post-fire year (Lunt et al. 2012). Recent fire management trends in native grasslands of western Victoria are for earlier burning during the high fire-risk period (October–December), before the onset of summer, as a strategy for built and agricultural asset protection (Dickson-Hoyle et al. 2021). The potential impacts of spring burning, especially on plant reproductive success, remain largely unexplored in native grasslands of western Victoria. Fires that occur during 'non-traditional' seasons may have different ecological consequences compared to those occurring in 'historically typical' seasons, affecting plant reproduction, seedling regeneration, and seedling survival (Pausas and Keeley 2014; Kelly et al. 2025). An understanding of the potential impacts of the seasonal timing of fire is vital for predicting and managing the outcomes of fire on native plant communities (Miller et al. 2019). Such an understanding may be enhanced by quantifying the phenology of native and exotic plant species, as well as the differences that may exist between life forms (Xavier et al. 2019; Pereyra Almena et al. 2024).

Phenological differences among species in a grassland flora are expected because plants can differ in their (i) photosynthetic pathway and (ii) life form, both of which constrain seasonal growth and resource allocation. Cool-season C3 grasses and forbs, for example, typically grow during winter and early spring under cool, moist conditions, before senescing or retreating to below-ground organs as summer drought stress intensifies (Morgan 1999). As a consequence, flowering in these species is predicted to occur early, primarily in spring. In contrast, warm-season C4 grasses and forbs are physiologically adapted to higher temperatures and therefore initiate growth later in the year, when air temperatures are warmer (Groves 1965; McDougall 1989). Delayed seasonal growth in these taxa is expected to shift flowering later, extending from late spring into summer.

Life form provides an additional axis for predicting flowering phenology. Annual species germinate during cooler, wetter periods and complete their life cycles rapidly, leading to early flowering in spring. Geophytes, including orchids and lilies, emerge from annual dormancy in winter by drawing on resources stored in underground organs, allowing rapid growth and early flowering before seasonal drought develops (Gott 1983; Chapin et al. 1990; Gott et al. 2015). In contrast, hemicryptophytes must first rebuild above-ground leaf area in winter before allocating resources to reproduction and are therefore expected to flower later (Raunkiaer 1934). Together, differences in photosynthetic pathway and life form may provide a framework for understanding interspecific variation in flowering timing in grassland plant communities.

Here, we document the flowering phenology of temperate grassland species across one growing season. To our knowledge, only Groves (1965) has previously recorded community-level flowering periods in this ecosystem, showing seasonal differences among life forms. We hypothesised that (i) flowering would peak in spring, coinciding with cool-season growth of C3 species, and be lowest in summer when moisture is limiting; (ii) life forms would differ in the timing of peak flowering due to their contrasting responses to water stress; and (iii) flowering duration would vary among species. These hypotheses provide a basis for evaluating how shifts in fire season may influence both native and exotic grassland flora.

2 | Methods

2.1 | Study Setting

The study was conducted between Chatsworth and Woorndoo in western Victoria, Australia (Figure S1) on the lands of the Eastern Maar people. The study sites were native tussock grasslands dominated by the C4 grass *Themeda triandra* and are species-rich, comprising perennial C3 forbs (typically from the Asteraceae) and monocots (including orchids and lilies); native annuals are rare in this community (Sinclair et al. 2021). Exotic species were present at low density, typically comprising annual grasses and short-lived ruderal forbs. All sites were roadside remnants that have been rarely grazed by livestock; all have been burnt frequently in summer by local fire brigades for fuel reduction for more than six decades. Study sites were on the Victorian Volcanic Plain bioregion (basalt-rich soils) and the adjoining Dundas Tablelands bioregion (sediment-rich soils). Structurally and compositionally,

they were very similar. All study sites were within 16 km of one another.

The seasonal climate is characterised by cool, wet winters and hot, dry summers. Mean monthly maximum temperatures are highest in January and February at 26.2°C, and lowest in July at 13.1°C (Bureau of Meteorology http://www.bom.gov.au/climate/data). The average annual rainfall for the region is ~587 mm, with mean rainfall highest in August (austral winter) before the onset of spring, at which point mean monthly rainfall total declines over summer until the following autumn (Figure S2). During the study period (September 2023–January 2024), rainfall was 6% above the long-term average (Lake Bolac Meteorological recording station #89016; ~20 km from the study area).

2.2 | Sampling Strategy

We selected eight species-rich *Themeda triandra*-dominated native grasslands. These were last burnt between 2 and 4 years before this study. This may have affected the number of species observed flowering and the intensity of their flowering; Lunt (1994) showed that time-since-fire can have positive, negative, and neutral impacts on flowering intensity in grassland species, including daisies, orchids and lilies. At each site, three permanent plots were established in September 2023, each measuring 400 m^2. In each plot, five random permanent sampling quadrats (2 × 7 m) were established. Within each quadrat, each observed species was assigned a phenological state (vegetative, budding, flowering, seeding, or having shed seed) based on the phenological state that the *majority* of individuals were in. In this paper, we focus on flowering, whereby flower buds had opened or anthesis had begun (grasses). Hence, we have a total of 120 observation points per month (eight sites × three plots × five quadrats). The onset and duration of flowering of each species were determined by repeated sampling of the permanent quadrats across October, November (austral spring), and December 2023, and January 2024 (summer). Sampling took place from October when field inspection showed that multiple species first began flowering, and typically took place over four full days in the latter half of each month. Hence, there was a total of 480 observation points throughout the study (120 points per month × 4 months).

To compare differences in phenology that may arise from differences in life form, all species were assigned a Raunkiaer (1934) life form—chamaephytes, geophytes, hemicryptophytes, therophytes—according to McIntyre et al. (1995). The subdivisions of the Raunkiær system are premised on the location of the perennating bud of a plant during seasons with adverse conditions, where the growing season here is determined by water scarcity. Chamaephytes are perennial species with perennating buds positioned just above the soil surface. Geophytes survive adverse periods entirely below-ground as bulbs, corms, rhizomes, or tubers that store resources and support rapid emergence when conditions become favourable. Hemicryptophytes maintain perennating buds at the soil surface, relying on the regrowth of above-ground tissues after dormancy before allocating resources to reproduction. Therophytes are annual species that complete their life cycle within a single favourable season and persist through unfavourable periods solely as seeds.

2.3 | Statistical Approach

To evaluate temporal variation in the flowering phenology of native and exotic species, we modelled the number of species at peak flowering—defined as the month with the highest number of flowering individuals per species—across October to January. Analyses were conducted separately for native and exotic species using generalised linear models (GLMs) fitted with a Poisson error distribution and a log link. The response variable was the number of species per site reaching peak flowering in each month, and the predictor variable was month. Sampling was aggregated to the site level ($n = 8$ sites), as each site contained multiple plots and quadrats that were not independent. Consequently, no additional hierarchical structure was included. Models employed an effects coding (sum contrasts) scheme for month, where coefficients represent deviations of each month from the overall (grand) mean rather than comparisons to a single reference month. Model assumptions of normality, homogeneity, and dispersion were assessed using the DHARMa package (Hartig 2018). Intercept and effect size estimates with empirical 95% confidence intervals were estimated using a 10,000-iteration bootstrap approach (Table S1). Model fit was assessed with pseudo-R^2 based on model deviance (Table S1). An equivalent analysis was conducted for plant life forms, where life form was the response variable. All analyses were performed in R (R Core Team 2023) and visualised using ggplot2 (Wickham 2016). The code and data supporting this analysis are openly available on GitHub: github.com/LukeLikesDirt/flower-phenology-and-fire.

3 | Results

3.1 | Field Study

We observed a total of 107 species (77 native, 30 exotic), including 53 forb species (41 native), 53 graminoid species (35 native), and one native sub-shrub. Exotic species were dominated by therophytes (60%), while native species were dominated by hemicryptophytes (65%) and geophytes (21%) (Figure 1). The native hemicryptophytes *Themeda triandra, Tricoryne elatior*, and *Dichelachne crinita* were the most frequently observed species flowering, as were the exotic therophytes *Briza minor* and *Vulpia bromoides*, and the exotic hemicryptophyte *Hypochaeris radicata* (Figure 1).

3.2 | Peak Flowering

Peak flowering for native species was significantly higher in spring (October–November) than in summer (December–January), showing a strong seasonal effect with a log ratio difference of approximately 1 (Figure 2). In contrast, exotic species flowering peaked in October and exhibited a moderate log-linear decline over the study period, with the effect of month decreasing by approximately log-ratio 0.75 per month (Figure 2). Both models showed excellent fit, with pseudo-R^2 values of 0.98 for native species and 0.99 for exotic species, indicating that month explained most of the variation in flowering patterns.

Generalised linear models showed that the timing and intensity of peak flowering differed markedly among plant life

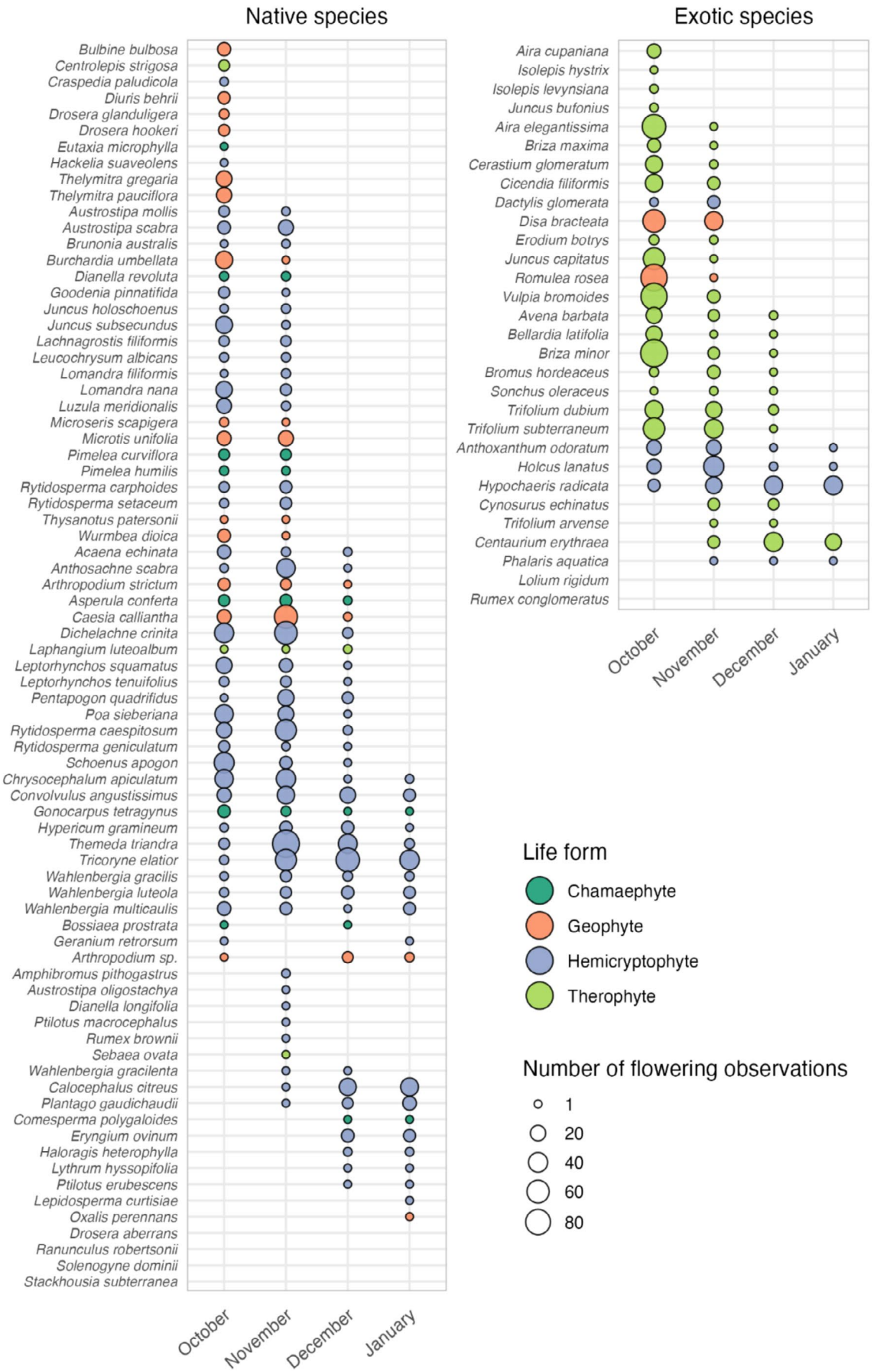


FIGURE 1 | Number of flowering observations per species in each month. The size of the bubbles corresponds with the total number of quadrats where each species was observed flowering, and colour corresponds with their lifeform.

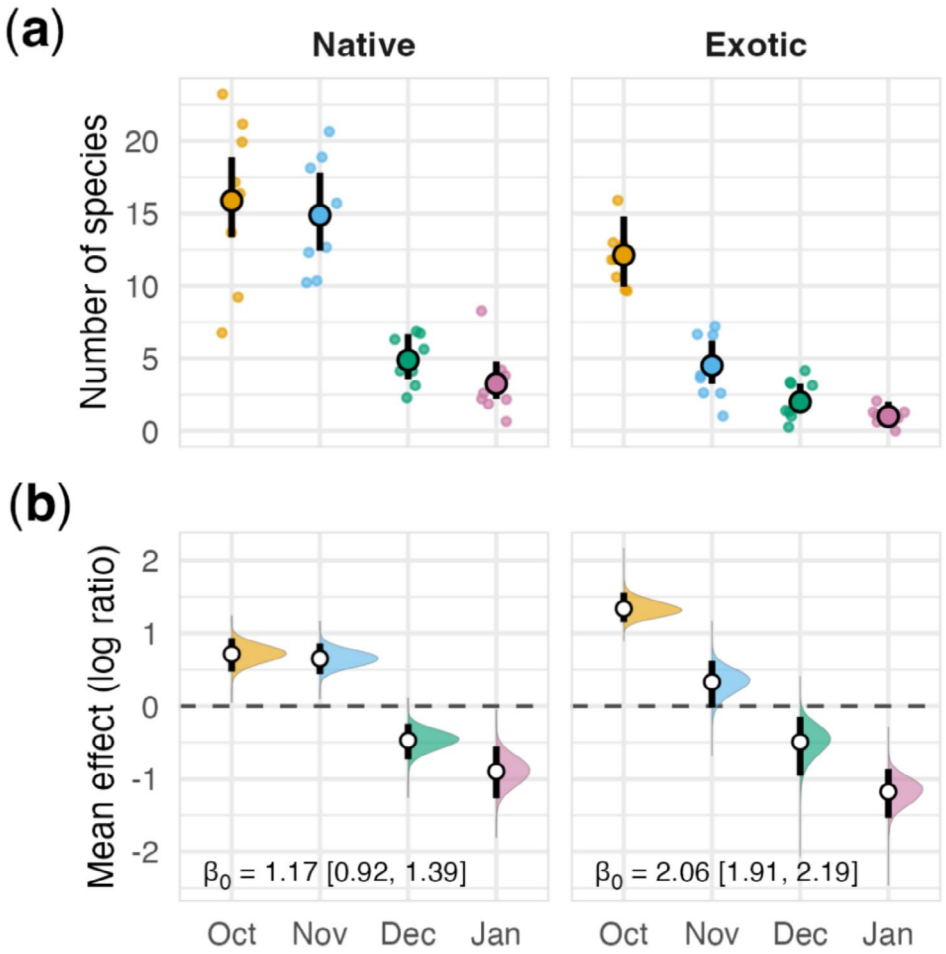


FIGURE 2 | Differences in the mean number of native and exotic species at peak flowering. (a) Estimated mean number of species flowering with 95% confidence intervals (CIs); scattered points represent observed values. (b) Effect sizes of months relative to the grand mean (β_0) with 95% CIs, showing the magnitude and direction of seasonal deviations. Effect sizes were derived from bootstrapped model coefficients (10,000 iterations) to illustrate model uncertainty and robustness. Significant differences between months are indicated where effect size CIs do not overlap.

forms (Figure 3). Hemicryptophytes accounted for most of the species in the dataset and therefore, unsurprisingly, exhibited the highest number of species in peak flower throughout the study period. Hemicryptophyte flowering showed a strong seasonal effect, with a pronounced peak in late spring (October–November) and a sharp decline through summer (December–January) (Figure 3). Therophytes and geophytes displayed similar early-season flowering peaks in October, followed by steep declines in flowering intensity toward and throughout summer (November–January) (Figure 3). In contrast, chamaephytes exhibited the lowest flowering intensity and little seasonal variation, with a weak and non-significant negative seasonal effect (Figure 3). Model fit was generally high for geophytes ($R^2 = 0.94$), hemicryptophytes ($R^2 = 0.94$), and therophytes ($R^2 = 0.99$), indicating strong seasonal structuring, but substantially lower for chamaephytes ($R^2 = 0.33$), consistent with their weak seasonal response.

3.3 | Phenology of Individual Species

While there are peaks of flowering activity at the community level for the native and exotic flora, we identified four types of phenology that individual species express (Figure 1). For native species, phenological patterns included: early-season (strictly spring-flowering only; 47% of species), late-season (strictly summer-flowering only; 9% of species), long-flowering (12% of species), and spring–summer overlap flowering (27% of species). Exotic species were predominantly early-season flowering (47% of species) or spring–summer overlapping (37% of species). Few are long-flowering (10% of species), and none exclusively flower in summer. Four native species and two exotic species did not flower in the study period.

4 | Discussion

We found that temperate native grasslands are dominated by plant species that have peak flowering in spring, and that variation in phenology is mostly attributable to life form, with differences evident among native and exotic species. Annuals (typically exotic species) and geophytes (typically native species) have concentrated early spring flowering because they likely emerge earliest after winter rains; they are the species most likely to be vulnerable to spring burns. Hemicryptophytes, by contrast, have a more extended flowering phenology and hence may be less vulnerable to spring burning (but would nonetheless be affected if burns coincide with peak flowering).

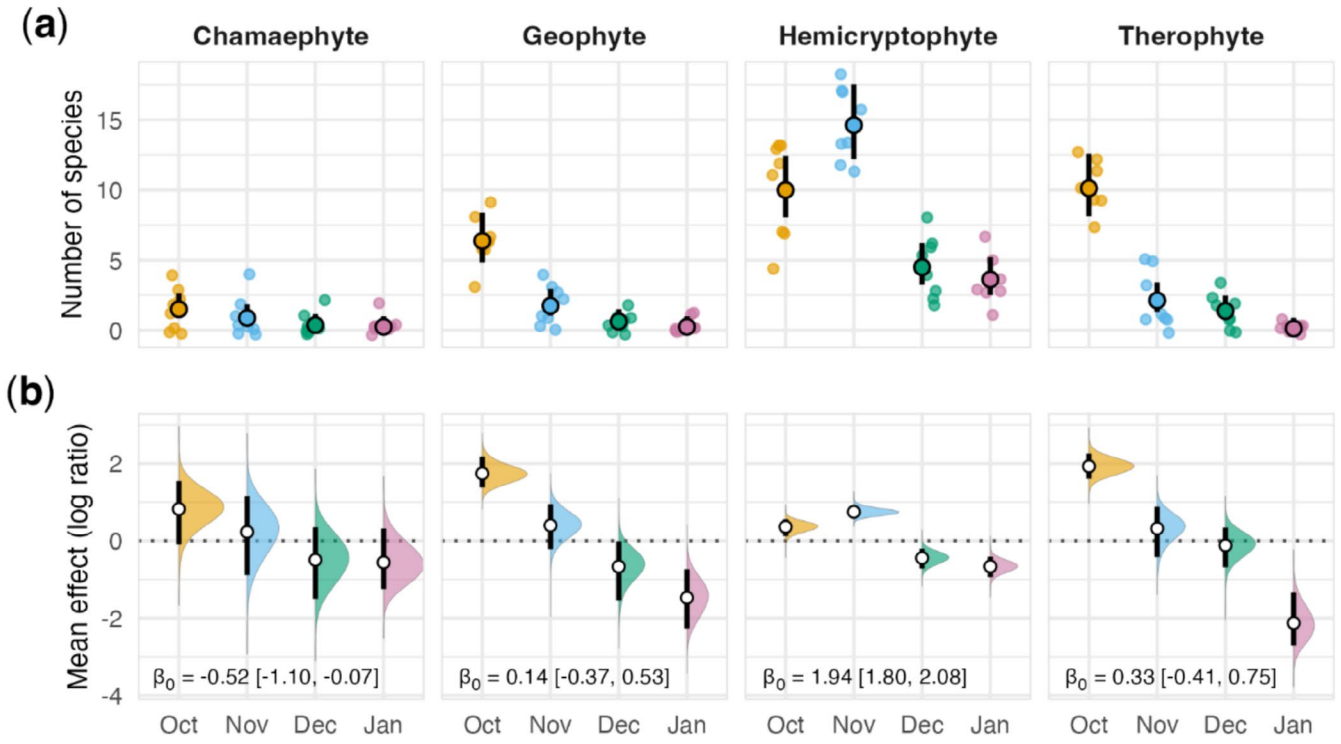


FIGURE 3 | Differences in the mean number of species at peak flowering across plant life forms. (a) Estimated mean number of species flowering with 95% confidence intervals (CIs); scattered points represent observed values. (b) Effect sizes of months relative to the grand mean (β_0) with 95% CIs, showing the magnitude and direction of seasonal deviations. Effect sizes were derived from bootstrapped model coefficients (10,000 iterations) to illustrate model uncertainty and robustness. Significant differences between months are indicated where effect size CIs do not overlap.

Chamaephytes had a low flowering intensity in grasslands and hence may not be strongly constrained by seasonality of fire. Few species were long-flowering in this flora, and none exclusively flower in summer, likely because *Themeda triandra* is the only species in our study system known to be C4. Some species were not seen flowering at all. This may be because they do so in winter (e.g., *Drosera aberrans*; VicFlora 2025), before we began surveying phenology, or because they do not flower every year (Morgan 1998).

Flowering of native species was strongly skewed toward spring, with peak flowering highest in October and November, a pattern previously observed for temperate native grasslands near Melbourne, Australia (Groves 1965). A spring flowering peak is typical in winter-rainfall plant communities dominated by C3 species where constraints associated with the bounds of the growing season, such as water limitation, can predict flowering (Debussche et al. 2004), and peak flowering is predicted to be highest in the middle of the growing season (Morales et al. 2005). The significant decline in flowering observed for native grassland plants between November and December is likely to reflect the limitation imposed on species by increasing soil moisture stress (Morgan 1999); at this time, as temperatures rise, precipitation declines, evaporation increases, and biomass is at its highest (Groves 1965; McDougall 1989). Seasonally defined resource limitations are known to act as a strong selection pressure on phenology in a wide range of plant communities (Sun and Frelich 2011). Despite the spring flowering peak in this community, the distinctly different flowering times between some species suggest that variation in plant root and shoot traits enable varied strategies and reproductive phenologies outside of the peak period (Laughlin 2023), when water resources may be limited.

Early flowering grassland species are likely favoured by reduced competition for both light and soil moisture prior to the onset of growth by dominant warm-season C4 grasses. In south-eastern Australian grasslands, the canopy development of warm season grasses like *Themeda triandra* strongly limits light availability to subordinate herbaceous species later in the growing season (Morgan 1997, 1998; Callahan and Pigliucci 2002). Flowering early therefore potentially provides a temporal escape from competition, allowing species to acquire resources and reproduce before canopy closure and summer soil moisture stress intensify. In our study system, many of the earliest-flowering taxa were diminutive forbs (< 40 mm tall), including *Drosera glanduligera*, *Drosera hookerii* and *Wurmbea dioica*. Spring flowering was also common for C3 therophytes, most of which are exotic. They germinate with environmental cues (e.g., when temperature decreases and available moisture increases with autumn rainfall; Cheplick 1998), allowing them to establish quickly and access resources early in the growing season (Thomson et al. 2017).

Early flowering was also observed in taller lilies and orchids, including *Thelymitra gregaria*, *Thelymitra pauciflora*, *Diuris behrii*, *Burchardia umbellata*, and *Bulbine bulbosa*. All of these species are geophytes with underground storage organs, a trait that likely facilitates rapid early-season growth and flowering by providing immediate access to stored carbon following emergence from dormancy (Gott 1983; Gott et al. 2015). This is followed by replenishment of below-ground reserves (Sheikh

et al. 2022) and then senescence (i.e., summer dormancy; Chapin et al. 1990).

Late-season flowering may be a response to competition, but rather than flowering early, species have developed stress-tolerant traits that enable delayed flowering. Traits that enable physiological function in water-limited environments are likely important for late-flowering species. Late-flowering species, such as *Eryngium ovinum*, *Oxalis perennans*, *Ptilotus erubescens*, and *Plantago gaudichaudii*, typically have taproots (Conn et al. 1999; Jeanes 1999; Michael 1999; Walsh 1996) which may enable access to water held deeper in the soil and hence make these species more drought-resistant (Castañeda et al. 2019). These species may also have a higher leaf tissue density (low leaf dry matter content), a trait which has enabled later flowering in some species as it has been shown to improve tolerance to drought (Tucker et al. 2011) and is important in withstanding low nutrient uptake experienced later in the season (Craine et al. 2012).

Alternative explanations for the timing of flowering are that day length (photoperiod) or winter temperatures (vernalisation) control phenology (Lang 1952; Andrés and Coupland 2012). We can expect that the triggers for flowering vary across the flora, and species will have developed sensitivities to triggers based on factors such as their life-history, growth form, and broader plant strategies. Repeating the observations we have made in other years would enable characterisation of those species that have variable phenological patterns (induced by variation in inter-annual climate, e.g., Jarrad et al. 2008) versus those that are more predictable in their flowering because they are cued by factors such as day length.

Peak flowering for exotic species was in October, with a sharp decline in flowering by the following month (Figure 2). October also supported a peak in native species flowering, evidencing a lack of clear phenological separation between the groups. Native and exotic species have been found flowering synchronously in grasslands, suggesting that invasions in grasslands are more dependent on moisture sensitivities than species adapting to flower at different temperature cues, and thus times of year (Wolkovich et al. 2013). Our finding that both native and exotic groups flower in October suggests that temperature is likely a secondary factor, with soil moisture being a stronger predictor of flowering time. The high proportion of annual therophytes in the exotic species group means that the majority of these species have the capacity to grow and reproduce quickly to avoid competition for resources. This explains the steep drop in the number of exotic species flowering after October. Only a few exotic species flowered over longer durations; these were predominantly perennial hemicryptophytes (e.g., *Hypochaeris radicata*).

4.1 | Implications for Fire Management

In grassland ecosystems, characterising flowering phenology is critical to understand how the timing of fire influences plant reproduction and community dynamics (Ansquer et al. 2009). We built on a previous study of phenology by Groves (1965) to better understand the timing and duration of flowering by both native and exotic species, with the aim of interpreting these patterns and their implications for conservation management of these threatened ecosystems.

Our study indicates that a greater proportion of native species flower earlier in the season, suggesting that the emerging trend of lighting spring (early season) fires is likely to coincide with, and thereby disrupt, their reproductive phases. As a result, earlier burning may significantly reduce seed set in the native flora, undermining their capacity for seed regeneration. The continued application of spring burns may thus contribute to a decline in local populations. Historical accounts, such as Scarlett and Parsons (1982), have similarly linked the rarity of late-flowering species—like grassland peas on the Victorian Volcanic Plains—to the loss of reproductive structures due to early summer fires. A shift to repeated early-season fire may threaten a much wider range of plant diversity than does summer fire.

Conversely, many exotic species in these grasslands are fast-cycling therophytes that complete their life cycle early in the season. Strategic use of spring burns may reduce their populations by preventing seed set and reducing contributions to the soil seed bank (Prober et al. 2004, 2005). This presents a potential management tool to improve grassland condition (Stuwe 1986), but also highlights the trade-offs involved; efforts to control exotics must be carefully balanced against risks to native and threatened flora.

Although a limited number of native species may re-flower following spring burns (Morgan 1996), the capacity for post-fire flowering is not well understood and is likely species-specific, depending on both plant traits and fire timing (Howe 1994; Kelly et al. 2025). Further research is needed to identify which species are capable of compensatory flowering and under what environmental conditions. Without this knowledge, the continued trend toward earlier burning—whether driven by policy, climate, or operational convenience—could exacerbate biodiversity loss in already threatened grassland communities.

By aligning fire regimes with the phenological cycles of native species, fire can be used as a tool to maintain plant diversity. As climate change lengthens fire seasons, and managed fires are implemented further outside historically typical fire seasons, reproductive success may become more vulnerable to failure. It is important to consider the effect of fire season, however, with the other aspects of the fire regime. A spring fire may negatively impact species reproduction in a single season, but these effects may only become detrimental if done at high frequency given most species have a short secondary juvenile period and can flower in the year following fire (Lunt 1994; Morgan 1996). With this consideration, a one-off spring fire may not be detrimental to plant community composition, assuming plant survival. Studies of fire impacts early in the growing season on individual species responses are needed to accurately quantify this. Importantly, the absence of fire per se has been found to be one of the most significant drivers of native species loss in productive grasslands (Williams et al. 2006). Maintaining fire—despite shifts in its season of application—is likely to be preferable to its removal altogether.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The code and data supporting this analysis are openly available on GitHub: github.com/LukeLikesDirt/flower-phenology-and-fire.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Model coefficients for generalised linear models (GLMs) on differences in peak flowering across months. Models were fitted separately for each status (exotics, natives)

and life forms (chamaephytes, geophytes, hemicryptophytes, therophytes) using a Poisson GLM with log link. The response variable was the number of species at peak flowering per site ($n = 8$ sites), with month as a predictor. Nagelkerke's pseudo-R^2 are shown for each status and life form to indicate model fit. Month was coded using effect coding (sum contrasts), and the intercept therefore represents the grand mean across months. **Figure S1:** Location of the study area, and sites, in western Victoria, in relation to regional Bioregions (a landscape classification using attributes like climate, geomorphology, geology, soils and vegetation). **Figure S2:** Long-term average temperature and precipitation data (1990–2024) from the Lake Bolac Meteorological recording station (#89016; www.bom.gov.au), ~20 km from the study area.