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RESEARCH ARTICLE

Southern hemisphere plants show more delays than advances in flowering phenology

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Abstract

1. Shifts in flowering phenology have been studied in detail in the northern hemisphere and are a key plant response to climate change. However, there are relatively fewer data on species' phenological shifts in the southern hemisphere.
2. We combined historic field data, data from herbarium specimens dating back to 1842 and modern field data for 37 Australian species to determine whether species were flowering earlier in the year than they had in the past. We also combined our results with data compiled in the southern and northern hemispheres, respectively, to determine whether southern hemisphere species are showing fewer advances in flowering phenology through time.
3. Across our study species, we found that 12 species had undergone significant shifts in flowering time, with four species advancing their flowering and eight species delaying their flowering. The remaining 25 species showed no significant shifts in their flowering phenology. These findings are important because delays or lack of shifts in flowering phenology can lead to mismatches in trophic interactions between plants and pollinators or seed dispersers, which can have substantial impacts on ecosystem functioning and primary productivity. Combining our field results with data compiled from the literature showed that only 58.5% of southern hemisphere species were advancing their flowering time, compared with 81.6% of species that were advancing their flowering time in the northern hemisphere. Our study provides further evidence that it is not adequate for ecologists to assume that southern hemisphere ecosystems will respond to future climate change in the same way as ecosystems north of the Equator.

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4. *Synthesis*. Field data and data from the literature indicate that southern hemisphere species are showing fewer advances in their flowering phenology through time, especially in comparison to northern hemisphere species.

KEYWORDS
climate change, flowering, global change ecology, herbarium, northern hemisphere, phenology, reproductive ecology, southern hemisphere

1 | INTRODUCTION

Climate change has led to substantial changes in temperature across the globe (Hartmann et al., 2013; Intergovernmental Panel on Climate Change (IPCC), 2021). Changes in temperature can shift the timing of biological events (phenology). For example, breeding phenology in boreal birds has advanced by an average of 4 days over four decades (Hällfors et al., 2020), and plants in North America have advanced their flowering time by an average of 7 days in 154 years (Miller-Rushing & Primack, 2008). These shifts in phenology can have substantial effects on species' survival, reproduction and trophic interactions (Kharouba et al., 2018). For example, both male and female *Adrena nigroaenea* bees are emerging earlier than the orchid *Ophrys sphegodes*' peak flowering time since the 1600s due to increases in air temperature in Britain (Hutchings et al., 2018). This is problematic for *O. sphegodes*' pollination as this orchid typically required solitary males for sexually deceptive pollination before the females have emerged (Hutchings et al., 2018). The present study aims to provide new data on changes in flowering time in Australia, to ask what type of species are most likely to show advances or delays in flowering time, and to compare the rates of flowering time change in the southern hemisphere with those in the northern hemisphere.

There are hundreds of studies on phenological changes in species from the northern hemisphere (Menzel et al., 2006; Miller-Rushing & Primack, 2008). However, we know much less about how southern hemisphere species, particularly plants, have responded to warming climates (Chambers et al., 2013, 2016). We currently have data for long-term flowering phenology shifts through time for just 195 of the ~21,000 (Chapman, 2009) flowering plant species in Australia (Gallagher et al., 2009; Keatley et al., 2004; Keatley & Hudson, 2007; Rawal et al., 2014; Rumpff et al., 2010). These data come from just five studies in four different ecosystems (alpine, Eucalypt woodland, sclerophyll woodland and coastal vegetation). These studies in the southern hemisphere show relatively few species advancing their flowering and some species delaying their flowering (Gallagher et al., 2009; Rumpff et al., 2010). The present study complements these existing studies by providing new data for 37 species from 19 families from sclerophyll woodland in northern Sydney, testing the hypothesis that Australian species have shifted to earlier flowering times over the last 177 years.

We also asked which types of species were most likely to be advancing their flowering. Obtaining long-term data on change in flowering time is difficult, particularly for parts of the world where there are few historic data available. Being able to predict which species are at the highest risk of being left behind under future climate change would have benefits for protecting flora across Australia and for understudied regions and ecosystems elsewhere in the world. We therefore investigated whether phylogeny, native/introduced status or growth form could help predict flowering time change.

To determine the types of species that were advancing their flowering time, we first asked whether there was a significant phylogenetic signal in flowering shifts. Research in the northern hemisphere has found strong phylogenetic signals in shifts in flowering time (Davies et al., 2013; Du et al., 2017). For example, many lineages of Asterales flowered later in the year through time and many lineages within Myrtales flowered earlier in the year through time (Davies et al., 2013). Strong phylogenetic signals in flowering time shifts may allow future predictions for species at risk of phenological mismatches based on species' taxonomy.

Second, we tested the hypothesis that introduced plants in Australia are advancing in their flowering time more rapidly than native plants. Introduced species often have a competitive advantage over native species due to their high levels of plasticity and ability to adapt more rapidly to changes in environmental conditions (Cao et al., 2018). Consistent with this, invasive species advanced their average flowering time 11 days earlier than native species and 9 days earlier than non-native species in Thoreau's Woods in the northern hemisphere (Willis et al., 2010), and non-native species showed longer flowering periods and higher flowering synchrony than native species in subtropical China (Cao et al., 2018). If introduced species show large shifts in their flowering phenology due to climate change, they may be able to outcompete native species in many natural ecosystems, threatening ecosystem richness and diversity. However, there has never been a test of the hypothesis that introduced species may be advancing their flowering times more quickly than native species in the southern hemisphere.

Third, we hypothesised that trees would shift flowering time more rapidly than shrubs or herbs. Trees are typically more sensitive to shifts in temperature due to long-term environmental selection, and may respond faster to shifts in climate than herbs and shrubs (Yang et al., 2018). However, species with a herbaceous growth form tend to grow and reproduce faster, and have less time between generations and faster adaptation and evolution (Lanfear et al., 2019; Salguero-Gómez et al., 2016; but see Oduor et al., 2016), which could lead to faster shifts in phenology over time. Growth form has been shown to be related to short-term (within year) flowering phenology (Cortés-Flores et al., 2017) and long-term shifts in flowering phenology (Wang, Yang, et al., 2020) in the northern hemisphere, with trees advancing their flowering time more rapidly than herbs and shrubs (Wang, Yang, et al., 2020).

Relationships between growth form and flowering time shifts in the southern hemisphere have not yet been quantified and our study aims to fill this knowledge gap.

Climate change is not uniform across hemispheres, with the northern hemisphere having outpaced its southern counterpart in recent climatic warming due to the higher volume of ocean in the southern hemisphere (Friedman et al., 2013; Intergovernmental Panel on Climate Change (IPCC), 2021). Differences in both the rate of warming (Friedman et al., 2013) and the taxa (Box, 2002; Sanmartín & Ronquist, 2004) between the two hemispheres could drive differences in responses between northern and southern hemisphere species. Studies in the southern hemisphere have found limited shifts in species' flowering phenology (Gallagher et al., 2009; Rumpff et al., 2010), and we hypothesised that species may be less likely to show shifts in flowering timing than northern hemispheric species. Thus, our final aim was to determine whether a lower proportion of species have advanced their flowering phenology in the southern hemisphere than in the northern hemisphere.

2 | MATERIALS AND METHODS

2.1 | Flowering phenology data

We collected flowering phenology data from the northern Sydney region, NSW, Australia (Supporting Information: Figure S1a). This region was selected as detailed flowering time data from the early 1960s were available for over 400 species (Price, 1963). The mean temperature in our study area increased by 1.1°C from 1910 to 2019, while spring and summer temperatures have increased by 1.6°C (Supporting Information: Figure S2a). Rainfall has remained relatively stable on average; however, variability in rainfall has increased (Supporting Information: Figure S2b,c) and previous studies have shown that droughts and heatwaves in the Sydney region have increased since the early 1900s (CSIRO, 2007; CSIRO, & Australian Government Bureau of Meteorology (BOM), 2020; Jyoteeshkumar Reddy et al., 2021).

Price (1963) recorded flowering at weekly intervals giving a high degree of sensitivity in assessing flowering time shifts. Unfortunately, while we know that Price began sampling in 1960, she only specified that data collection was 'across a number of years' before she published her data in 1963 (Price, 1963, p. 171). We therefore set Price's data to 1961, the most likely median sample date for species from her study. However, we ran analyses with Price's dataset to 1960, 1961 and 1962, and the results of the relationship and associated significance were unchanged.

Price's data indicated the timing of 'abundant flowering' or the 'main flush of flowering' (Price, 1963, p. 171) and we interpreted and used these data as 'full flowering' from this period. Only full flowering data are presented throughout this paper. However, we also recorded the initiation of flowering and end of flowering. Analyses of these variables yield results that are quantitatively very similar to those for full flowering (Supporting Information S3: Tables S3a–c).

We collected modern field data in sites selected to try to match the localities and ecosystems that would have been monitored by Price (1963). Fieldwork was carried out under the New South Wales National Parks and Wildlife Service licensing (permits S13105 and SL100569). Fieldwork occurred from August to February (end of southern hemisphere winter, through to spring and summer) in 2010, 2011, 2018 and 2019 for a subset of 37 species, in the northern Sydney region from the Price (1963) dataset. These species were selected from a range of families and growth forms and chosen based on their presence in the northern Sydney region and abundance at the locations sampled (typically we monitored >30 individuals, however, for some species there were lower numbers of individuals; see Supporting Information: Table S1a for sample sizes of each species). For each species, we monitored flowering at weekly intervals to match sampling methods in Price (1963). Each species was determined to be in full flower if at least 50% of individual plants were in flower.

We supplemented the historic data and field data with flowering phenology data collected from herbarium specimens from the John T. Waterhouse Herbarium (UNSW, Sydney, Australia), The Downing Herbarium (Macquarie University, Australia), the John Ray Herbarium (The University of Sydney, Australia) and the National Herbarium of New South Wales (Royal Botanic Gardens, Sydney, Australia). Herbarium specimens have been shown to yield similar results to field data and can be used in conjunction to increase sample sizes and time frames (Jones & Daehler, 2018). Herbarium specimens were only included if they had sufficient geolocation information for us to be certain that they were collected from the sample region (Supporting Information: Figure S1a). We scored each specimen for flowering status in accordance with field data scoring and species were in full flower when >75% of the specimen's reproductive organs/buds had turned to flowers. Although previous studies have used 50% as the threshold for full flowering (e.g. Daru et al., 2019; Park et al., 2018), we believe that 75% (also used in a previous study; Davis et al., 2015) more accurately captured full flowering in our species: as each specimen was only one section of a plant, a higher threshold for full flowering was necessary for comparison with our field data. Most specimens had date data resolved to the exact day of observation. We also included specimens with dates resolved to at least the month of flowering and for these specimens we arbitrarily appointed the 15th day of the month (the median of the month) as the specimen observation date. To ensure that these specimens with incomplete date data did not have an impact on our data, we also ran our main analysis to test the advancement of flowering time in Sydney without these points (reducing our total dataset from 2529 data points to 2314). Many of these points were herbarium specimens that were not in full flower, so they did not impact our flowering time analysis which only used specimens in flower. This is reported in Supporting Information: Table S3d.

To determine whether there were differences in the types of species that were more rapidly shifting their flowering phenology through time, we assigned a growth form (herb, shrub or tree) to each species following the Flora of New South Wales (Harden, 2002). For species that were on the borderline between growth forms (e.g. 'shrub/tree'), we classified the species based on the predominant growth form of the individuals monitored in the northern Sydney region (pers. obs.

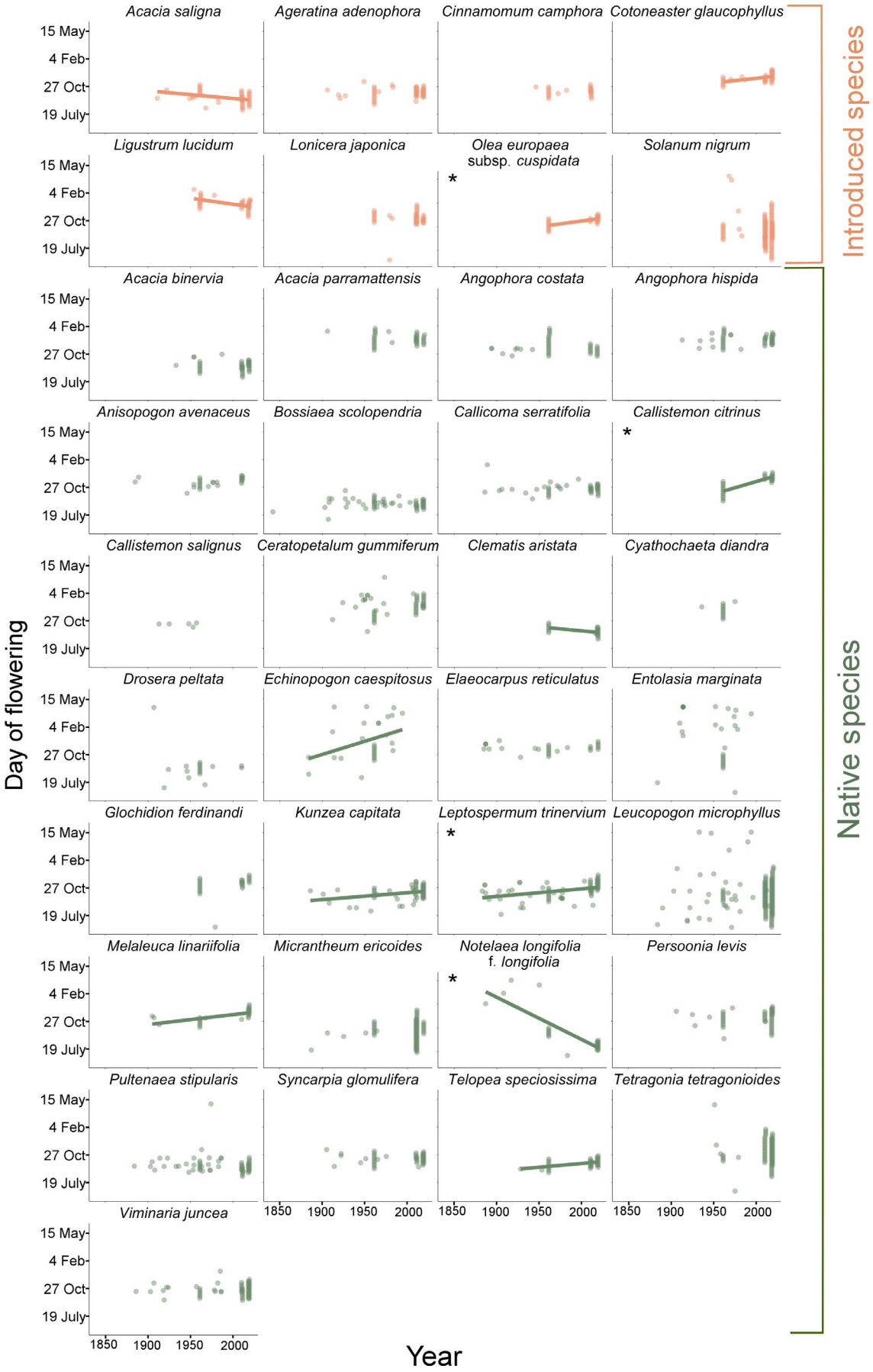
Acacia saligna
Ageratina adenophora
Cinnamomum camphora
Cotoneaster glaucophyllus
Ligustrum lucidum
Lonicera japonica
Olea europaea subsp. cuspidata
Solanum nigrum
Acacia binervia
Acacia parramattensis
Angophora costata
Angophora hispida
Anisopogon avenaceus
Bossiaea scolopendria
Callicoma serratifolia
Callistemon citrinus
Callistemon salignus
Ceratopetalum gummiferum
Clematis aristata
Cyathochaeta diandra
Drosera peltata
Echinopogon caespitosus
Elaeocarpus reticulatus
Entolasia marginata
Glochidion ferdinandi
Kunzea capitata
Leptospermum trinervium
Leucopogon microphyllus
Melaleuca linariifolia
Micrantheum ericoides
Notelaea longifolia f. longifolia
Persoonia levis
Pultenaea stipularis
Syncarpia glomulifera
Telopea speciosissima
Tetragonia tetragonioides
Viminaria juncea
15 May
4 Feb
27 Oct
19 July
1850
1900
1950
2000
Day of flowering
Year
Introduced species
Native species

FIGURE 1 Shifts in full flowering time for 8 introduced species and 29 native species. Each point represents either a field sample (sampled in the years 1960, 2010, 2011, 2018 and 2019) where a species was in full flower (at least 50% of individual plants were in flower) or where a herbarium specimen was in full flower (when >75% of the specimen's reproductive organs/buds had turned to flowers). Each year may have multiple time points either due to a species remaining in full flower across multiple weeks or multiple herbarium specimens having been collected from different locations. Green regression lines denote significant relationships and asterisks (*) denote relationships that remained significant after correcting for multiple hypothesis testing

S.E.E. and R.A.J.B; Supporting Information: Table S1b). Two species (*Clematis aristata*; Ranunculaceae and *Lonicera japonica*; Caprifoliaceae) were classified as woody climbers and, as they were the only species of this growth form, we excluded them from our growth form analysis.

We also recorded each species' native/introduced status following the Flora of New South Wales (Harden, 2002). Our study included 29 native species, seven introduced species that originated from other countries and one species (*Acacia saligna)* that was introduced to New South Wales from Western Australia (Kodela & Harden, 2002) and was considered as an introduced species in further analyses.

2.2 | Data analysis

All data analyses were carried out in R Studio, version 3.6.3 (R Core Team, 2018) and code is freely available on GitHub (https://github.com/SEveringham/flowering-phenology-changes-in-Sydney).

To determine whether plants flowered earlier in the year over time we ran linear regressions, using the *lm* function in base R (R Core Team, 2018), with flowering date as the response variable, and year of observation as the predictor variable. As species in the southern hemisphere flower across the December–January year transition, we transformed flowering time Julian date data to a cyclical format, by adding 365 days to dates that fell before the 1st of June. That is, the season of flowering went from June (day 152 of the year) to the end of May.

We quantified phylogenetic patterns in flowering phenology using a phylogenetic least squares (PGLS) framework. A covariance matrix was obtained from the relationships and branch lengths of our species when pruned from the Smith and Brown (2018) megatree. Our tree was created using the *phylo.maker* function in the V.PHYLOMAKER package (Qian & Jin, 2016). We then tested for a phylogenetic signal in flowering phenology shifts across our species using two metrics—Pagel's λ and Blomberg's K (Münkemüller et al., 2012).

To determine whether there was a significant difference in flowering phenology shifts between native and introduced species, we used a meta-analysis using the *rma.uni* function in the METAFOR package (Viechtbauer, 2010) with species absolute flowering phenology shift through time (the slope coefficient from each species' regression regardless of direction) as the response variable and a categorical predictor variable for whether the species was native or introduced, with data points weighted by species' variance.

Finally, to test the hypothesis that trees would shift in their flowering phenology more rapidly than herbs or shrubs, we performed a meta-analysis with species absolute flowering shift (irrespective of the direction of the shift—i.e. irrespective of whether the species were advancing or delaying) as the response variable and growth form as a categorical predictor variable with weighting by species' variance.

2.3 | Differences between southern and northern hemisphere shifts in flowering phenology

We conducted a literature search in December 2020 following protocols from König et al., (2017) using Web of Science and Google Scholar with keywords 'phenology', 'plants' in combination with 'climate change', 'temperature' or 'global warming'. This yielded flowering phenology shift data (days per decade) from studies worldwide, including reviews, meta-analyses and other literature (e.g. König et al., 2017; Mo et al., 2017; Supporting Information S4 contains detailed information on compiled data). We only included studies that explicitly quantified shifts in phenology through time, had at least 10 years of data, quantified shifts in full flowering or first flowering date and were samples of native, non-agricultural species (i.e. no crop species). Species were classified as advancing or delaying in their flowering time independent of the significance of this relationship. Two studies from the southern hemisphere (Rawal et al., 2014; Rumpff et al., 2010) were not included in our analyses as they only reported data on the species that were significantly advancing through time and/or did not provide results or raw data on each species' phenological shift direction (i.e. we could not differentiate between if these species were not significantly advancing shifting or if they were delaying their phenology through time). We also included flowering shift data from the 27 native species in our current study. Our search yielded data for 830 species from seven studies in the northern hemisphere (562 of which originated from a recent meta-analysis; a full list of individual studies can be found in König et al., 2017) and 118 species across four studies (including the present study) from the southern hemisphere (Table S4a).

To determine whether a lower proportion of plants were advancing their flowering time in the southern hemisphere than in the northern hemisphere, we used a logistic generalised mixed-effect model with hemisphere as the predictor variable, a binomial response variable of species' advancing (or delaying) and a random factor for study using the *glmer* function in the LME4 package (Bates et al., 2015). We obtained a pseudo-R^2 value from this model using the *r.squaredGLMM* function in the MUMIN package (Bartoń, 2013; Burnham & Anderson, 2002; Nakagawa et al., 2017).

3 | RESULTS

We found both significant advances and significant delays in species' flowering phenology through time (Figure 1; Table S3a). Four species had a significant advance in flowering time. This included two native species: *C. aristata* (Ranunculaceae), which advanced 3.2 days per decade over the period from 1961 to 2019 (R^2 = 0.35,

$p = 0.004$, Figure 1), and *Notelaea longifolia* f. *longifolia* (Oleaceae), which advanced 17.8 days per decade over the period from 1887 to 2019 ($R^2 = 0.67$, $p < 0.001$, Figure 1). The two introduced species that significantly advanced their flowering timing were *Acacia saligna* (Fabaceae; $R^2 = 0.14$, $p = 0.012$, Figure 1), which advanced 2.8 days per decade over the period of 1911–2019, and *Ligustrum lucidum* (Oleaceae; $R^2 = 0.26$, $p = 0.001$, Figure 1), which advanced 4.3 days per decade over the period from 1949 to 2019. After correcting for multiple hypothesis testing (using a Bonferroni–Holm correction), only the advancement of flowering time in *Notelaea longifolia* f. *longifolia* remained significant ($p < 0.001$).

Two introduced species (*Olea europea* subsp. *cuspidata*, Oleaceae, and *Cotoneaster glaucophyllus*, Rosaceae) and six native species (*Callistemon citrinus*, *Leptospermum trinervium*, *Melaleuca linariifolia*, *Kunzea capitata* (all Myrtaceae), *Telopea speciosissima*, Proteaceae, and *Echinopogon caespitosus*, Poaceae) showed significant delays in flowering time. However, only three of these species' shifts remained significant after correcting for multiple hypothesis testing (using a Bonferroni–Holm correction)—this included *C. citrinus*, which was delayed by 8.7 days per decade from 1961 to 2019 ($R^2 = 0.66$, $p < 0.001$, Figure 1), *O. europea* subsp. *cuspidata*, which was delayed by 4.6 days per decade from 1961 to 2019 ($R^2 = 0.42$, $p = 0.001$, Figure 1), and *L. trinervium*, which was delayed by 2.7 days per decade from 1901 to 2019 ($R^2 = 0.16$, $p = 0.001$, Figure 1).

Due to our unexpected result, whereby few species in our study advanced their flowering time (and some delayed flowering time, however, many showed now change through time), we performed a post-hoc analysis to determine whether climatic conditions prior to the flowering season affected flowering shifts through time, and whether between year variation in climatic conditions might have acted to obscure temporal trends in flowering time. We collected climatic data on the average temperature and average precipitation of the 3 months prior (90 days) to the beginning of the minimum full flowering date for each species; see Appendix S5 for details). Consistent with the idea that changes in flowering date across years are associated with changes in climatic conditions, we found that 5 of our 37 species showed significant correlations between flowering time and the average temperature preceding the flowering season, with three of these five species showing earlier flowering in warmer years (Table S5a). Similarly, 10 species showed significant correlations between flowering time and average precipitation preceding flowering, with seven of these species showing earlier flowering in wetter years (Table S5b). Analyses were also consistent with the idea that the changes through time that we did see are associated, at least in part, with changes in climate. When we included the average temperature preceding the flowering season in the models with year, the effect of year became non-significant for 7 of the 12 species that previously showed significant flowering shifts through time (*C. glaucophyllus*, *Olea europaea* subsp. *cuspidata*, *C. aristata*, *E. caespitosus*, *L. trinervium*, *M. linariifolia*, *T. speciosissima*; Table S4a). For two species (*Acacia saligna* and *C. glaucophyllus*) of the 12 species that had significant flowering shifts through time, when the average precipitation preceding the flowering seasons was added to the analysis, the year of observation did not remain significant (Table S4b). Likewise, mean temperature preceding the flowering season explained more of the variance than year in the multiple linear regression for 21 out of 37 species (Table S4c) and average precipitation explained more variance in flowering date than the year of observation for 17 out of the 37 species (Table S4c) which may be causing less significant long-term shifts in flowering time.

There was no significant phylogenetic signal in shifts in flowering time (Pagel's $\lambda = 0.035$, $p = 0.830$ and Blomberg's $K = 0.208$, $p = 0.88$, Supporting Information: Figure S6a).

Contrary to our hypotheses, introduced species did not shift their flowering more than native species ($R^2 < 0.001$, $Z = -0.018$, $p = 0.28$, Figure 2a) and there were no significant differences between trees, shrubs and herbs in their flowering time ($R^2 < 0.001$, $p = 0.41$, Figure 2b).

A significantly smaller proportion of southern hemisphere than northern hemisphere plants advanced in their flowering time ($R^2 = 0.04$, $p = 0.006$, Figure 3). Out of the 118 species that have been analysed for flowering phenology shifts through time in the southern hemisphere, only 72 (58.5%) showed advances, whereas, in the northern hemisphere, 677 of 830 species (81.6%) showed significant advances in their flowering phenology (Figure 3).

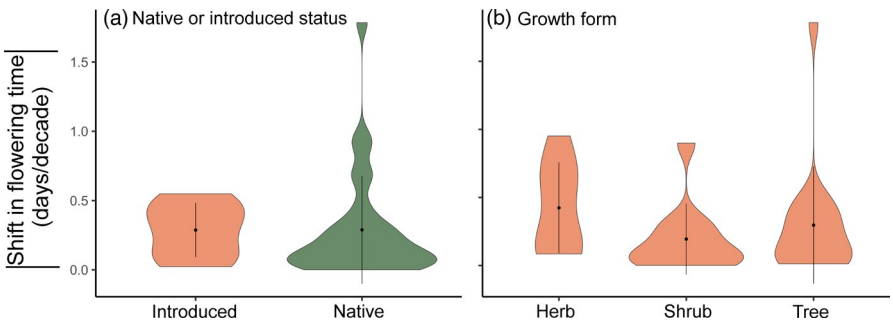

FIGURE 2 (a) Difference in the shifts in full flowering time in native (green) vs introduced (orange) species in our study. (b) Differences in the shifts of full flowering time between growth forms (herb, shrub, tree). The shift in flowering phenology is the absolute value of the slope from a linear model correlating flowering time with year (see methods, and Figure 1)

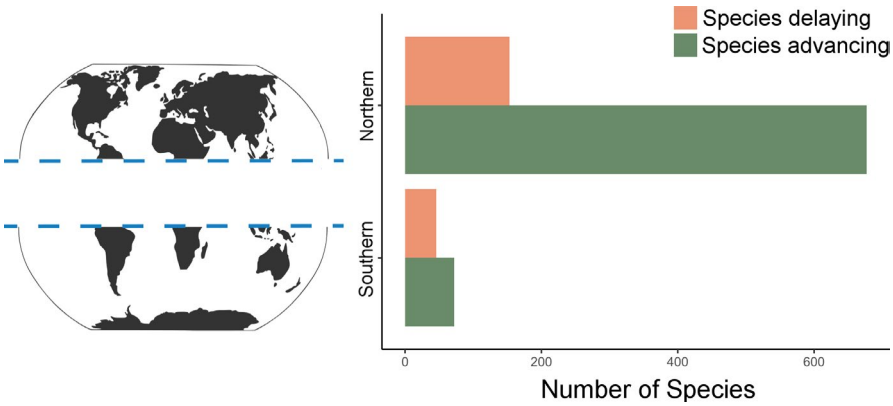

FIGURE 3 Difference in the number of species advancing and delaying their flowering time between the northern and southern hemispheres. Shifts in flowering phenology include all slope relationships of advances (slope >0) and delays (slope <0) determined from the relationships between the date of flowering and year of each species, regardless of the significance of these relationships. World map adapted from free image (OnlyGFX.com, author: 'zolee', 2015)

4 | DISCUSSION

A small increase in temperature can have a substantial impact on species' phenology, and previous studies have shown multiple-day advances in flowering for increases in just 1°C of temperature (Fox & Jönsson, 2019; Pearson, 2019). In northern Sydney, mean annual temperatures increased by 1.1°C from 1910 to 2019 (see Supporting Information for long-term weather data). However, only four of the 37 species in our study had significantly advanced their flowering phenology. These advances ranged from 2.8 days earlier flowering to 17.8 days earlier flowering and were determined over various time frames from 58 years to 132 years. In all, 25 species showed no significant change in flowering time, and eight species showed significant delays (Figure 1). Our results indicated that these long-term shifts may not be occurring in our study as many of our species are responding to changes in temperature and precipitation in the season preceding flowering time.

While temperature in the 3 months preceding flowering is an important variable driving phenological change both in the long-term and on a yearly scale, precipitation in the 3 months preceding flowering showed more correlations with flowering dates (Table S5b). There have been more frequent and more intense droughts and increased rainfall variability over the study period both in our study region, and at the continental scale in Australia (CSIRO, 2007; CSIRO, & Australian Government Bureau of Meteorology (BOM), 2020; Jyoteeshkumar Reddy et al., 2021; Trancoso et al., 2020). For two species in our study, seasonal trends in precipitation before the flowering season were obscuring shifts in flowering through time and seasonal precipitation explained more of the variance in flowering time than the year of observation for almost half of our species. Limited water availability may have led species in northern Sydney to delay their flowering in particular years, obscuring long-term shifts in flowering, as limited water may reduce a plants' ability to invest in reproduction (Aspinall & Husain, 1970), or because delaying flowering to a time when there is higher soil moisture yields greater reproductive success (Yang & Kim, 2016).

Another possible explanation for the lack of significant flower time advancement for some species and no relationships between flowering time and climatic variables for other species observed in our study could be the effect of photoperiod. Photoperiod (or day length) has been found to be an important factor that controls flowering time in other species; however, it has only been tested for northern hemisphere species (across Europe; Ma et al., 2020 and North America; Marchin et al., 2015) and southern hemisphere agricultural species (e.g. canola; Whish et al., 2020 and wheat; Sadras & Monzon, 2006). There are no data on species' photoperiod sensitivity in flowering time for the species considered in our study. Further studies could quantify flowering phenology photoperiod sensitivity in these species and test its effect on flowering time. Photoperiod may also interact with changes in temperature (Wang, Wang, et al., 2020) to produce unpredictable results in species flowering time shifts. If species' flowering phenology is more tightly controlled by photoperiod than by changes in temperature in the southern hemisphere, this could result in temporal mismatches as some species would not shift their flowering time to favourable climatic conditions. Likewise, some insect pollinators and seed dispersers may shift in phenology irrespective of photoperiod, putting plant species, that depend on these organisms, at risk under future climate change.

A lack of significant advancement in flowering time found in species in our study may also be due to the less frequent sampling intervals. Price's flowering time dataset (Price, 1963) is the highest resolution (weekly sampling) of long-term field data on flowering time in Australia. We resampled at the same intervals, which allows us to see significant changes in some of our species (Figure 1). However, previous studies have shown that additional changes may not be perceived when sampling at weekly intervals (Miller-Rushing et al., 2008). Future studies could resample at 3- or 2-day intervals and potentially increase the ability to detect species-level trends. Similarly, there are limitations in compiling datasets from alternative sources such as herbaria that may impact the detection of trends in flowering phenology. Herbarium specimens are a valuable source

of data when used in conjunction with field data (Jones & Daehler, 2018). However, herbarium specimens can be patchy in time for particular species (e.g. *Cinnamomum camphora* and *Acacia binervia*; Figure 1) and this may lead to a lack of detection of an earlier or later flowering trend in some species for which historical data are lacking. Investment into natural history collections and long-term monitoring of species is therefore critically needed to determine the impacts of future climate changes on southern hemisphere species.

Species in the southern hemisphere, including those quantified in our study, are showing significantly less flowering phenology advancement through time than are species in the northern hemisphere (Figure 3). The disparity between phenological change in the northern and southern hemispheres highlights the need for more research to be performed in the southern hemisphere, particularly in regions where long-term flowering phenology shifts have not been quantified such as sub-Saharan Africa. Understanding the mechanisms underpinning the differences in flowering phenology shifts is also an important direction for future research. One possibility is that the lower rate of change in the southern hemisphere might be because the northern hemisphere (particularly the arctic) has experienced much more warming since the 1980s than the southern hemisphere (Friedman et al., 2013; Intergovernmental Panel on Climate Change (IPCC), 2021). Differentiated rates of climate change have been shown to be of importance within continental Europe, with western and central Europe showing more advances in phenology due to warmer Atlantic air mass flow in spring, whereas eastern Europe is showing more delays in phenology due to influence from Siberian high-pressure systems (Ahas et al., 2002). Moreover, different climate factors might limit growth and flowering in different parts of the world. Perhaps increases in drought and heatwaves have a greater impact on species' phenology than increases in mean temperature for water-limited regions. Consistent with this idea, water availability is the key limiting factor during the growing season in much of Australia, including our study region (CSIRO, 2007), while much of the research performed in the northern hemisphere focuses on regions in North America (Bertin, 2015; König et al., 2017) and the United Kingdom (Fitter & Fitter, 2002; König et al., 2017) that may not experience limiting water availability at the same time as large increases in temperature as is experienced in Australian ecosystems. Additionally, shorter-term temperatures in the month prior to flowering have shown strong correlations with flowering time (Fitter & Fitter, 2002; Sparks et al., 2000) and these may play a greater role than mean annual temperatures. A worthwhile direction for future studies would be to identify the most limiting climatic factors on species flowering phenology, rather than assuming plants will flower earlier in the year due to increased mean temperature.

Climate change is altering pollinator emergence and phenology (Bartomeus et al., 2011). Thus, advances in flowering phenology may keep flowering time aligned with pollinator availability. However, species that do not advance their flowering, or do not advance quickly enough, can suffer mismatches between pollinator emergence and flowering time, which can have substantial detrimental effects on plant fitness (Forrest & Thomson, 2011; Hutchings et al., 2018; Kharouba et al., 2018; Scaven & Rafferty, 2013). The six native species and two introduced species in our study that were significantly delaying their flowering phenology (Figure 1) may miss an early emergence of insects that pollinate them at their typical earlier flowering emergence (Ramos-Jiliberto et al., 2018). Likewise, species that were delayed in their end of flowering may produce fruits too late or at the wrong time for potential specialised fruit/seed dispersers.

Our study showed few patterns in the types of species that are shifting their flowering phenology most rapidly nor any relationships between flowering shifts and species' phylogeny. Unfortunately, this means that our ability to predict which types of species or taxon groups will keep pace with climate change and shift their phenology is still limited in the southern hemisphere. Although there were no significant differences in flowering phenology between the growth forms (Figure 2), 6 out of the 12 significant flowering time shifts occurred in tree species (e.g. *Notelaea longifolia* f. *longifolia*), five significant shifts occurred in shrubs/woody climbers and only one herbaceous species (*E. caespitosus*) showed a significant shift in flowering time (Figure 1). Our findings complement previous research in the northern hemisphere, where studies have shown flowering phenology advances in a higher proportion of taller tree species than in shorter herbaceous species (Yang et al., 2018). Longer-lived trees may be shifting phenology through plasticity rather than genetic adaptation through multigenerational evolution. Shorter-lived species such as the herbaceous species and grasses may still be able to shift their flowering phenology through adaptation, especially for species with shorter generation times. Although all species observed in the field component of our study are perennial, further studies with additional species from both annual and perennial forms could test whether there were stronger relationships between life history and flowering phenology rather than the growth form of the species. Our results showed limited phylogenetic patterns in the flowering time shifts in our species and this is in contrast with previous research found in northern hemisphere plants (Davies et al., 2013; Rafferty & Nabity, 2017; but see CaraDonna & Inouye, 2015; Wolkovich et al., 2013) and may indicate that southern hemisphere species are phylogenetically less able to respond to climate change. A lack of phylogenetic signal in flowering phenology shifts may also be due to stronger effects of local climatic conditions and processes of community assembly (CaraDonna & Inouye, 2015). A global comparison of photoperiod shifts in flowering time in both hemispheres and how these relate to phylogeny would be a timely future direction to determine if southern hemisphere species are phylogenetically constrained from responding to future climate change in their flowering time.

In conclusion, we have shown for the first time that species in the southern hemisphere are significantly less likely to be advancing their flowering times in response to climate change than species from the northern hemisphere. This highlights the need for more studies of how plant and animal species are responding to climate change in the southern hemisphere. Different species showed shifts in phenology in different directions and at different rates. These

varied responses to climate change may result in substantial changes in species interactions in the future. These phenological shifts may cause mismatches that not only leave plants at risk to future climate change, but also the animals that depend on them.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

S.E.E. collected the data, analysed the data and led the writing of the manuscript; R.A.J.B. collected the data; M.E.B.S. collected the data and analysed the data; E.S. analysed the data and A.T.M. conceived the ideas and designed the methodology. All authors contributed critically to writing the manuscript and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

All data are publicly available on Dryad Digital Repository https://doi.org/10.5061/dryad.msbcc2g09 (Everingham et al., 2021).

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