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Bright and Long: Day Length Modulates the Phenology of Two Myrtaceae Species in Upper Montane Mixed Ombrophilous Forest

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ABSTRACT

The Upper Montane Mixed Ombrophilous Forest is a humid montane ecosystem characterised by cold winters and a rich Myrtaceae flora. We investigated the vegetative and reproductive phenology of *Myrceugenia euosma* (O. Berg) D. Legrand and *Siphoneugena reitzii* D. Legrand and its relationships with climatic variables over 35 months in southern Brazil. Using activity and intensity indices, circular statistics and generalised linear models, we assessed seasonality and climatic influences on phenophases. Both species exhibited continuous vegetative phenology. Reproductive phenophases were annual, seasonal and synchronous within species but temporally segregated between them. This phenological behaviour suggests niche partitioning that may reduce competition for pollinators and dispersers. Vegetative phenophases showed limited climatic dependence, with leaf flush in *S. reitzii* responding only to current day length. Reproductive phenophases were positively related to day length in both species, with distinct temporal lags. Comparisons of the mean onset and peak angles indicated interannual variation in most phenophases. Phenological advances were more frequent (13 events, 6–32 days) than delays (8 events, 6–59 days), suggesting climate-related shifts. These results indicate that abiotic factors act as environmental filters shaping the phenological patterns of sympatric Myrtaceae in montane environments.

1 | Introduction

The Upper Montane Mixed Ombrophilous Forest, also known as the Araucaria Forest, is a high-altitude (above 1000 m) phytophysiognomy of the Atlantic Forest Domain that occurs on the Southern Plateau of Brazil (IBGE 2012) and is characterised by high floristic diversity. This forest type harbours gymnosperms, such as *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae) and *Podocarpus lambertii* Klotzsch ex Endl. (Podocarpaceae), as well as a rich assemblage of angiosperms from the families Lauraceae, Meliaceae, Myrtaceae and Winteraceae. These taxa are adapted to the specific conditions of this altitudinal

environment (Martins-Ramos et al. 2011; IBGE 2012; Higuchi et al. 2013). The region exhibits moderate climatic seasonality, with annual variation in temperature and day length, while rainfall is evenly distributed throughout the year (Martins-Ramos et al. 2011; Higuchi et al. 2013). In addition, low winter temperatures and the occasional occurrence of snow add a seasonal component that can influence vegetation phenology (Liebsch and Mikich 2009).

In the Mixed Ombrophilous Forest and similar phytoformations, including temperate and montane forests of South America, temperature and humidity modulate phenological

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patterns (Marques et al. 2004; Morellato et al. 2024). In these environments, phenophases generally occur year-round, although peak periods may vary. Vegetative phenophases typically show peaks of leaf flush during the rainiest months, whereas leaf fall tends to occur in drier months. Flowering and fruiting also commonly occur during the rainiest months (Marques et al. 2004; Paise and Vieira 2005; Liebsch and Mikich 2009), although fruiting may extend throughout the year (Marques et al. 2004). These studies were conducted at the community level and were based on monthly presence-absence records of phenophases. Understanding these phenological dynamics is particularly relevant for families such as Myrtaceae, which exhibit broad adaptive diversity across vegetation types, including the Upper Montane Mixed Ombrophilous Forest (Gomes et al. 2020; Wagner and Fiaschi 2020).

With approximately 140 genera and 6000 species worldwide (Wilson 2011), Myrtaceae is the most representative family in Brazil, encompassing 29 genera and 1219 species, of which 811 are endemic (Flora e Funga do Brasil 2025). In the Upper Montane Mixed Ombrophilous Forest, Myrtaceae stands out for its diversity and abundance in both the canopy and the understory (IBGE 2012), playing key ecological roles as a food source for avifauna and contributing to forest regeneration (Gomes et al. 2017). Among the genera occurring in this phytophysognomy, *Myrceugenia* and *Siphoneugena* are particularly prominent. The former occurs in subtropical to temperate regions of South America, whereas the latter, which comprises only eight species, ranges from Puerto Rico to southern Brazil, in humid montane environments above 900 m a.s.l. (Kausel 1947; Proença 1990; Lughadha and Proença 1996; Higuchi et al. 2013). Both genera share pollination by pollen-collecting visitors and dispersal of fleshy fruits by birds (Costa et al. 2017; Corrêa, Sá, Santos, et al. 2024).

Among the representatives of these genera, *Myrceugenia euosma* (O. Berg) D. Legrand and *Siphoneugena reitzii* D. Legrand are co-occurring and abundant in the Caveiras River basin, southern Brazil (Higuchi et al. 2013; Gomes et al. 2017), where they play important ecological roles for the epiphytic community (Montibeller-Silva et al. 2020). In addition, both species have ornamental, biochemical and pharmaceutical potential and act as bioindicators of acidic soils (Souza et al. 2011; Gomes et al. 2020; Cavalheiro et al. 2023). Therefore, this study aimed to characterise the vegetative and reproductive phenology of *M. euosma* and *S. reitzii* in the Upper Montane Mixed Ombrophilous Forest and to evaluate the influence of abiotic variables on their phenological behaviour. Specifically, we addressed the following questions: When do vegetative and reproductive phenophases occur in *M. euosma* and *S. reitzii*? Are these phenophases seasonal? Which abiotic variables modulate their phenological behaviour during the studied period in the Upper Montane Mixed Ombrophilous Forest?

2 | Material and Methods

2.1 | Study Site

The study was conducted at Fazenda das Nascentes, part of the *Reserva Particular do Patrimônio Natural* (RPPN) Complexo Serra da Farofa, located in the municipalities of Urupema, Paine

and Rio Rufino, in the state of Santa Catarina, southern Brazil (Appendix S1). An RPPN is a category of Brazilian protected area established under the National System of Conservation Units to protect biodiversity on private land. The RPPN Complexo Serra da Farofa comprises six distinct areas and covers 4965.86 ha of forests in advanced regeneration, protecting several headwaters of the Caveiras River, a tributary of the Canoas River.

Fazenda das Nascentes (27°54'53.7" S, 49°52'51.0" W; 1502 m a.s.l.), with an area of 1659.20 ha, is characterised by Haplic Nitrosol and Humic Cambisol and by high atmospheric humidity associated with frequent rainfall (Pires et al. 2014). Forest formations vary across the area, with a predominance of Upper Montane Mixed Ombrophilous Forest. Its cloud forest physiognomy occupies the highest relief, whereas natural grasslands occur in lower portions (Costa et al. 2017) (Appendix S1). Undergoing natural regeneration for more than 30 years, the area supports a diverse flora, characterised by the high abundance of *M. euosma* and *S. reitzii*, together with other representative species such as *Araucaria angustifolia* (Bert.) Kuntze, *Cinnamomum amoenum* (Nees) Kosterm., *Dicksonia sellowiana* Hook., *Drimys angustifolia* Miers, *Ilex paraguariensis* St. Hil., *Ocotea pulchella* (Nees and Mart.) Mez, *Vernonanthura discolor* (Spreng.) H. Rob. (Martins-Ramos et al. 2011; Montibeller-Silva et al. 2020).

The regional climate is classified as mesothermal humid subtropical (Cfb) under the Köppen system (Alvares et al. 2018), with moderate seasonality, mild summers, no dry season, recurrent severe frosts and rainfall well-distributed throughout the year. Mean annual rainfall is 1656 mm, and mean annual temperature is 14.3°C (meteorological data from 1991 to 2022; Climate-Data 2022), with occasional snowfall during colder months (Montibeller-Silva et al. 2020).

During the study period (January 2021 to November 2023; Figure 1), the area experienced pronounced climatic variability, particularly in rainfall, which ranged from 37.8 to 391.2 mm per month. Rainfall peaks occurred discontinuously across seasons, with timing and intensity varying among years. Annual rainfall was close to the historical average in 2021 (1743 mm) and above average in 2022 (2256 mm—wetter autumn and spring) and 2023 (2327 mm—wetter winter and spring). Mean annual temperature was below the historical average, ranging from 11.5°C to 12.5°C, with minimum and maximum values of 7.5°C and a of 16.6°C, respectively. Photoperiod varied by approximately 3.5 h, from about 10 h in June to 14 h in January (Figure 1). Climate data were obtained from Epagri-Ciram (2023), with rainfall and temperature from meteorological station 106, located 4 km from the study area, and day length calculated using the Sunrise and Sunset Calculator (Time and Date 2023) based on the geographic coordinates of Urupema, Santa Catarina.

2.2 | Description and Ecology of the Species

Myrceugenia euosma has a shrubby to arboreal habit, reaching 3–8 m in height, whereas *S. reitzii* is a larger tree, attaining approximately 10 m, with a highly branched trunk. Both species have simple leaves with entire margins and opposite,

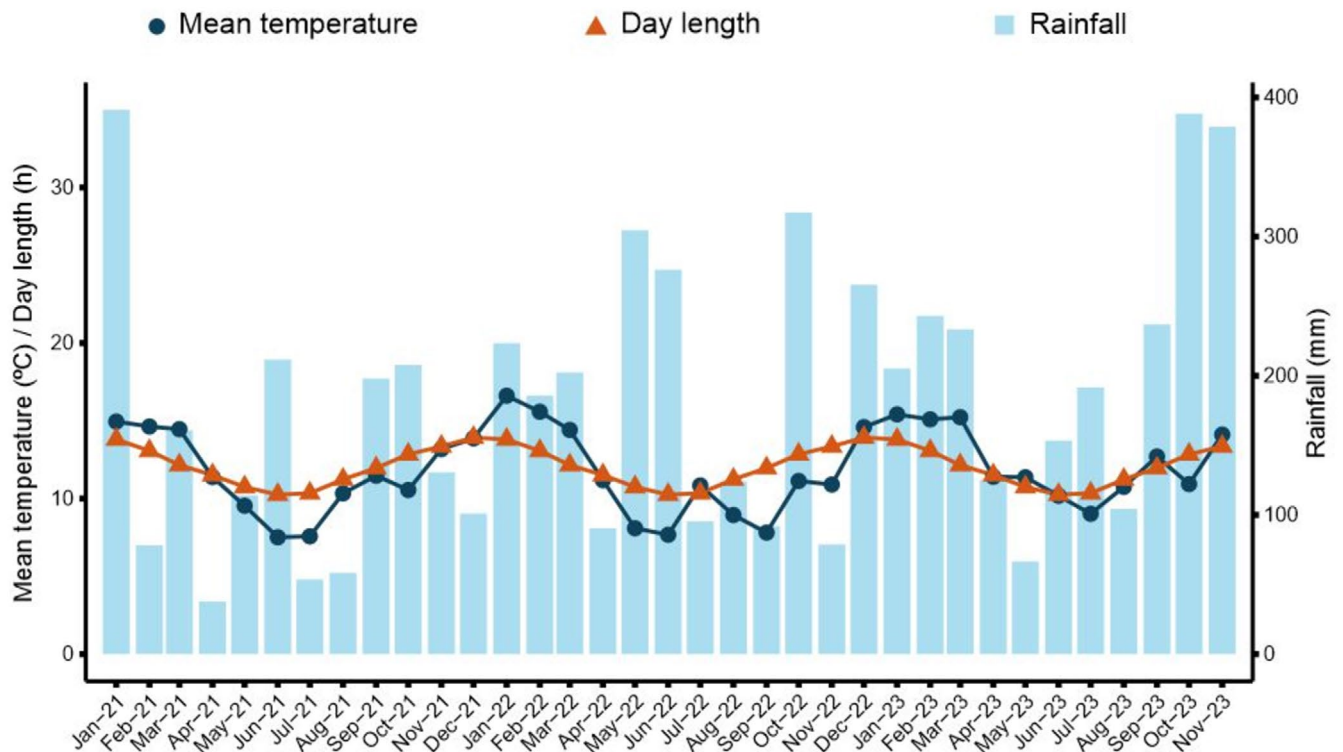


FIGURE 1 | Abiotic variables recorded during the phenological monitoring period (January 2021–November 2023) at Fazenda das Nascentes, located at the boundary of the municipalities of Painei, Rio Rufino and Urupema, Santa Catarina State, southern Brazil. Blue line (●) = mean temperature; orange line (▲) = day length; blue bars = rainfall.

decussate phyllotaxis, a characteristic of the Myrtaceae family (Sobral 2003). Leaves of *M. euosma* are dark green on the adaxial surface and bear trichomes on the abaxial surface, which impart a golden hue (Figure 2a–f). In *S. reitzii*, leaves are brownish-green, darker adaxially and lighter abaxially, with pubescent trichomes on both surfaces. Young leaves exhibit the reddish coloration typical of the family, associated with the presence of anthocyanin pigments (Figure 2g–l) (Wagner and Fiaschi 2020).

Inflorescences are axillary, and flowers are bisexual and morphologically similar in both species, with white petals and numerous stamens (Figure 2d,j). In both cases, pollen is the main floral reward and attracts native bees, which act as legitimate pollinators (Corrêa, Sá, Santos, et al. 2024). Fruits are globose to oblong purple berries (Figure 2e,f,k,l), with juicy pulp that serves as a food source for local avifauna (Costa et al. 2017; Cosmo et al. 2017; Wagner and Fiaschi 2020).

2.3 | Phenological Data Collection

We conducted biweekly observations on 69 individuals, including 33 of *M. euosma* and 36 of *S. reitzii*. Sampling was based on the phytosanitary and structural criteria proposed by Fournier and Charpentier (1975), and only individuals with a minimum height of 3 m and a diameter at breast height (DBH) greater than 5 cm were selected. Phenological observations included vegetative phenophases (leaf flush and leaf fall) and reproductive phenophases (flower buds, flowers at anthesis, immature fruits and mature fruits) (Figure 2). Phenophase intensity was quantified

using a semi-quantitative five-category scale (0–4), with 25% intervals between categories (Fournier 1974). Reproductive samples from the monitored individuals were incorporated into the Lages Herbarium of the Universidade do Estado de Santa Catarina (LUSC) under accession numbers 11 454–11 473.

2.4 | Data Analysis

2.4.1 | Phenological Behaviour Classifications

From the intensity index, we calculated the activity index, defined as the percentage of individuals expressing each phenophase (Bencke and Morellato 2002a). Category 0 was considered absence, whereas categories 1–4 were considered presence. Based on the activity index, we classified phenophase synchrony as asynchronous (<20% of individuals expressing the phenophase), low synchrony (20%–60%) or high synchrony (>60%) (Bencke and Morellato 2002b). Phenophase frequency over the studied period was classified as continuous, sub-annual, annual or supra-annual. For annual phenophases, duration was further classified as brief (<1 month), intermediate (1–5 months) or extended (>5 months), following Newstrom et al. (1994).

Patterns of leaf canopy retention were classified following Williams et al. (1997). This approach categorises species based on the minimum proportion of canopy cover observed during the annual cycle. Accordingly, species were classified as evergreen (high canopy cover year-round), brevideciduous (moderate seasonal leaf reduction, with canopy cover never falling



FIGURE 2 | Phenophases evaluated in *Myrceugenia euosma* (a–f) and *Siphoneugena reitzii* (g–l): (a, g) leaf flush; (b, h) leaf fall; (c, i) flower buds; (d, j) flowers at anthesis; (e, k) immature fruits; (f, l) mature fruits.

below approximately 50%), semideciduous (canopy cover falling below 50% during part of the year) or deciduous (complete leaf loss during part of the year).

2.4.2 | Statistical Approach

Seasonality of phenophases was assessed using circular statistics (Morellato et al. 2010; Zar 2010). For this purpose, onset and peak periods were determined for each individual and converted into angular values. From these angles, the following parameters were obtained: mean angle, subsequently converted into a mean date; circular standard deviation; and the length of the mean vector (r) (Zar 2010). The r value represents the concentration of angles around the mean date and ranges from 0 (no seasonality) to 1 (all individuals expressing the phenophase simultaneously). The Rayleigh test (Zar 2010) was used to assess unimodality of the angular distribution and to evaluate the existence of seasonality (Morellato et al. 2000). To test for differences in phenophase timing among years, homogeneity of the mean onset and peak angles for each phenophase was evaluated using the Watson-Williams test (Zar 2010). All analyses were performed in R version 4.5.2 using the *circular* package (Agostinelli and Lund 2017).

The association between abiotic variables (day length, rainfall and mean temperature; explanatory variables) and vegetative and reproductive phenophases (response variables) was evaluated for the month of phenophase occurrence and for time lags of 1–3 months prior to occurrence. Biweekly values of the phenophase activity index were used in these analyses, considering the entire study period (January 2021 to November 2023). For each abiotic variable, we selected the time lag showing the strongest cross-correlation with the phenophase activity index to minimise collinearity among consecutive months. Effects of the selected abiotic variables on the phenophases were evaluated using generalised linear models (GLM) with a Poisson distribution and a logarithmic function. We applied a model-averaging procedure to select the set of predictors that best explained variation using the *MuMIn* package (Barton 2025). Model diagnostics were performed using the *DHARMa* package (Hartig 2024), and when necessary, models were refitted using a negative binomial or zero-inflated negative binomial distribution. Goodness of fit was assessed using a pseudo- R^2 metric (Nakagawa and Schielzeth 2013). Analyses were conducted using the *car* (Fox and Weisberg 2019), *glmmTMB* (Brooks et al. 2017; McGillicuddy et al. 2025), *MASS* (Venables and Ripley 2002) and *performance* (Lüdtke et al. 2021) packages.

3 | Results

3.1 | Vegetative Phenology

Leaf flush occurred throughout the study period in both species; however, *S. reitzii* showed a more concentrated pattern during specific periods (October–December 2021, November–January 2022 and October–November 2023; Figure 3a). Despite these peaks, leaf flush frequency was classified as continuous in both species. In *M. euosma*, this phenophase showed high synchrony in all months, with at least 60% of individuals active. Activity peaks (100% of individuals) occurred in March, April and November 2021 and 2022, and February 2022 (Figure 3a). In *S. reitzii*, leaf flush ranged from low to high synchrony throughout the year, with 33%–90% of individuals active in most months. Activity peaks (> 90%) were generally recorded in November and December of the 3 years (Figure 3a).

Leaf flush intensity peaks coincided with activity peaks in both species but reached higher values in *S. reitzii* (70%–92%) than in *M. euosma* (45%–60%) (Figure 3b). During these events, crowns of *S. reitzii* trees were fully covered by new reddish leaves (Figure 2g), making individuals conspicuous in the landscape. An additional intensity peak in *M. euosma* occurred in October 2021 (approximately 70%), when 96% of individuals were active (Figure 3b).

Leaf fall also occurred throughout the study period in both species and was classified as continuous (Figure 3c). *Myrceugenia euosma* exhibited high synchrony in most months, except July–August 2021 and October–November 2022. Activity peaks

(> 90% of individuals) occurred in different months across the year (Figure 3a). In *S. reitzii*, leaf fall varied from low to high synchrony, with 30%–86% of individuals active, and the proportion of individuals losing leaves was generally lower than in *M. euosma* (Figure 3c).

In both species, leaf fall did not result in marked reductions in canopy cover, which remained relatively stable over time. Based on intensity index, canopy fullness in *M. euosma* remained above 75% in most observations, falling below this threshold on only occasionally. In contrast, *S. reitzii* maintained a canopy fullness above 75% throughout the entire study period. Accordingly, both species were classified as evergreen. In *M. euosma*, intensity peaks of leaf fall (21%–41%) overlapped with activity peaks, with the highest values recorded in September 2022 (41%) and in June–July 2023 (36%) (Figure 3d). In *S. reitzii*, leaf fall intensity showed little variation, ranging from 9% to 22% during the study period (Figure 3d).

3.2 | Reproductive Phenology

The flowering periods of *M. euosma* and *S. reitzii* are sequential and did not overlap. In *M. euosma*, flower buds were recorded from September to December, whereas in *S. reitzii* they occurred from January to April (Figure 4a). In both species, this phenophase had an annual frequency with intermediate duration. Synchrony was generally high in *M. euosma*, with activity peaks in September–October 2021 (100% of individuals) and November 2022 (94%). In contrast, synchrony in *S. reitzii* was mostly low or asynchronous, except for activity peaks in February (83% in 2021, 86% in 2022 and 75% in 2023) and March (58%–63%).

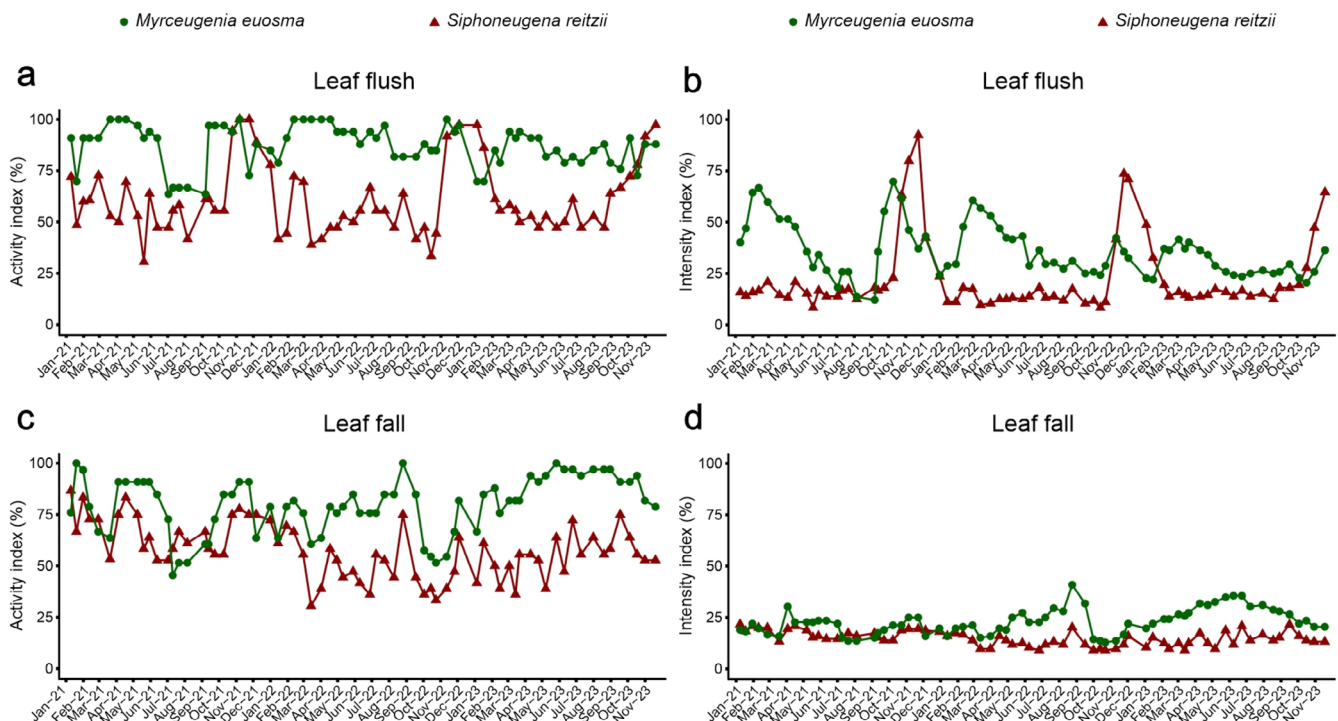


FIGURE 3 | Vegetative phenology of *Myrceugenia euosma* and *Siphoneugena reitzii* in southern Brazil. Activity and intensity indices of leaf flush (a, b) and leaf fall (c, d). Green line (●) = *M. euosma*; red line (▲) = *S. reitzii*.

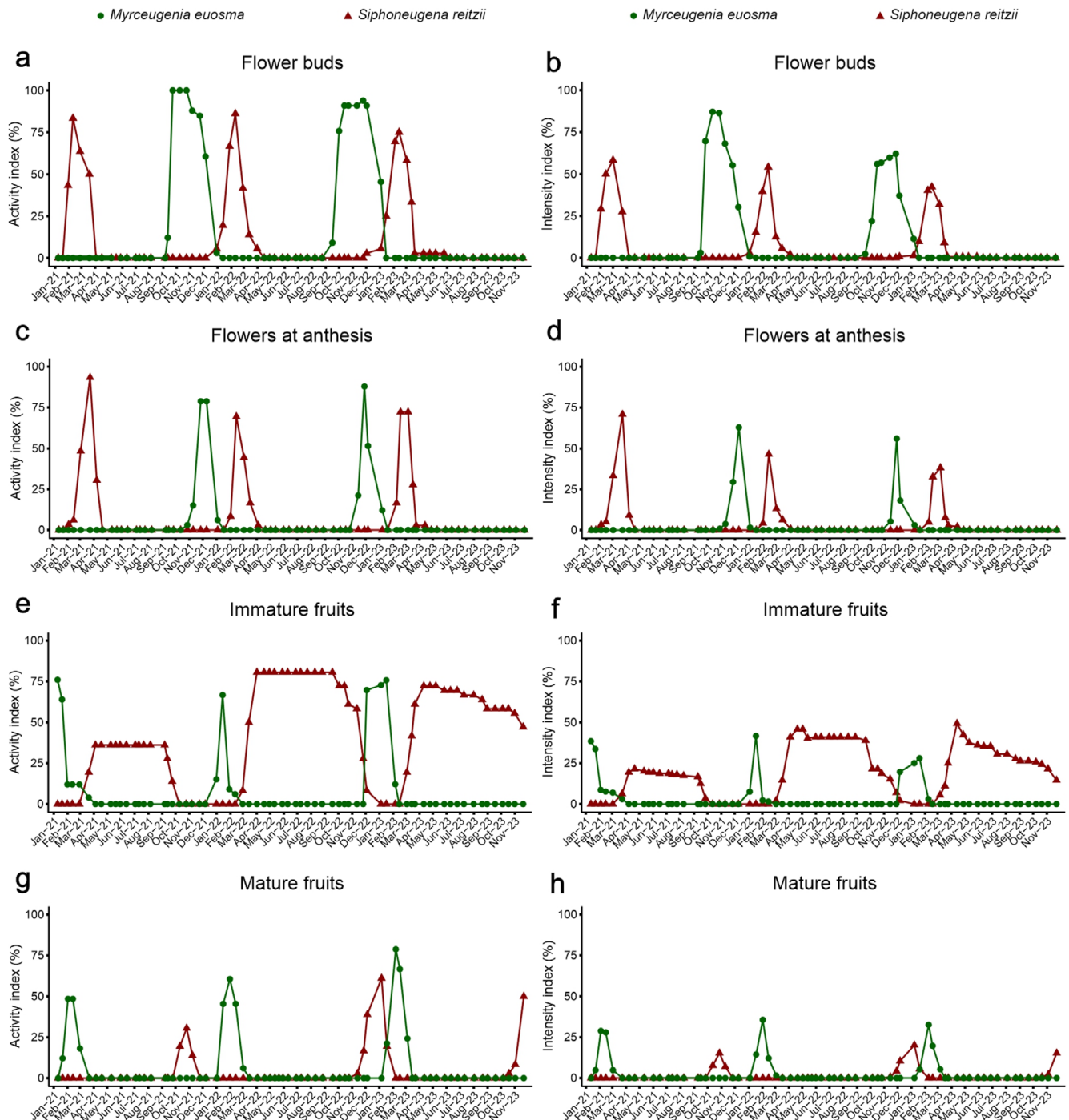


FIGURE 4 | Reproductive phenology of *Myrceugenia euosma* and *Siphoneugena reitzii* in southern Brazil. Activity and intensity indices of flower buds (a, b), flowers at anthesis (c, d), immature fruits (e, f) and mature fruits (g, h). Green line (●) = *M. euosma*; red line (▲) = *S. reitzii*.

In both species, intensity peaks generally coincided with activity peaks (Figure 4b). *Myrceugenia euosma* showed flower buds intensity peaks in October 2021 (87%) and November 2022 (62%) (Figure 4b). In *S. reitzii*, the highest intensity was recorded in March 2021 (58%), occurring after the activity peak. In subsequent years, intensity peaks occurred in February 2022 (58%) and 2023 (42%), overlapping activity peaks (Figure 4a,b).

Flower opening was observed from November to January in *M. euosma* and from February to April in *S. reitzii* (Figure 4c), resulting in an annual frequency with intermediate duration

in both species. High synchrony at anthesis was recorded in December for *M. euosma* (79% in 2021 and 88% in 2022) and mainly in March for *S. reitzii* (93% in 2021, 69% in 2022 and 72% in 2023). An additional peak (72%) was observed in February 2023 for *S. reitzii* (Figure 4c).

Intensity peaks of flowers at anthesis overlapped activity peaks in both species (Figure 4d). *Myrceugenia euosma* reached intensity peaks of 63% in 2021 and 56% in 2022. In *S. reitzii*, intensity peaks declined over the study period, from 71% in 2021 to 47% in 2022 and 38% in 2023.

The onset of immature fruit development occurred approximately 30 days after the peaks of flower anthesis in both species. Fruit formation and maturation were predominantly sequential between species, with brief overlap of immature fruits in March 2021 and December 2022 (Figure 4e). The duration of this phenophase varied among years. In *M. euosma*, immature fruits were recorded from December or January to February (Figure 4e), characterising an annual frequency with intermediate duration. In *S. reitzii*, this phenophase extended from March to October or December (Figure 4e), indicating an annual frequency with extended duration. Synchrony of immature fruits was generally high, except in *S. reitzii* in 2021. Activity peaks occurred in January for *M. euosma* (67% in 2022 and 70% in 2023) and persisted for longer periods in *S. reitzii*. In this species, synchrony varied markedly among years, with a low and prolonged peak in 2021 (36%; April–September), followed by higher peaks in subsequent years (81% from April to September 2022 and 72% from April to May 2023) (Figure 4e).

In *M. euosma*, intensity peaks of immature fruits coincided with activity peaks but declined between years (42% in 2022 and 28% in 2023) (Figure 4f). In *S. reitzii*, despite extended periods of high activity, intensity peaks occurred between April and May (22% in 2021, 46% in 2022 and 49% in 2023), approximately 1 to 2 months after the flowering peak (Figure 4d,f).

The period of mature fruit availability was sequential between species in the first reproductive cycle (2021–2022) and partially overlapping in January of the second cycle (2022–2023) (Figure 4g). In *M. euosma*, mature fruits occurred from January to March in all study years, whereas in *S. reitzii* they were recorded from October to December 2021 and from November 2022 to January 2023 (Figure 4g). Thus, mature fruit availability showed an annual frequency with intermediate duration in both species. This phenophase was generally asynchronous or exhibited low synchrony, with few months showing activity peaks. In *M. euosma*, the highest activity values occurred in February (49% in 2021, 61% in 2022 and 79% in 2023). In *S. reitzii*, activity peaks were observed in November 2021 (31%) and January 2023 (61%) (Figure 4g).

Intensity peaks of mature fruits overlapped activity peaks in both species. During these peaks, fruit intensity was consistently higher in *M. euosma* (29% in 2021, 36% in 2022 and 33% in 2023) than in *S. reitzii* (15% in 2021 and 20% in 2023) (Figure 4h).

3.3 | Seasonality and Association With Abiotic Variables

Circular analyses revealed strong seasonality at both the onset and peak of all reproductive phenophases in the studied species. This pattern was supported by high mean vector values ($r \geq 0.96$ in *M. euosma* and $r \geq 0.84$ in *S. reitzii*), low circular standard deviations and significant Rayleigh tests ($p < 0.01$) (Appendix S2). Vegetative phenophases were not analysed using circular statistics because they showed continuous patterns throughout the study period, which prevented the identification of discrete onset and peak angles.

Comparisons of mean onset and peak angles between years indicated interannual differences for most phenophases in both species (Appendix S2). In *M. euosma*, no interannual differences were detected only for the onset of flowers at anthesis and for the onset and peak of mature fruit (2021 vs. 2023). In *S. reitzii*, no differences were found for the onset (2022 vs. 2023) and peak (2021 vs. 2023) of flower buds, the onset of flowers at anthesis (2022 vs. 2023) or the peak of immature fruits. Mean dates showed both advances and delays in the onset and peak phenophases across years. Advances were more frequent (13 episodes, ranging from 6 to 32 days) than delays (8 episodes, ranging from 6 to 59 days). The longest advances were observed for the onset of immature fruits in *M. euosma* (32 days) and for the peak of flowers at anthesis in *S. reitzii* (28 days, comparing 2022 with 2021). The longest delays occurred in the onset (58 days) and peak (59 days) of mature fruits in *S. reitzii*.

Phenophases of both species responded primarily to day length, either in the month of occurrence or in preceding months. In *M. euosma*, vegetative phenophases showed no significant associations with the abiotic variables tested. In contrast, reproductive phenophases were positively associated with day length (Table 1). Mean temperature in the month of occurrence showed a positive association with immature fruits. In *S. reitzii*, leaf flush was positively associated with current-day length, although the model explained a relatively low proportion of variance (28%). Leaf fall showed no significant association with any abiotic variable. Among reproductive phenophases, day length with a three-month lag was the strongest predictor for flower buds and flowers at anthesis, whereas current-day length had a positive effect on mature fruits. Immature fruits showed no significant association with any of the abiotic variables evaluated (Table 1).

4 | Discussion

Through 3 years of monitoring two sympatric Myrtaceae species in an Upper Montane Mixed Ombrophilous Forest, this study reveals three central patterns: (i) a continuous vegetative phenology largely independent of short-term climatic variation, (ii) a strongly seasonal reproductive phenology tightly associated with day length, and (iii) a marked temporal segregation of flowering and fruiting between co-occurring species. Together, these results indicate that endogenous controls dominate vegetative dynamics in this humid subtropical environment, whereas photoperiod acts as the primary cue synchronising reproductive events. The complementary timing of reproductive phenophases further suggests a mechanism that may reduce interspecific competition for pollinators and dispersers, contributing to species coexistence in this forest system. Below, we discuss the ecological and physiological implications of these patterns in light of current hypotheses on plant phenological regulation.

Both species exhibited continuous leaf flush throughout the year, a pattern commonly reported for Myrtaceae in humid forests (Marques and Oliveira 2004) and for tree species in subtropical forests (Marques et al. 2004), differing mainly in the timing of peak activity. Continuous leaf production is likely associated with the absence of a pronounced dry season,

TABLE 1 | Results of the models evaluating the association between abiotic variables and vegetative and reproductive phenophases of *Myrceugenia euosma* and *Siphoneugena reitzii*.

Phenophase	Model	Parameter	Abiotic variables								R ²
			temp0	temp1	temp2	temp3	dayl0	dayl1	dayl2	dayl3	
Myrceugenia euosma											
Leaf flush	nb	χ^2	—	—	4.05	—	—	—	—	0.21	0.05
		p value	—	—	0.0441	—	—	—	—	0.64	
		b	—	—	0.01	—	—	—	—	0.01	
Leaf fall	p	χ^2	—	—	—	—	3.39	—	—	—	0.04
		p value	—	—	—	—	0.06	—	—	—	
		b	—	—	—	—	−0.03	—	—	—	
Flower buds	zinb	χ^2	—	—	—	2.52	8.87	—	—	—	0.68
		p value	—	—	—	0.11	0.0029	—	—	—	
		b	—	—	—	−0.6118	1.7137	—	—	—	
Flower at anthesis	nb	χ^2	34.93	—	—	—	58.72	—	—	—	0.94
		p value	3.408e-09	—	—	—	1.816e-14	—	—	—	
		b	−0.2031	—	—	—	6.21	—	—	—	
Immature fruits	nb	χ^2	56.06	—	—	—	25.01	—	—	—	0.83
		p value	7.01e-14	—	—	—	5.70e-07	—	—	—	
		b	0.58	—	—	—	2.01	—	—	—	
Mature fruits	zinb	χ^2	—	—	—	—	—	—	14.23	—	0.97
		p value	—	—	—	—	—	—	0.000161	—	
		b	—	—	—	—	—	—	4.26	—	
Siphoneugena reitzii											
Leaf flush	nb	χ^2	—	—	—	—	26.96	—	—	—	0.28
		p value	—	—	—	—	2.077e-07	—	—	—	
		b	—	—	—	—	0.12	—	—	—	
Leaf fall	p	χ^2	—	—	—	—	—	—	—	—	—
		p value	—	—	—	—	—	—	—	—	
		b	—	—	—	—	—	—	—	—	
Flower buds	nb	χ^2	—	—	—	—	—	—	—	75.32	0.80
		p value	—	—	—	—	—	—	—	2.2e-16	
		b	—	—	—	—	—	—	—	2.59	
Flower at anthesis	nb	χ^2	—	—	—	118.55	—	—	—	232.46	0.98
		p value	—	—	—	2.2e-16	—	—	—	2.2e-16	
		b	—	—	—	−0.16	—	—	—	6.05	
Immature fruits	zinb	χ^2	1.32	—	—	—	—	2.31	—	—	0.27
		p value	0.25	—	—	—	—	0.13	—	—	
		b	−0.03	—	—	—	—	−0.12	—	—	

(Continues)

TABLE 1 | (Continued)

Phenophase	Model	Parameter	Abiotic variables								R^2
			temp0	temp1	temp2	temp3	day10	day11	day12	day13	
Mature fruits	zinb	χ^2	3.67	—	—	—	8.94	—	—	—	0.95
		<i>p</i> value	0.05	—	—	—	0.002	—	—	—	
		<i>b</i>	−0.49	—	—	—	4.20	—	—	—	

Note: Numbers following each variable indicate the time lag used in the analyses. Bold *p*-values denote significant explanatory variables. Italicised *p* values indicate variables that improved model fit according to the likelihood ratio test, although the Wald test was not significant, likely due to inflated standard errors. Estimated coefficients (β) are presented on the model scale.

Abbreviations: —, variable excluded in cross-correlation analysis; day1, day length; nb, negative binomial; *p*, Poisson; rain, rainfall; temp, mean temperature; zinb, zero-inflated negative binomial.

allowing sustained photosynthesis and growth in response to relatively predictable climatic conditions (Talora and Morellato 2000). *Myrceugenia euosma* showed consistently high leaf flush intensity throughout the study period. Within this continuous pattern, two peaks were observed during the annual cycle, the second coinciding with the onset of flowering. This behaviour is characteristic of *Myrceugenia* and reflects a strategy of coordinated allocation to vegetative and reproductive growth, associated with the concomitant formation of axillary foliar buds and flower buds (Landrum 1980). In contrast, *S. reitzii* followed a pattern described for other arboreal Myrtaceae, such as *Eugenia umbeliflora* O. Berg (Marques and Oliveira 2004) and *E. pyriformis* O. Berg (Viana et al. 2020). These species belong to closely related clades (Vasconcelos et al. 2019; Lucas et al. 2019) and typically show leaf flush concentrated in specific months, a pattern that may favour carbon assimilation prior to flowering (Marques and Oliveira 2004). The occurrence of leaf flush peaks before peaks of flower anthesis in both species supports this interpretation. This phenological sequence is consistent with the transition of leaves from sinks to sources of photoassimilates (Luo et al. 2024). When leaves mature before flowering, they become photosynthetically active and contribute resources required to sustain floral and fruit development (Richardson et al. 2013).

Leaf fall in both *M. euosma* and *S. reitzii* was continuous and of low intensity, a pattern commonly reported for Myrtaceae (Ortiz et al. 2019; Viana et al. 2020; Castro et al. 2020). This behaviour classifies both species as evergreen (Williams et al. 1997), a trait frequently observed in subtropical climates with mild winters, despite seasonal variation in temperature and light availability (Bergamaschi 2007). Unlike some subtropical forest trees that show pronounced leaf fall during drier months (Marques et al. 2004), the species studied here exhibited sparse and moderate peaks that never exceeded leaf flush intensity or substantially reduced canopy cover. Prolonged leaf retention is likely supported by continuous water availability, which allows sustained photosynthetic activity even during cooler periods (Silva et al. 2021).

The weak association between vegetative phenophases and climatic variables observed in both species is consistent with patterns reported for evergreen rainforest species, in which leaf turnover tends to be continuous (Morellato et al. 2000; Ferrera et al. 2017). In humid environments with relatively low thermal variability, resources required for leaf maintenance remain available year-round, and vegetative phenology is largely

governed by endogenous controls, such as continuous branch growth and hormonal regulation (Reich 1995; Bauer et al. 2014). This intrinsic regulation, together with the deep root systems characteristic of Myrtaceae, which buffer short-term fluctuations in surface water availability by accessing deeper soil layers (Dye 1996; Whitehead and Beadle 2004; Ferrera et al. 2017), results in staggered leaf production and senescence among individuals, rather than strong synchronisation with short-term climatic variation.

The flowering of *M. euosma* (November–January) and *S. reitzii* (February–April) exhibits seasonal, sequential and non-overlapping anthesis patterns. The concentration of floral resources (pollen) in distinct periods (December for *M. euosma* and February–March for *S. reitzii*) likely enhances floral advertisement to generalist pollinators, such as native bees and *Apis mellifera* (Corrêa, Sá, Santos, et al. 2024; Otárola and Rocca 2014). This temporal pattern, combined with a shared floral morphology (bisexual flowers, white petals, polystemony), is consistent with a generalised pollination syndrome that promotes attraction and pollen transfer efficiency (Wolowski et al. 2016). Although such temporal segregation among morphologically similar species supports the hypothesis of niche partitioning to reduce competition for shared pollinators (Fenner 1998), its ecological relevance likely extends beyond this species pair. At the community level, staggered flowering periods may reduce interspecific competition with other co-flowering species offering similar resources, contributing to the structuring of temporal flowering niches and promoting pollinator fidelity and reproductive success (Smith-Ramírez et al. 1998; Staggemeier et al. 2010).

Photoperiod was the primary abiotic driver of flowering in both species. Day length is a key phenological cue in the Mixed Ombrophilous Forest (Marques et al. 2004; Athayde et al. 2009; Liebsch and Mikich 2009), where temperature variability and unpredictable frosts reduce the reliability of thermal signals, making photoperiod a more consistent and anticipatory cue for seasonal reproduction (Paise and Vieira 2005; Jackson 2009). This pattern is consistent with findings for other subtropical Myrtaceae, including *Myrcia brasiliensis* Kiaersk and *Myrciaria tenella* (DC.) O. Berg (Bauer et al. 2014; Ferrera et al. 2017). Despite this shared driver, the species adopt distinct temporal strategies. In *M. euosma*, flowering was associated with current-day length, suggesting an immediate photoperiodic trigger that synchronises anthesis with favourable seasonal conditions. In contrast, increases in day length acted as antecedent signals

for *S. reitzii*, likely triggering flower bud organogenesis (Singh et al. 2017), an energetically demanding process that may require several months to complete. This advance preparation has been described for high-altitude plants and for other Myrtaceae from the Mixed Ombrophilous Forest (Athayde et al. 2009; Inouye and Wielgolaski 2025).

The temporal segregation in the fruiting of *M. euosma* and *S. reitzii* is ecologically relevant given that both species produce morphologically similar fruits (Corrêa, Sá, Santos, et al. 2024) and share disperser guilds, predominantly birds of the genus *Turdus* (Costa et al. 2017). This partitioning suggests selective pressure to reduce competition for dispersal services, a process widely documented in zoochorous plant communities (Staggemeier et al. 2010; Zimback et al. 2023), as well as for germination sites following seed deposition (Primack 1987; Fenner 1998). The generally low intensity of mature fruits recorded over the 35-month study period likely reflects the combined effects of early fruit removal by frugivorous birds (Costa et al. 2017), potential constraints on pollination efficiency (Corrêa, Sá, Oliveira, et al. 2024) and natural interannual variability in fruit production, a common feature of tropical and subtropical tree species (Kelly and Sork 2002).

At the individual level, the temporal separation between peaks of flowering and fruiting within each species suggests a trade-off in resource allocation. By avoiding the simultaneous energetic demands of pollinator attraction and fleshy fruit development, plants may optimise the allocation of carbon and nutrients to maximise reproductive success (Bazzaz et al. 1987). This intraplant phenological partitioning complements the niche segregation observed at the community level, highlighting a multi-scale strategy for coping with the energetic constraints imposed by montane environments.

Fruiting in both species showed distinct photothermal dependencies, consistent with patterns reported for other Myrtaceae in Mixed Ombrophilous Forests (Marques and Oliveira 2004; Athayde et al. 2009; Paise and Vieira 2005; Ferrera et al. 2017; Leão-Araújo et al. 2019; Gomes et al. 2023). In *M. euosma*, immature fruit development was associated with concurrent warmth and long days, whereas fruit maturation responded to earlier photoperiodic signals. This pattern is typical of species that require favourable climatic conditions for rapid fruit development, as observed in *Campomanesia adamantium* (Cambess.) O. Berg and *Myrcia neoregeliana* Sobral (Leão-Araújo et al. 2019; Gomes et al. 2023). In contrast, fruit development in *S. reitzii* was largely independent of abiotic variables until ripening, which responded to immediate increases in day length, possibly reflecting a thermoperiodic adaptation to climate instability in montane environments (Paise and Vieira 2005; Bergamaschi 2007).

The occurrence of advances in multiple phenological events should be interpreted with caution, as the 35-month monitoring period does not allow discrimination between long-term directional shifts and natural interannual variability. The observed advances may reflect non-exclusive factors, including particular climatic conditions during the study period, internal cycles of resource accumulation or a response to ongoing climate change, as reported for temperate forests (Menzel et al. 2006). Notably, the

early flowering peak of *S. reitzii* (28 days earlier between 2021 and 2022) may be associated with the increase in temperature recorded prior to flowering. The apparent sensitivity of these species to interannual thermal variation highlights their potential value as bioindicators of climatic change in high-montane ecosystems (Santos et al. 2020).

Overall, *M. euosma* and *S. reitzii* exhibit continuous vegetative phenology coupled with strongly seasonal and temporally segregated reproductive events, with flowering and fruiting primarily modulated by day length. The consistency of these patterns with previous studies in Mixed Ombrophilous Forests (Marques et al. 2004; Paise and Vieira 2005; Liebsch and Mikich 2009) indicates that seasonal and non-overlapping reproductive strategies are widespread among zoochorous plants in this biome. In addition, our results reinforce the limited role of rainfall as a phenological driver in subtropical forests distant from the equator, where photoperiod and temperature emerge as the main abiotic regulators (Athayde et al. 2009; Ferrera et al. 2017; Marchioreto et al. 2007). By documenting these dynamics in a comparatively understudied montane ecosystem, this study expands current understanding of phenological drivers and provides a foundation for future research integrating ecophysiology and plant–animal interactions in Myrtaceae.

Author Contributions

Bruno Jan Schramm Corrêa: conceptualisation, data curation, formal analysis, investigation, methodology, software, validation, visualisation, writing – original draft, writing – review and editing. **Adriano Valentin-Silva:** formal analysis, methodology, validation, visualisation, writing – review and editing. **Alexandra Cristina Schatz Sá:** data curation, investigation. **Jaçanan Eloisa de Freitas Milani:** writing – review and editing. **Adelar Mantovani:** conceptualisation, methodology, project administration. **Roseli Lopes da Costa Bortoluzzi:** conceptualisation, funding acquisition, project administration, resources, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available on request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Species and study site