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Ferns and Lycophytes as new challenges

Climatic triggers of the phenophases of *Elaphoglossum macrophyllum* in Southern Brazil

Vanessa Graeff [1,6,8], *Andressa Müller*[1,7], *Fernando Junges*[2], *Danielle Bauer*[3], *Marciel Teixeira de Oliveira*[4] & *Jairo Lizandro Schmitt*[1,5]

Abstract
Although ferns have a prominent floristic position with their richness center in Atlantic Forest in Brazil, the effect of climate on their phenophases is still poorly known. This group shows different phenological patterns due to the great latitudinal extent, the strong climatic seasonality of this forest, and the leaf dimorphism found in some species. In this scenario, we evaluated the phenological events of *Elaphoglossum macrophyllum* and related them to climatic factors. Fertility, leaf renewal, and leaf senescence in *E. macrophyllum* were analyzed based on the monthly survey of 152 plants growing for two years in the subtropical Atlantic Forest, Brazil. The three analyzed phenophases showed the same intra-annual pattern regarding continuity, regularity, and seasonality along the two years, revealing a phenological pattern for the specie. The generalized additive models for location, scale, and shape (GAMLSS) indicated that photoperiod was the most important trigger for fertility and leaf renewal. Temperature, as an important phenology modulator, was related to leaf renewal and senescence. Our data indicate that *E. macrophyllum*, an endangered species in southern Brazil, withstands the consequences of seasonal climatic variations without the individual mortality, total leaf shedding, or fertility loss.
Key words: Atlantic Florest, climate, dimorphism, fern, phenology.

Resumo
Embora as samambaias tenham posição florística de destaque, com seu centro de riqueza na Mata Atlântica brasileira, o efeito do clima sobre suas fenofases ainda é pouco conhecido. Este grupo apresenta comportamentos diferenciados em sua fenologia devido à grande extensão latitudinal, à forte sazonalidade climática desta mata e ao dimorfismo foliar presente em algumas espécies. Nesse cenário, avaliamos os eventos fenológicos de *Elaphoglossum macrophyllum* e os relacionamos a fatores climáticos. Fertilidade, renovação foliar e senescência foliar em *E. macrophyllum* foram analisadas a partir do levantamento mensal de 152 plantas crescendo por dois anos na Mata Atlântica subtropical, Brasil. As três fenofases analisadas apresentaram comportamento recorrente quanto à continuidade, regularidade e sazonalidade nos dois anos, evidenciando um padrão fenológico para a espécie. Os modelos aditivos generalizados para localização, escala e forma (GAMLSS) indicaram que o fotoperíodo foi o gatilho mais importante de fertilidade e renovação foliar. A temperatura, como importante modulador da fenologia, esteve relacionada à renovação e senescência foliar. Nossos dados indicam que *E. macrophyllum*, uma espécie ameaçada de extinção no sul do Brasil, resiste às variações climáticas das estações sem a morte dos indivíduos, perda total de folhas ou perda de fertilidade.
Palavras-chave: Floresta Atlântica, clima, dimorfismo, samambaia, fenologia.

[1] Universidade Feevale, Prog. Pós-graduação em Qualidade Ambiental, Vila Nova, Novo Hamburgo, RS, Brasil.
[2] Universidade Feevale, Curso de Ciências Biológicas, Vila Nova, Novo Hamburgo, RS, Brasil. ORCID: <https://orcid.org/0009-0003-4519-702X>.
[3] Universidade do Vale do Rio dos Sinos, Prog. Pós-graduação em Biologia, Cristo Rei, São Leopoldo, RS, Brasil. ORCID: <https://orcid.org/0000-0001-6693-9246>.
[4] Universidade Federal de Pernambuco - UFPE, Lab. Fisiologia Vegetal, Cidade Universitária, Recife, PE, Brasil. ORCID: <https://orcid.org/0000-0001-9706-5625>.
[5] Universidade Federal de Alagoas, Campus Arapiraca, Unidade Educacional Penedo, Prog. Pós-graduação em Diversidade Biológica e Conservação nos Trópicos, Penedo, AL, Brasil. ORCID: <https://orcid.org/0000-0001-9867-9645>.
[6] ORCID: <https://orcid.org/0000-0003-3930-4186>. [7] ORCID: <https://orcid.org/0000-0002-8098-9749>.
[8] Author for correspondence: graeffvanessa@hotmail.com

Introduction

Neotropical forests are the most important repository of biological diversity and are essential for global climatic regulation (Kilpatrick *et al.* 2017). Among these, the Atlantic Forest in Brazil shows great latitudinal extent and strong climatic seasonality along the country's east coast (Stehmann *et al*. 2009). It is highly fragmented (Ribeiro *et al*. 2009), is considered one of the top five worldwide hotspots for conservation priority (Mittermeier *et al.* 2004) and has an estimated species richness of about more than 20,000 plant species, of which 40% are endemic (Ribeiro *et al*. 2009; Stehmann *et al*. 2009).

In the Brazilian Atlantic Forest, ferns deserve being mentioned as their center of richness is in this biome (Moran 2008; Mittermeier *et al*. 2004) with more than 1,410 species, representing approximately 79% of the inventoried diversity (Prado *et al.* 2015; BFG 2018; Flora e Funga do Brasil 2023, continuously updated). The phenological studies of ferns in Brazil have only monitored 40 species, which represents less than 3% of the country's richness. Such studies were mainly conducted in the southern and northeastern regions (Müller & Schmitt 2019).

The life cycle of ferns does not depend on animal dispersers, which makes climate the main trigger for the manifestation of their phenophases (Barrington 1993). Phenology is the integrative environmental science that investigates the repetition of biological events and correlates them with precipitation, temperature, and photoperiod, which are the main triggers of phenophases in plants (Morellato *et al*. 2016). This science is a tool used to understand the dynamics of populations and the influence of climatic variables on plants (Menzel *et al*. 2006; Rosenzweig *et al*. 2008). Leaf seasonality in ferns may be associated with differences between plants with monomorphic and dimorphic leaves, with the latter tending to have at least the most seasonal fertility phenophase (Mehltreter & Palacios-Rios 2003; Padoin *et al*. 2016).

Elaphoglossum (Dryopteridaceae), is a fern genus that includes ca. 600 species around the world, its greatest species richness is found in the Neotropical region where more than 450 species are found (Mickel 1990; PPG I 2016). In Brazil, 90 species have been reported (Matos 2023). This genus is typically characterized by simple entire leaves with dimorphism, acrostichoid sori, free veins, and phyllopodia. Most species are epiphytes, but there are also terrestrial and epipetric ones (Lagomarsino *et al*. 2012; Moran *et al*. 2010; Rouhan *et al*. 2004; Vasco *et al*. 2013).

Elaphoglossum macrophyllum (Mett. *ex* Kuhn) Christ. (Dryopteridaceae) is an herbaceous species distributed in South America, from Venezuela to the south of Brazil (speciesLink 2023). The laminae are elliptical/lanceolate with a cuneate base, and their spores have cristate, perforated perispores with sparse thorns on the ridges (Kieling-Rubio 2012; Matos 2023). In Brazil, this species occurs along the Atlantic coast, and it can grow on soil, tree trunks, or rocks from 50 to 1,350 meters above sea level (masl) (Tropicos 2020; Kieling-Rubio 2012; Matos 2023). According to Kieling-Rubio (2012), in the Atlantic Forest fragments of Brazil's South Region, *E. macrophyllum* prefers preserved environments and presents few populations with a discontinuous distribution. Consequently, the species is included in the Red List of the native flora of the state of Rio Grande do Sul, in the category "Endangered" (Rio Grande do Sul 2014).

Our study monitored of *Elaphoglossum macrophyllum*, the first dimorphic terrestrial species monitored in the Brazilian subtropical climate. In this study, we aim to address the following questions: (i) Does *E. macrophyllum* present different phenological behavior from the monomorphic species monitored under subtropical climate? (ii) When compared to monomorphic species, is the seasonality of this species greater due to its leaf dimorphism? (iii) Which climatic triggers can affect phenology the most? and (iv) What are the characteristics and classifications of the phenophases of this species in the scenery of the Brazilian Atlantic Forest?

It is expected that *Elaphoglossum macrophyllum* will have more synchronous and seasonal behavior in its fertility than in leaf changes and in relation to monomorphic species, due to the short lifespan of fertile leaves, characteristic of dimorphic species. In addition, triggers such as photoperiod and temperature are expected to be greater in subtropical climates.

Material and Methods

Study area and climate

The study was conducted in a fragment of the Subtropical Atlantic Forest in the municipality of Campo Bom, Rio Grande do Sul, Brazil (29°40'23.37"S and 51°01'56.65"W, 45 mals). The fragment has an estimated area of 60 ha and since it is isolated, it is under the direct influence of the edge effect in all its cardinal limits. Previous studies in this location revealed biological elements, such as high epiphyte diversity, which classify this area as a secondary forest with advanced ecological succession (Endres Júnior *et al*. 2015; Lippert *et al*. 2022; Quevedo *et al.* 2014; Brasil 1994).

The climate of the region is humid subtropical without a defined dry season (Cfa) according to Köppen. The annual mean temperature of the warmest month is above 22 °C (a) and presents well-distributed monthly rainfall (Peel *et al*. 2007; Alvares *et al.* 2013). The climatic monitoring was obtained from the Meteorological Station of Campo Bom (29º41'18,08"S and 51º03'52,84"W 25.8 mals). Previous data, from 2001 to 2014 showed that the mean annual precipitation was 1,872.6mm and the mean temperature was 19.6 °C.

Data on photoperiod are from the interactive annual report of the National Observatory for the capital city of the state of Rio Grande do Sul, Porto Alegre (latitude 30) (Observatório Nacional 2014). The soil of this region is classified as Dystrophic Red Argisol and Eutrophic Haplic Planosol (Streck *et al*. 2002) and the annual leaf-litter decomposition constant is 0.994 (k) (Bauer *et al*. 2017).

Sampling

Plots were demarcated totaling 20 parallel and adjacent 25m² (5 m × 5 m) parcels in two transects reaching 500 m², where 152 individuals of *Elaphoglossum macrophyllum* were marked. The plants were monthly monitored for two years, from September 2012 to August 2014. The species individuals were monitored regarding the number of leaves with developing sporangia, newly formed leaves, and senescent leaves, to assess the rates of fertility, leaf renewal, and leaf senescence.

Statistical analysis

Phenology was determined both qualitatively by the (i) Activity Index which assesses the presence or absence of the phenophase resulting in a frequency (Morellato *et al*. 2010), and quantitatively by the (ii) Fournier's Intensity Index (1974), in which the obtained data were classified based on a 5-category scale (0 to 4) with a 25% interval between each category. In order to calculate the Fournier's Intensity Index per month, the sum of all intensity categories given to each individual was divided by the maximum sum that the community could get (total number of individuals by area multiplied by four), resulting in a proportion. From the observation of the plants' behavior, the species' phenophases were classified into categories of continuous, discontinuous, regular, and irregular as proposed by Müller & Schmitt (2019).

In order to assess the seasonality of phenological events, an analysis of circular statistics was used. The months were converted into angles and each day of the year corresponded to about 0.9836º, resulting in 12 intervals of ~30º. The mean angle (μ) or the mean date is the time of the year in which the phenological activity of the individuals is more concentrated. The circular standard deviation and the vector r indicate the intensity of the concentration (0 to 1) around the mean angle. The vector r can be considered a measurement of the seasonality degree. The Rayleigh test was applied to indicate the significance ($P > 0.001$) of the mean angle (Morellato *et al*. 2000). These analyses were calculated by using the software ORIANA v.3 (Kovach 2009).

The contribution of the climatic variables to the phenological events of the plants was determined by building a Generalized Additive Model for Location, Scale, and Shape (GAMLSS) with Poisson error distribution, cubic smoothing spline function, and stepwise selection. For this purpose, predictive models were selected in order to reproduce the phenological events. Fertility, leaf renewal, and leaf senescence of the plants were count data and the Poisson error distribution was selected as a parameter for model adjustment. Photoperiod, temperature, and precipitation, as well as continuous variables, were standardized (mean 0, variance 1) before their inclusion in the complete model to obtain estimations of the comparable parameters (beta). Akaike's Information Criterion was used to choose the model with the best adjustment. The GAMLSS was generated using the package GAMLSS (Rigby & Stasinopoulos 2007) in the statistical software R (R Development Core Team 2017).

Results

Individuals of *Elaphoglossum macrophyllum* presented irregular discontinuous phenophases for fertility and leaf renewal, wherein individuals did not produce fertile leaves and/or new leaves in at least one month of the monitoring (Fig. 1a-b). Leaf senescence was continuous with leaf death rates in all months during the two years of monitoring. The frequency of this phenophase was irregular and its intensity was regular (Fig. 1c).

Fertility was the phenophase that presented a higher relation to seasonal changes (Tab. 1) with a peak of green sporangia in the warm months of the year coinciding with late spring and early summer (December). During autumn (March-April), an interruption of the phenophase was recorded. The mean date of this phenological event was only one day apart when comparing both years, occurring in a synchronous pattern (Tab. 1).

Leaf renewal showed a shorter mean vector length in relation to fertility and had a difference of one month in the mean date indicating lower seasonality rates (Tab. 1). This phenophase occurred with two annual peaks, the first one during the spring (September) and the second one during the summer (January-March) (Fig. 1b). Leaf senescence was continuous and not seasonal. No individual underwent total leaf shedding, but leaf death was recorded in all 24 monitored months with discrepant frequencies between summer and winter (Fig. 1c).

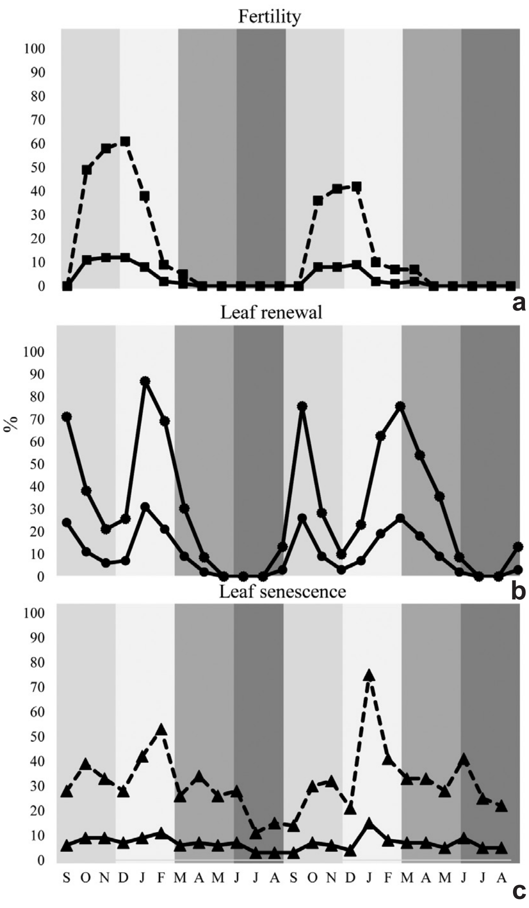

Figure 1 – a-c. Activity index (continuous line) and Fournier's Intensity Index (discontinuous line) of the population of *Elaphoglossum macrophyllum,* in the Subtropical Atlantic Forest, Brazil – a. fertility; b. leaf Renewal; c. leaf senescence monitored for two years. Shades of gray follow the seasons: spring (S–D), summer (J–M), autumn (M–J) and winter (J–S).

Climate monitoring in the first and second years, indicated precipitation of 1,911.8 mm and 1,964.8 mm, respectively, and the most intense precipitation event (370.7 mm) occurred in the late winter in August/2013 followed by 200–250 mm distributed mainly in early spring and summer (Fig. 2) The mean temperature was 19.2 °C and 20.2 °C (Fig. 2) and the photoperiod varied from 10.24 h to 14.31 h (ON 2014).

The GAMLSS model indicated that the photoperiod was the most important trigger for fertility and leaf renewal. Thus, photoperiod showed the greatest positive coefficients and demonstrates that 12 hours of sunlight per day generates an increase in the frequency and intensity of both phenophases. The temperature was the most important climatic trigger for leaf senescence since the positive coefficient confirms that at temperatures above 20 °C, there was a greater frequency and intensity of leaf death.

As for the leaf renewal, the negative coefficients of the mean temperature demonstrate that less leaf renewal occurs when the temperature reaches 20 ºC in the spring-summer transition. When this temperature is reached, this phenophase continues between spring and summer. It was observed that precipitation volumes above 250 mm preceded the beginning of fertility periods as well as volumes above 200 mm during this period may have contributed to the continuity of fertility during the two years of monitoring (Tab. 2).

Discussion

Our results evidenced the discontinuous phenological pattern of *Elaphoglossum macrophyllum* during the two years of monitoring which demonstrates a tendency to seasonality. The intensity of fertility was twice greater than the leaf renewal and occur in a unimodal way which intensified the seasonality of this phenophase because of the homogeneous behavior of the individuals. On the other hand, leaf renewal was bimodal and resulted in a decrease in the intensity of seasonality due to more the heterogeneous behavior of the population.

Table 1 – Mean date (μ), mean vector (r) and values of the Rayleigh test of the phenological events of the population of *Elaphoglossum macrophyllum* in the Subtropical Atlantic Forest, Brazil.

	Fertility		**Leaf renewal**		**Leaf senescence**	
	1st year	**2nd year**	**1st year**	**2nd year**	**1st year**	**2nd year**
No. of observations	46	31	116	122	83	76
Mean vector (μ)	75.2°	69.1°	95.1°	118.0°	117.8°	141.5°
Mean date	12/05/2012	12/06/2013	12/25/2012	01/24/2014	01/18/2013	02/19/2014
Circular standard deviation	37.5°	41.8°	72.4°	82.9°	105.1°	97.2°
Mean vector length (r)	0.80	0.76	0.45	0.35	0.18	0.23
Rayleigh Test (*Z*)	29.9	18.2	23.4	15	2.8	4.2
Rayleigh test (p)	< 0.001	< 0.001	< 0.001	< 0.001	0.058	0.014

The production of sporangia occurred in the same period in both years during three between spring and summer months and decreased in autumn. This behavior reflects the strong seasonality in which the species dedicated a third of its annual cycle to phenophase (fertility). The fertility seasonality is reinforced by leaf dimorphism considering fertile leaves have a shorter life span in comparison to sterile ones since their function is only reproduction (Lee *et al*. 2008, 2009). This characteristic of seasonal phenophase is also found in dimorphic species such as *Blechnum acutum* (Desv.) Mett. (Padoin *et al*. 2016), *Danaea wendlandii* Rchb. (Sharpe & Jernstedt 1990), *Acrostichum danaeifolium* Langsd. & Fisch. (Mehltreter & Palacios-Rios 2003) and *Thelypteris angustifolia* (Willd.) Proctor (Sharpe 1997).

The fertility found in *Elaphoglossum macrophyllum* individuals was greater when compared with monomorphic species *Ctenitis submarginalis* (Langsd. & Fisch.) Ching (Müller *et*

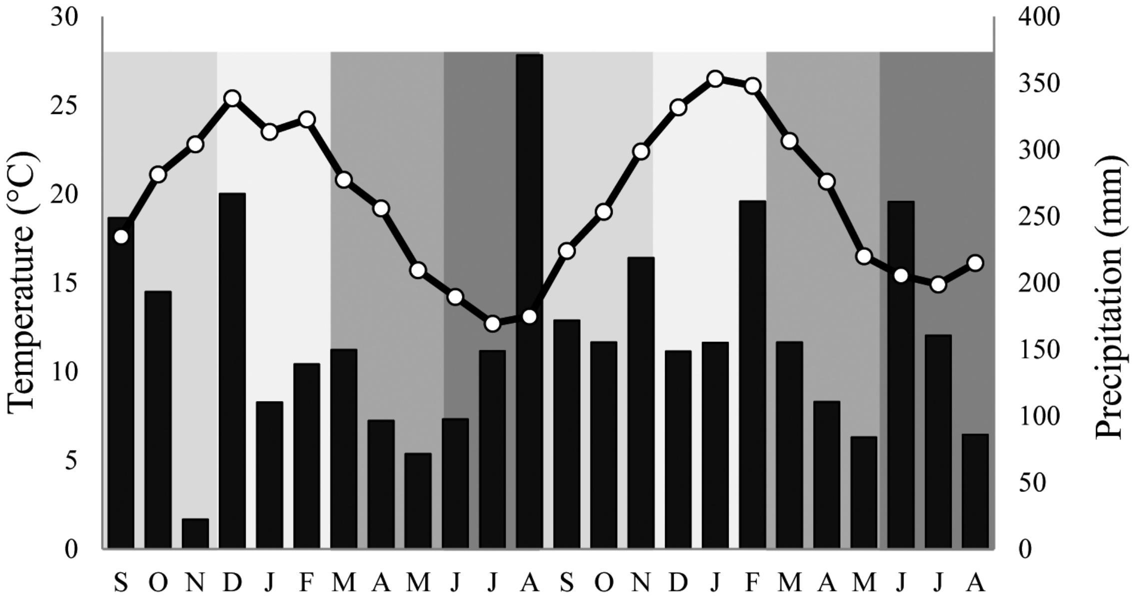

Figure 2 – Mean temperature and monthly precipitation in the two monitored years. Source: Campo Bom Meteorological Station (29º41'18,08"S and 51º03'52,84"W. alt. 25.8 m). Bars represent the volume of rainfall and the continuous line represents variation in temperature.

Table 2 – Result of the GAMLSS model for fertility, leaf renewal, and leaf senescence of the population of *Elaphoglossum macrophyllum,* in the Subtropical Atlantic Forest, Brazil.

Phenophase	Predictor variable	β	SE	t value	*P*	GD	AIC	SBC
Fertility	Intercept	-60.4	4.04	-14.9	7.99	31.90	47.90	57.32
	Photoperiod	4.76	0.31	15.2	< 0.001			
	Precipitation	0.02	0.01	1.9	0.07			
	Temperature	-0.06	0.06	-1.11	0.28			
Leaf renewal	Intercept	-8.49	2.5	-3.4	0.003	148.02	164.02	173.44
	Photoperiod	1.16	0.33	3.44	0.003			
	Temperature	-0.21	0.10	-2.1	0.05			
	Precipitation	0.0001	0.003	0.49	0.62			
Leaf senescence	Intercept	1.34	0.99	1.35	0.18	108.72	116.72	121.43
	Temperature	0.09	0.04	2.25	0.03			
	Photoperiod	-0,1	0.13	-0.7	0.45			
	Precipitation	-0.0008	0.001	-0.76	0.45			

Significant parameters are ordered by descending order of importance according to the estimated value (β). GD = Globally Deviation; AIC = Akaike's Information Criterion; SBC = Schwarz Bayesian criterion.

al. 2022) and *Lindsaea lancea* (L.) Bedd. (Müller *et al*. 2016) monitored in southern Brazil. In addition, phenophase was triggered and modeled by environmental variables, such as photoperiod and temperature (Morellato *et al*. 2016). This inherent attribute is part of the species' life history, and its seasonal and collective occurrence aims to ensure the species' succession, which reinforces seasonality even more (Mehltreter 2008; Groot *et al*. 2012).

Despite this collective effort in sporangia production and, in addition to the fact that the ferns produce a larger number of positive photoblastic spores that persist in the soil for long periods, sexual reproduction is somewhat rare (Esteves 2013; Arens 2001). The preferential dispersion is vegetative (Jones *et al*. 2007) or near mother plants (Wolf *et al*. 2001), which restricts its distribution to short distances, since its spores are really small (Jones *et al*. 2006, 2007).

This can also be influenced by ferns preferring places with high soil humidity for their development (Silva & Schmitt 2015). The soil in the studied forest is subjected to a quick process of leaf litter decomposition (Bauer *et al*. 2017), providing more favorable conditions for individuals to settle near the mother plant in the forest understory, where *E. macrophyllum* grow up (Quevedo *et al*. 2014).

The senescent behavior of the leaves of *Elaphoglossum macrophyllum* followed the leaf renewal cycle, the highest frequency of this phenophase was recorded during summer, after the first event of leaf renewal that occurred in the previous spring. The continuous rhythm of leaf senescence is common in monomorphic and dimorphic ferns monitored at the population and community level in southern Brazil (98%) such as *Blechnum brasiliense* Desv. (Schmitt & Franz 2005), *Dicksonia sellowiana* Hook. (Schmitt *et al*. 2009), *Cyathea atrovirens* (Langsd. & Fisch.) Domin (Schmitt & Windisch 2012), *Cyathea corcovadensis* (Raddi) Domin (Neumann *et al*. 2014), *Blechnum acutum* (Padoin *et al*. 2016) (Müller & Schmitt 2019).

As in the mentioned species, the phenological event in *Elaphoglossum macrophyllum* was enhanced during spring, when the peak of leaf renewal and fertility also occurred. Thus, a larger number of expanded leaves is associated with an increased frequency of leaf death. Moreover, this same period of the year has the highest temperatures, more daylight hours, and more water deficit and these environmental variables cause stress on the plant and may compromise its physiological activity and the incidence (Yordanov *et al*. 2000).

Senescence decreased in the winter months when there is a limitation of temperature and photoperiod, as well as decreased rates of leaf expansion, senescence tends to be less influenced, especially during winter (Müller *et al.* 2022). However, the senescence was not interrupted as in *L. lancea* (Müller *et al*. 2016).

In this study, fertility, and leaf renewal were induced from a minimum of 12 daily hours of light, during the winter-spring transition and the same occurred in those periods of maximum photoperiod (December 14:01 hrs and January 13:82 hrs), coinciding with the second peak of leaf renewal and fertility maintenance since the beginning of the warm seasons. When the mean temperature reaches 20 °C, there is an intensification of senescence and leaf renewal decline reducing the second leaf renewal event by 10%. It is already registered that the increase in temperature also causes a reduction in the rates of leaf renewal and fertility in fern species growing in southern Brazil (Müller & Schmitt 2019; Müller *et al*. 2020).

Photoperiod and temperature are variables that signal climatic seasons for the organisms (Way & Montgomery 2015), and in southern Brazil, they occur simultaneously, triggering and modeling the phenophases of fern phenology (Körner & Basler 2010; Neumann *et al*. 2014; Müller *et al*. 2016; Padoin *et al*. 2016).

Considering the prediction of an increase of 1.5 °C in the Earth's temperature in the next years (WMO 2014), the specie *Elaphoglossum macrophyllum* would have a tendency to produce fewer leaves in the period of leaf renewal, as well as have an increase in leaf senescence rates, which could reduce their colonization capacity within a scenario of extinction threat and reduction of habitats (Kieling-Rubio 2012; Rio Grande do Sul 2014). The production of sporangia tends to be less vulnerable to climate change because it demonstrated a relationship only with photoperiod, which is a constant variable year by year (Jackson 2009).

However, the following climatic triggers: photoperiod and temperature occurred together with an increase in precipitation during the spring months. According to the GAMLSS model, the greatest positive coefficients of this variable showed that at least 150 mm of rainfall is necessary to trigger fertility, which indeed occurred at the beginning of this phenophase. This influence of precipitation is stronger in plants growing in the tropical Atlantic Forest, which has a well-defined dry season (Flanagan & Adkinson 2011).

Fertility, leaf renewal, and leaf death of *Elaphoglossum macrophyllum* showed recurrent behavior in both years of monitoring highlighting a phenological pattern. Fertility and leaf renewal were discontinuous and irregular and showed seasonality while leaf death was continuous, regular, and non-seasonal.

Our results support the idea that the main trigger for *Elaphoglossum macrophyllum* is photoperiod because the statistical approach here used highlighted its preponderance over temperature and precipitation. Recognizing the climatic variables that model the life cycle of this species is relevant to determine its places of occurrence or places that may be colonized by these plants in case of a threat to the species in southern Brazil.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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