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Weather variables affecting the behaviour of Insect flower visitors and main pollinators of *Erythroxylum myrsinites* Martius (Erythroxylaceae)

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Abstract

Basic research assessing environmental effects on entire pollinator communities are still uncommon, particularly for rare and commercially unattractive plant-pollinator partners. We investigated the community of flower visitors of *Erythroxylum myrsinites* to check for potential pollinators and to check the extent of weather influence of visitor behaviour, registered as the number of visitors attending flowers of *E. myrsinites.* We then calculated species' dominance and constancy and assessed location of pollen attachment in each visitor's body. We correlated weather variables with the composition and abundance of visits carried out by the entire community and by most constant and dominant species. The wasps *Polybia sericea*, *P. ignobilis* and *P. fastidiosuscula* showed the highest values of constancy, dominance and attached pollen. There was a community-level effect of atmospheric pressure, solar radiation and wind speed on the number of visits. Atmospheric pressure affected the number of visits of eudominant species *P. fastidiosuscula* and *P. sericea*, while solar radiation affected the number of visits of *P. ignobilis*. Our results demonstrate the influence of weather variables on flower visiting insects and suggest the importance of native wasps in pollen transport and potential pollination.

Introduction

Honeybees visiting flowers is such a common picture that it is hard to remember it is just a part of the pollination story. First, not all pollinators are honeybees. Pollination stands as one of the most important classes of animal–plant interaction, as ~85% of angiosperms are pollinated by animals (Ollerton et al., 2011). Such interactions were key drivers of the evolutionary radiation of both angiosperms and insects across the world (Crepet et al., 1991; Grimaldi, 1999). Within Hymenoptera, one of the largest insect orders, honeybees and other bee species are frequently cited as major pollinators (Cardinal et al., 2012; Kevan & Baker, 1983; Potts et al., 2010), but other insects such as wasps are also important pollinators (Heithaus, 1979; Freitas & Sazima, 2006; Sühs et al., 2009;

Somavilla et al., 2010; Rader et al., 2016). Second, not all insects visiting flowers are pollinators. Among other resources, flower visitors seek for pollen or nectar (Faegri & van der Pijl, 1971; Proctor et al., 1996) and are only pollinators if visits are frequent and pollen is regularly transferred to another flower (stigma) of the same species (Rech et al., 2014) or within the same individual. Last, the study of unusual plant-pollinator systems and factors driving pollination success may still uncover gaps in the "story of pollination".

Pollination success can be driven by factors such as flower and pollinator morphology and plant phenology or pollinator behaviour. Over short temporal and spatial scales, successful reproduction of plant pollinated species can result from the activity and identity of pollinators, whereas the behaviour and activity of pollinators can be constrained by

abiotic factors (Case & Barrett, 2004). Air temperature and humidity, atmospheric pressure, solar radiation and wind intensity may influence insect visits, insect flight activity or even whether the insects leave their nests at all (Abrol, 1988; Burrill & Dietz, 1981; Fijen & Kleijn, 2017; Kearns & Inouye, 1993; Lundie, 1925; Nielsen et al., 2017). However, studies usually focus on the effect of weather variables either on few or a single species (e.g. honeybees: Burrill and Dietz, 1981; Lundie, 1925). This leaves a gap in the understanding of how weather affects the behaviour of entire pollinator communities (Fijen & Kleijn, 2017), particularly for rare and economically unattractive plant-pollinator partners.

Erythroxylum myrsinites Mart. (Erythroxylaceae) is a shrub native to South America, occurring in Argentina, Brazil, Paraguay and Uruguay (Amaral Jr., 1980). In Brazil, *E. myrsinites* is found in Southern and South-Eastern regions, in the Atlantic Forest vegetation domain (Loiola & Costa-Lima, 2015) and is considered endangered in parts of its range (São Paulo 2016). Even though pollination of *E. myrsinites* is still underexplored, bees, wasps, and flies are known to be the main flower visitors and pollinators of several species of *Erythroxylum* (Barros, 1998; Freitas & Sazima, 2006; Rosas & Domínguez, 2009).

Here we gathered information on the flower visitors of *E. myrsinites* and assessed what drives the activity and number of visitors on its flowers. By assuming pollination systems are normally evolutionary conserved (Macior 1982; Johnson et al. 1998; but see Ollerton 1996) and based on previous studies for *Erythroxylum* spp. (Barros, 1998; da Silva et al., 2007; Freitas & Sazima, 2006), we hypothesized that bees, wasps, and flies are the main flower visitors of *E. myrsinites*. Regarding the drivers of visitors' activity, we expected air temperature and relative humidity, atmospheric pressure, solar radiation and wind intensity (e.g. Nielsen et al. 2017) to affect the community of visitors by influencing the number of visiting insects. By checking these hypotheses, we tried both to improve basic knowledge of a poorly known plant species and its interacting insect community and to apply community-level modelling techniques to assess environmental drivers of the behaviour of flower visitors.

Materials and methods

Study system

The study was conducted in municipality of Santa Cruz do Sul (29º41'S – 52º26'W), Southern Brazil. Vegetation type is seasonal deciduous forest, being inside the Atlantic Forest domains. Following Koeppen's classification (Köppen, 1931), the regional climate is *Cfa* (subtropical humid). *Erythroxylum myrsinites* individuals were found growing in the edge of an isolated forest remnant of ca. 9 ha at 45 m above sea level.

Study plant

Erythroxylum myrsinites is a light-demanding shrub and grows on moist soils, reaching up to 3 m in height (Amaral Jr., 1980). Flowers are solitary, small, light cream coloured and slightly perfumed (Amaral Jr., 1980). It is a distylous plant with brevistylous and longistylous flowers, very similar in size, produced from August to April (Amaral Jr., 1980). This kind of floral dimorphism, in which anthers and stigmas of the two floral morphs are in different positions, may promote pollen flux between the two flower types and increase cross-pollination (Barros, 1998). The fruit is a small drupe (ca. 7 mm length and 3.5 mm wide), red, monospermic and probably bird-dispersed. Fruiting spans from September to May (Amaral Jr., 1980).

Sampling methods and data collection

Flower visitors of seven individuals of *E. myrsinites* were collected during their complete flowering period between September and October 2008 (a different flowering period reported in literature). Visitors were collected with entomological nets, between 9h00 and 17h00. This temporal sampling extent was determined after preliminary observations where the period with the highest visitor activity was identified. Two additional observations were done at night to check if there were any nocturnal visitors, and no flower visitors were observed. Each sampling event lasted 30 min. Total time of observations and collections spanned over 32 h and was distributed along 16 days. Insects were deposited in individual vials and stored in the entomological collection of University of Santa Cruz do Sul (CESC). Subsequently, all collected individuals were examined under a stereoscopic microscope (at 40x) for identification and to verify if there was pollen attached to their integument and in which body part pollen grains were located (corbicula, face, frontal legs, mesosome, metasome, propleuron and scopa). From a fraction of these individuals, pollen was removed and visualised in optical microscope (at 1000x) to confirm if pollen grains belonged to *E. myrsinites* (same procedure than in Sühs et al. 2009).

Weather data (air temperature and relative humidity, solar radiation, wind intensity and atmospheric pressure) were collected by a weather station (Davis®, model Vantage Pro Plus), located ca. 500 m away from the study site. Data was collected every 30 min and were provided by University of Santa Cruz do Sul (UNISC).

Data analysis

To verify the first hypothesis of this study, we recorded the identity, dominance, and constancy of flower visitors. As a complementary information regarding flower visitor behaviour, we also verified the number of individuals with pollen attached and the location of pollen on visiting species. Dominance (D) was calculated as: $D = (i / t) \times 100$, where i = total number of individuals of i species; t = total number of collected individuals. Dominance was used to classify species in the following scheme: D > 10% = Eudominant; D > 5 ≤ 10% = Dominant; D > 2 ≤ 5% = Subdominant; D > 1 ≤ 2% = Recessive; D ≤ 1% = Rare (Sühs et al., 2009). Constancy (C)

was calculated as: C = (P / N) × 100, where P = number of collections (number of records containing the species) and N = total number of records (Thomazini & Thomazini, 2002). When C ≤ 25% the species was considered Accidental, when C > 25 ≤ 50%, Accessory; and when C > 50%, Constant. We then listed species as potential pollinators when they showed high values of dominance and constancy, and when they showed *E. myrsinites* pollen on their bodies.

We used generalized linear models for multivariate responses (GLM_{mv}) with negative binomial errors to test the effects of weather predictors (air temperature, atmospheric pressure, relative humidity, solar radiation and wind speed) on community composition and on species individual responses. Following preliminary exploratory analyses, we decided to include also quadratic terms for all weather variables. Correlation amongst explanatory variables was previously checked using variance inflation factor (VIF) and redundant variables removed when VIF > 4, so that all kept variables were uncorrelated. All weather predictor variables were standardized before the analysis to avoid collinearity. P-values were calculated through 999 PIT-trap resamplings. Even though we applied a high number of tests on univariate responses (each species against predictors), we reported unadjusted P-values, but interpret the results with caution. To reduce the risk of type-I errors, we inform and discuss only responses of most abundant species (eudominant). Initial model contained all predictors, including quadratic terms. Model simplification was performed through backward elimination. Model selection was based on the sum of computed Akaike information criterion (AIC - by selecting models with lowest sum-of-AIC values) and

validation was determined by graphical analysis of residuals. Analyses were performed on the R interface (R Development Core Team 3.0.1., 2013) using package *mvabund* (Wang et al., 2013) for model building.

Results

Erythroxylum myrsinites flowering period (since the opening of buds) lasted 19 days. The number of eudominant and subdominant visitors followed a bimodal pattern, peaking from 11h00 to 12h00 and from 13h00 to 14h00 and being low from 9h00 to 10h00, 12h00 to 13h00, and 16h00 to17h00 (Fig 1). We collected 376 visiting insects, 367 belonging to Hymenoptera and nine to Diptera. Nineteen species were recorded, 16 belonged to Hymenoptera and three to Diptera. Within Hymenoptera, ten species belonged to Vespidae, four to Halictidae and two to Apidae. Within Diptera, Syrphidae had two species and Stratiomyidae had one species (Table 1).

Three visiting species were classified as eudominant and constant, all three belonging to the genus *Polybia* (Vespidae). These three species were: *P. sericea* (number of collected individuals, N = 182; constancy, C = 87.5%); *P. ignobilis* (N = 57; C = 57.8%); and, *P. fastidiosuscula* (N = 56; C = 56.3%). Four species were classified as subdominant and accessories: *Apis mellifera* (N = 16, C = 21.9%), *Mischocyttarus rotundicollis* (N = 14, C = 18.8%), *Augochloropsis* sp. (N = 13, C = 15.6%) and *Brachygastra lecheguana* (N = 9, C = 14.1%). There were no species classified in the dominant and accidental classes. The remaining 12 species were classified as either recessive or rare regarding dominance (Table 1).
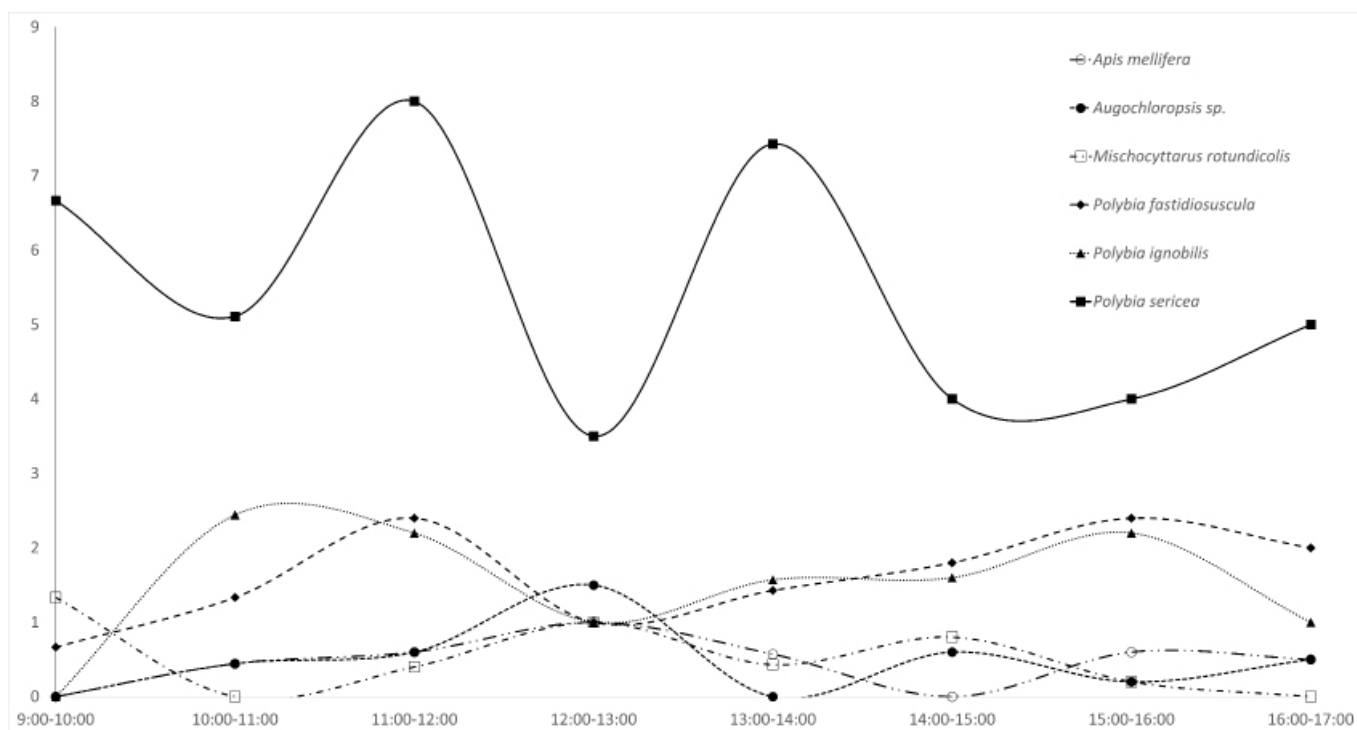

Fig 1. Number of individuals (NI) of eudominant and subdominant species collected per 0.5h periods over time of sampled days in *Erythroxylum myrsinites*' flowers, Southern Brazil.

Table 1. Recorded species in *Erythroxylum myrsinites*' flowers, Southern Brazil. N = number of individuals, Do = Dominance, Do Status = Dominance Status (Ed = eudominant, Sd = subdominant, Rc = recessive and Rr = rare). Co = Constancy, Co Status = Constancy Status (Co = constant and Ac = accessory). Pollen Location (number of records): C/S (corbicula or scopa); Fa (face); Fl (frontal legs); Ms (mesosome/thorax); Mt (metasoma/abdomen); Pp (propleuron). O.M. (individuals with pollen analyzed in optical microscope). NA (structure not available in taxon).

Taxon	N	Do (%)	Do Status	Co (%)	Co Status	Pollen Location						O.M. (%)
						C/S	Fa	Fl	Ms	Mt	Pp	
Hymenoptera												
Vespidae												
Agelaia multipicta (Haliday, 1836)	3	0.8	Rr	4.7	Ac	NA	0	0	0	0	0	0
Brachygastra lecheguana (Latreille, 1824)	9	2.4	Sd	14.1	Ac	NA	2	2	0	0	0	0
Mischocyttarus rotundicollis (Cameron, 1912)	14	3.7	Sd	18.8	Ac	NA	3	4	1	0	2	0
Pachodynerus guadulpensis (Saussure, 1853)	2	0.5	Rr	3.1	Ac	NA	0	0	1	0	1	0
Polistes cavapyta Saussure, 1853	1	0.3	Rr	1.6	Ac	NA	0	0	0	0	0	0
Polybia fastidiosuscula Saussure, 1854	56	14.9	Ed	56.3	Co	NA	4	3	9	0	10	0
Polybia ignobilis (Haliday, 1836)	57	15.2	Ed	57.8	Co	NA	23	32	35	0	22	26.3
Polybia platycephala Richards, 1951	1	0.3	Rr	1.6	Ac	NA	0	0	0	0	0	0
Polybia scutellaris (White, 1841)	1	0.3	Rr	1.6	Ac	NA	0	0	0	0	0	0
Polybia sericea (Olivier, 1792)	182	48.4	Ed	87.5	Co	NA	66	144	153	0	110	62.1
Apidae												
Apis mellifera L. 1759	16	4.3	Sd	21.9	Ac	10	6	5	0	1	5	62.5
Plebeia sp.	6	1.6	Rc	9.4	Ac	2	0	0	0	1	0	33.3
Halictidae												
Augochlorella urania (Smith, 1853)	1	0.3	Rr	1.6	Ac	0	0	0	0	0	0	0
Augochloropsis sp.	13	3.2	Sd	15.6	Ac	2	1	3	3	1	1	33.3
Dialictus sp.	2	0.5	Rr	3.1	Ac	1	0	1	0	0	0	50
Neocorynura aenigma (Gribodo, 1894)	3	0.8	Rr	4.7	Ac	1	0	0	0	1	0	66.6
Diptera												
Stratiomyidae												
Chorisops sp.	7	1.9	Rc	7.8	Ac	NA	0	0	0	0	0	0
Syrphidae												
Taxomerus sp.1	1	0.3	Rr	1.6	Ac	NA	0	0	0	0	0	0
Taxomerus sp.2	1	0.3	Rr	1.6	Ac	NA	0	0	0	0	0	0

We observed that 70% of the visiting insects had pollen attached to their integument. We analysed 229 wasps (Vespidae) in detail (totalling 60.9% of all collected wasps) and the most common body structures showing attached pollen were mesosome (62% of inspected individuals), forelegs (56.7%), propleuron (44.5%) and face (29.4%) (Table 1). Of the collected wasps, 26.6% had no pollen attached. The highest number of records of pollen in body structures was recorded for *Polybia sericea*, followed by *P. ignobilis* (Fig 2). For bees (Apidae and Halictidae), 24 individuals (totalling 58.5% of all collected bees) had pollen attached to their bodies. We found pollen of *E. myrsinites* attached to all visiting insects inspected in optical microscope (N = 147). Out of those insects, 77% belonged to the wasp species *P. sericea* (Fig 3) and 10.1% to *P. ignobilis* (Vespidae), and 12.9% belonged to bees (Apidae and Halictidae).

At the community level, the number of visiting insects correlated with atmospheric pressure (second-order parameter: LR = 42.5, p = 0.001), solar radiation (first-order: LR = 37.9, p = 0.001) and wind speed (first-order: LR = 35.5, p = 0.001; all results from the selected most parsimonious model described in detail in Table 2). Graphical analysis showed that residuals of the model were adequate. More information on model selection can be found in Supplementary file (Table S1).
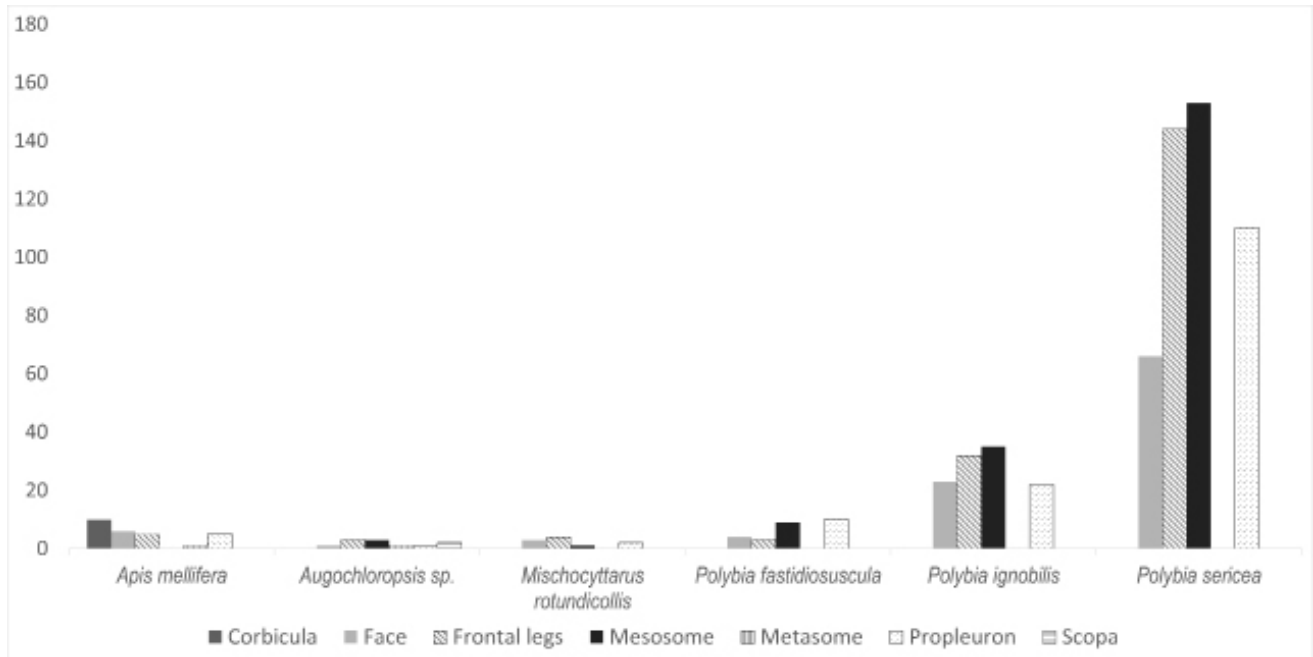
Fig 2. Number of records (NR) of pollen in body structures in individuals of eudominant and subdominant insect species in *Erythroxylum myrsinites*' flowers, Southern Brazil.

At the species level, weather variables had an overall effect on the eudominant species *Polybia fastidiosuscula* (LR = 8.21, p = 0.032) and *Polybia sericea* (LR = 8.09, p = 0.039), both affected by atmospheric pressure (second order). *P. gnobolis*, although affected by solar radiation (LR = 3.57, P = 0.041), was not affected by the set of weather variables (LR = 5.15, p = 0.125; Table 3). Wind speed did not affect significantly any eudominant visitor species. Graphical information about weather variables over the collection period is shown in Figure 4.

Fig 3. Images of *Polybia sericea* visiting *Erythroxylum myrsinites* flowers, Southern Brazil. The two images (A and B) show the visiting pattern of the wasp as well as pollen grains attached to its body.

Table 2. Selected most parsimonious Generalized Linear Model for multivariate response data (GLM$_{mv}$) built for abundance of visitors to *Erythroxylum myrsinites* flowers, Southern Brazil. LR = Likelihood Ratio. Significant *p*-values are in bold.

Variable	LR	*p*-value	Model AIC	Model test Statistics	Model *p*-value
Intercept	182.18	**0.001**			
Atmospheric pressure²	42.54	**0.001**	1141.2	101.5	**0.0009**
Solar Radiation	37.9	**0.001**			
Wind Speed	35.46	**0.001**			

Table 3. Univariate estimates of deviance and associated *P*-values of modelled variables for eudominant species recorded on *Erythroxylum myrsinites* flowers, Southern Brazil. LR = Likelihood Ratio. Significant *P*-values are in bold.

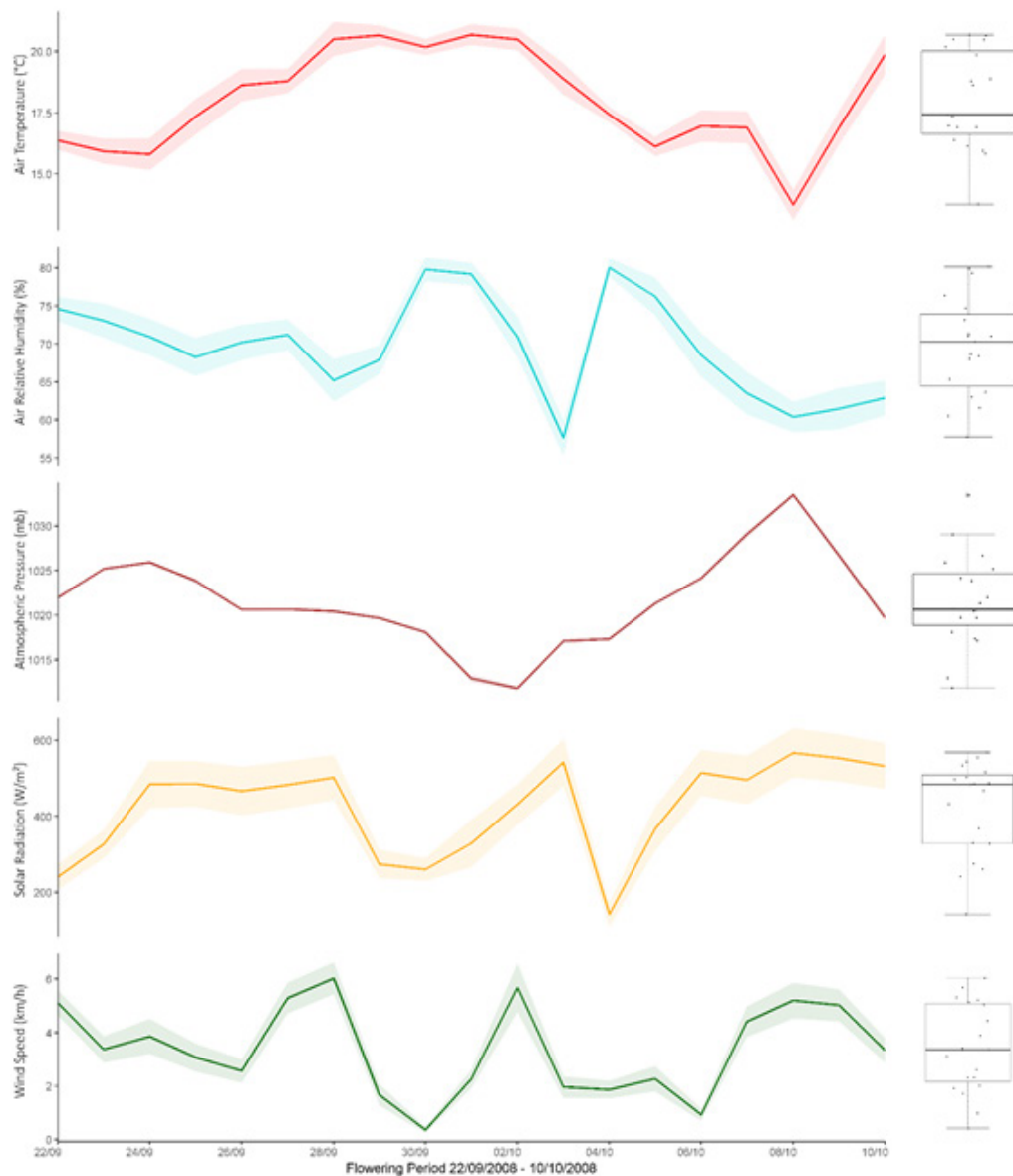| Model Parameters	*Polybia fastidiosuscula*		*Polybia ignobilis*		*Polybia sericea*	
	LR	*p*-value	LR	*p*-value	LR	*p*-value
Intercept	1.34	0.235	0	0.995	59.06	**0.001**
Atmospheric Pressure²	7.189	**0.008**	1.543	0.206	4.015	**0.049**
Solar Radiation	1.242	0.268	3.568	**0.041**	3.487	0.080
Wind Speed	2.747	0.097	1.331	0.233	0.858	0.368
Univariate Test Statistics	8.211	**0.032**	5.152	0.125	8.086	**0.039**

Fig 4. Variation of weather variables during the flowering period of *Erythroxylum myrsinites*, Southern Brazil. Lines represent daily averages and shaded areas the standard deviations.

Discussion

We found wasps are the most important flower visitors of *E. myrsinites*. The wasp *Polybia sericea* (Vespidae) was the most abundant species with high levels of constancy and pollen of the studied plant species attached to their integument, and thus can be considered the visitor with the highest potential to pollinate *E. myrsinites*. Other two species of wasps of the

same genus (*P. ignobilis* and *P. fastidiosuscula*) also had high abundance and constancy. These eudominant species had their visiting activity associated with atmospheric pressure, solar radiation, and wind speed.

The genus *Erythroxylum* has a variety of potential pollinators, especially flies, bees and wasps. We recorded all those groups visiting flowers of *E. myrsinites*, a pattern also reported by da Silva et al. (2007), for *E.* cf. *macrophyllum*. Bees and wasps were considered the main flower visitors of *E. campestre* St. Hil., *E. suberosum* St. Hil. and *E. tortuosum* Mart. (Barros, 1998). Wasps and flies were recognized as the main pollinators of *E. microphyllum* (Freitas & Sazima, 2006) and bees were considered the main pollinators for *E. havanense* (Rosas & Domínguez, 2009). In addition, our results suggest the wasp *Polybia sericea* potentially pollinates *E. myrsinites*, an additional instance to the intrinsic relationship between other species of *Erythroxylum* and wasps (Barros, 1998).

Wind intensity, air temperature and solar radiation are important weather variables influencing insect visits and may directly affect the community of flower visitors (Abrol, 1988; Kearns & Inouye, 1993; Kjøhl et al., 2011; Nielsen et al., 2017). Our results showed that atmospheric pressure, solar radiation, and wind speed affected the number of visits of the entire community of insects found on flowers of *E. myrsinites*. Except for wind speed, the same set of variables (either together or alone) affected eudominant species and, thus, can be important to regulate success of *E. myrsinites* pollination. Moreover, models were of quadratic form, suggesting the existence of optimal values (peaks) in the number of visits. Air temperature did not affect the community of visitors, which may be due to its low variation along the studied period. Although weather conditions and abiotic stress are important factors in determining the success of insect visits (Case & Barrett, 2004; Kearns & Inouye, 1993), few studies directly evaluated their effects on the community level.

Our results showed that 87% of collected individuals were wasps (Vespidae) while 11% were bees (Apidae and Halictidae). The same pattern was found for the species *Schinus terebinthifolius* Raddi, in the same forest fragment (Sühs et al., 2009). Visitation patterns found in both studies might be linked to local microclimatic conditions and visitor availability instead of a visitor preference for the flowers. However, the abundance and the seasonal pattern of common visitor species differ. In this study (during the spring), *Polybia sericea* was the most abundant species, with 55% of Vespidae individuals, followed by *P. ignobilis* and *P. fastidiosuscula*, both with 17% of collected Vespidae individuals. Conversely, these species individually accounted for less than 15% of collected Vespidae individuals and had great part of individuals collected in winter (Sühs et al., 2009). Although these studies were carried out in different years, it seems that there is a preference of distinct wasp species for flowers of either *E. myrsinites* or *S. terebinthifolius*.

There was a high production of fruits in all sampled individuals after the study, indicating that pollination event occurred. Although not tested, based on our results, we can infer that pollination probably was mainly crossed and done by insects because floral dimorphism in *Erythroxylum* species – considered a mechanism of self-incompatibility (Pailler et al., 1998) – promotes the pollen flux between the two types of flowers, enhancing cross-pollination (Barros, 1998), and a previously reported rejection of pollen tubes resulting from self-pollination and interbreeding for several species of *Erythroxylum* (Barros, 1998; Ganders, 1979). Nevertheless, we encourage future studies in evaluating the effectivity of different groups of flower visitors as pollinators, which besides depending on number and constancy of visits, also depends on the quantity of pollen grain still available for the pollination of the flowers transported on the body (*e.g.* Garibaldi et al., 2013).

Although carried out over a short time, this study provides novel data on flower visitors and possible pollinators of a little known and threatened plant species – at least in part of its range. Wasps were the main flower visitors, pollen carriers and potential pollinators of *Erythroxylum myrsinites*. The wasp *Polybia sericea* was considered the main potential pollinator of the species because of high values of dominance and constancy, and a high number of individuals with pollen attached to several of its body parts. On the community-level and for eudominant species, we found weather variables such as air humidity, atmospheric pressure, wind speed and solar radiation to affect the community of visitors. This study reinforces the role of wasps in pollen transport and potential pollination.

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Author's contributions

RB Sühs, ELH Giehl, A Somavilla – Conceptualization
RB Sühs, ELH Giehl, A Somavilla – Methodology
RB Sühs, A Somavilla – Formal analysis
RB Sühs, A Somavilla – Investigation
RB Sühs, A Somavilla – Data Curation
RB Sühs, A Somavilla – Visualization
RB Sühs, ELH Giehl, A Somavilla – Writing and revising

Supplementary Material

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