Journal of Pollination Ecology, 27(2), 2021, pp 28-35

ANERIOPHORA AUREORUFA (PHILIPPI, 1865) (DIPTERA: SYRPHIDAE): A FLY SPECIALIZED IN THE POLLINATION OF *EUCRYPHIA CORDIFOLIA* CAV. (CUNONIACEAE R. BR.), AN ENDEMIC SPECIES OF SOUTH AMERICAN TEMPERATE FOREST

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Abstract—The order Diptera is the second most important group of pollinators worldwide. Many flies are considered generalist pollinators, but specialist flower flies' associations are rare or uncommon. The present study aimed to determine the level of specialization in pollination for *Aneriophora aureorufa* (Philippi, 1865) (Diptera: Syrphidae), an endemic species of the South American temperate forests. The study evaluates also the species abundance in different sampling sites and environments. Our data suggest that *Aneriophora aureorufa* has an exclusive and extremely narrow association with the flowers of *Eucryphia cordifolia* Cav.¸ an endemic Chilean species. We reviewed the literature on Chilean pollinator species searching for information about *Aneriophora* Stuardo & Cortés 1952 and compared its exclusive association with other specialist flies. We conducted long-term fieldwork for 22 years in one location during the flowering season and over a period of one to six years in five additional locations. In our field study we recorded all insects which had contact with stigma and/or stamens of 25 plant species. We found that *Aneriophora* visits flowers of *E. cordifolia* in both low absolute abundance and low relative percentage, and occasionally visits flowers of two other species. In the northern distributional range of *A. aureorufa,* where *E. cordifolia* is absent, the hoverfly was recorded in flowers of *Laurelia sempervirens* (Ruiz & Pav.) Tul. (Chilean laurel, Atherospermataceae), but in low frequency (0.01 flowers/min). In a site where we have a long-term study, *A. aureorufa* represented only 0.2% of all flower visitors, and its abundance was higher in canopy forests, visiting 0.03 flowers/min. Based on our observations and the literature review we propose that (1) *Aneriophora* is one of the most specialized pollinator flies described until now; (2) the species is more frequent in old-growth forests than in forest edges or isolated trees.

Keywords: Pollinator conservation, endangered pollinators, Eucryphia cordifolia, Laurelia sempervirens, Myrceugenia planipes, old-growth forests

INTRODUCTION

The order Diptera is the second most frequent group of pollinators worldwide (Larson et al. 2001; Orford et al. 2015; Wardhaugh, 2015), and are described as pollinators in several ecosystems (Arroyo et al. 1982; Primack 1983; Larson et al. 2001; Klein et al. 2007; Orford et al. 2015; Smith-Ramírez et al. 2005, 2014, 2016). In temperate ecosystems, flies are more diverse than bees (Smith-Ramírez et al. 2005), playing a key role in the pollination of several plant species (Ssymank et al. 2008). Therefore, pollination by flies in forests is probably more prevalent than currently assumed, both in abundance and long-distance transfer of genetic material (Wardhaugh, 2015). For example, genetic studies show that the endangered tree *Gomortega keule* (Molina) Baill. in the Chilean Maulino forest can maintain gene flow and fruit production over long distances, mainly due to hoverfly pollination (Lander et al. 2009, 2010).

Flies are often considered to be generalist flower-visitors (Kearns, 2001), partly because specialist flies have rarely been mentioned in the literature (see Johnson, 2010; Manning & Goldblatt, 1997). By contrast, non-cleptoparasitic bees can reach up to 60% of some degree of floral specialization (Gottsberger & Silberbauer-Gottsberger, 2006; Wardhaugh, 2015; Wcislo & Cane, 1996). One of the most remarkable examples of fly pollination specialism is the

Received 27 May 2020, accepted 26 October 2020
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case of the long-proboscid fly *Moegistorhynchus longirostris* (Wiedemann, 1819) (Diptera: Nemestrinidae), a tangle-veined fly endemic to Cape Town in South Africa, which exclusively visits nine long-tubed flower species from three different plant families (Johnson, 2010; Manning & Goldblatt, 1997).

Syrphidae is probably the most important group of flower visitors within Diptera (Larson et al. 2001; Orford et al. 2015), being mostly generalists (Inouye et al. 2015; Raguso 2020; Ssymank, 2003). *Aneriophora* Stuardo & Cortés, 1952 is a monotypic genus (Eristalinae: Milesiini) that includes a charismatic species, *Aneriophora aureorufa* (Philippi, 1865). *A. aureorufa* is distributed from central (Maule) to southern Chile (Aysén Region) (Alaniz et al. 2018; Etcheverry, 1963; Thompson, 1972) but is also present on the south-central east border of Argentina (López-García et al. 2019).

A. aureorufa is one of the most notable and conspicuous flower fly species in South American temperate forests (SATF), characterized by being one of the largest species of the family (body length 14 mm). Its striking coloration and morphology shape have led it to be considered as a mimic of the austral American bumblebee, *Bombus dahlbomii* Guérin-Méneville, 1835 (Hymenoptera: Apidae) (Polidori et al. 2014). *A. aureorufa* is considered a threatened species due to the loss of 68% of its original habitat in the northern range of its distribution (Alaniz et al. 2018).

In this study, we present new reports of the plant species visited by *A. aureorufa*, we also describe the relative abundance of *A. aureorufa* in different environments and localities. We evaluate the specificity level of this dipteran since previous studies have reported that this hoverfly pollinates an endemic tree, *Eucryphia cordifolia* Cav. (Ulmo, Eucryphiaceae), distributed in almost the same range (Polidori et al. 2014; Smith-Ramírez et al. 2016).

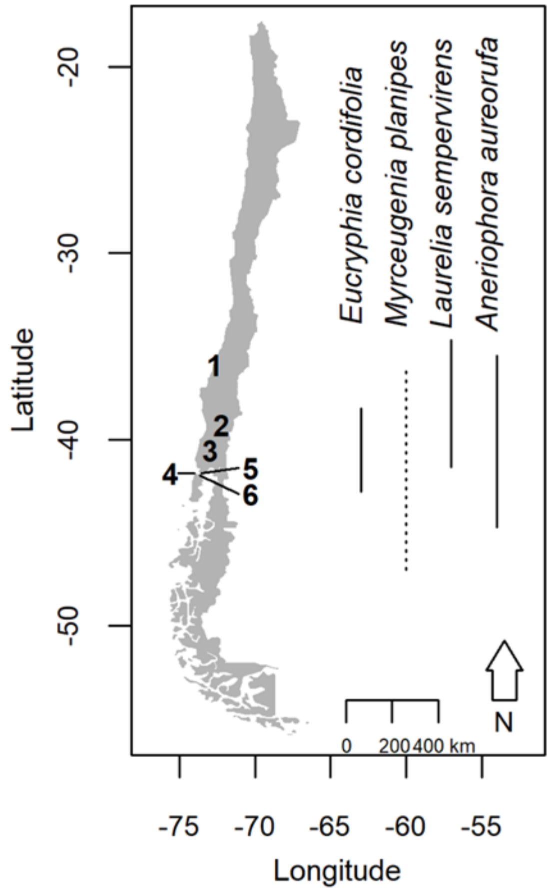

FIGURE 1. Map of the study sites and latitudinal distribution of tree species relevant for *Aneriophora aureorufa*. Vertical lines show latitudinal distribution of *Eucryphia cordifolia*, *Myrceugenia planipes*, and *Laurelia sempervirens* according to Donoso et al. (2006) in central and southern Chile. *Aneriophora aureorufa* distribution based on Etcheverry (1963) and Devoto (2006). Points indicate the sampling sites in the study. Numbers denote sampled sites used in this study: (1) Los Queules, (2) Villarrica, (3) Osorno, (4) Guabun, (5) Caulín and (6) Senda Darwin.

MATERIALS AND METHODS

Study sites

We conducted our fieldwork in six different sampling sites located in central and southern Chile from 1998 to 2019 (Table 1; Fig. 1). We studied six sites: The site 1 was Los Queules National Reserve; see site numbers in Fig. 1, and coordinates in Table 1). The site 2 was Villarrica, 500 km south of Los Queules. The site 3 was Osorno, located about 170 km south of Villarrica. The other three sites (sites 4, 5 and 6, respectively in Fig. 1) are in the north of Chiloé Island; from west to east these are: Guabun, Senda Darwin, and Caulín (Fig. 1). The last two sites are separated by 8 km and are located at more than 30 km away from Guabun. In some sites, we focused only on *E. cordifolia* trees, which are known to attract a wide range of flower visitor species (Smith-Ramírez et al. 2014), meanwhile, in Villarrica, we focused on *Laurelia sempervirens* (Ruiz & Pav.) In other sites, we included several species of native plants to the temperate rain forest of Chiloé Island (Guabun and Senda Darwin; Smith-Ramírez et al. 2005) and the Maulino native forest (Table 1). In Caulín and Osorno, the study was concentrated on forest fragments and isolated trees surrounded by a matrix of cattle grazing meadows. The total study period extended from 1998 to 2019, in the spring (in the northern distribution of *A. aureorufa*) and summer seasons (in central-south distribution). The dominant trees in Los Queules were *Aextoxicon punctatum* Ruiz & Pav., *Peumus boldus* Molina, *Cryptocarya alba* (Molina) Looser, *Nothofagus dombeyi* (Mirb.) Oerst., *G. keule*, and *Luma apiculata* (DC) Burret.

Flower visits

In Chiloé Island we sampled flower visitors of 25 plant species, including different life forms (tree, shrub, vine, and herb), characterized by having open, bell-shaped, and small tubular flowers; we excluded long tubular flowers (ornithochory flowers) which cannot be visited by *A. aureorufa*. We considered all flower visitors who simultaneously made contact with anthers and/or stigmas, as pollinators. Observations were made in tree canopies at 0.5 to around 3 m from the ground, including only trees of no more than 12 m tall. The observation time per species is presented in Table 1. We observed a minimum of one individual (*L.*

TABLE 1. Plant species sampled for flower insect visitors in different years and sites in Chile. Coordinates and elevation of each site are given. Species on which *Aneriophora aureorufa* was observed are highlighted in bold; m. a. s. l. = meter above sea level.

Year	Location	Plant species	Individuals per sampled plant	Observation time (minutes)	Reference study
1998-2000	Northern Chiloé (Senda Darwin) 41.89°S, 73.67°W 30 m. a. s. l.	*Amomyrtus luma* Cav.	8	1950	Smith-Ramírez et al. 2005
		Amomyrtus meli (Phil.) D. Legrand & Kausel	8	850	Smith-Ramírez et al. 2005
		Anagallis alternifolia Cav.	12	280	Smith-Ramírez et al. 2005
		Berberis darwinii Hook.	8	440	Smith-Ramírez et al. 2005
		Berberis microphylla G. Forst.	8	320	Smith-Ramírez et al. 2005
		Caldcluvia paniculata (Cav.) D. Don	6	300	Smith-Ramírez et al. 2005
		Gaultheria mucronata (L. f.) Hook. & Arn.	8	400	Smith-Ramírez et al. 2005
		Gaultheria phillyreifolia (Pers.) Sleumer	9	580	Smith-Ramírez et al. 2005
		Gevuina avellana Molina	6	840	Smith-Ramírez et al. 2005
		Hydrangea serratifolia (Hook. & Arn.) F. Phil.	6	220	Smith-Ramírez et al. 2005
		Luma apiculata (DC.) Burret	8	1180	Smith-Ramírez et al. 2005
		Luzuriaga polyphylla (Hook.) J.F. MacBr.	8	520	Smith-Ramírez et al. 2005
		Luzuriaga radicans Ruiz & Pav.	8	460	Smith-Ramírez et al. 2005
		Myrteola nummularia (Poir.) O. Berg	8	1160	Smith-Ramírez et al. 2005
		Myrceugenia ovata var. *nannophylla* (Burret) Landrum	8	850	Smith-Ramírez et al. 2005
		Myrceugenia ovata (Hook. & Arn.) O. Berg var. *ovata*	8	1845	Smith-Ramírez et al. 2005
		Myrceugenia parvifolia (DC.) Kausel	8	780	Smith-Ramírez et al. 2005
		Myrceugenia planipes (Hook. & Arn.) O. Berg	6	1180	Smith-Ramírez et al. 2005
		Ovidia pillopillo (Gay) Meisn.	6	200	Smith-Ramírez et al. 2005
		Tepualia stipularis (Hook. & Arn.) Griseb.	7	1020	Smith-Ramírez et al. 2005
		Ugni candollei (Barnéoud) O. Berg	6	80	Smith-Ramírez et al. 2005
		Ugni molinae Turcz.	7	760	Smith-Ramírez et al. 2005
2001		*Podanthus mitiqui* Lindl.	6	620	Unpublished data
2001-2013, 2015-2019	Northeast Chiloé (Caulín) 41.82°S, 73.59°W 55 m. a. s. l.	*Eucryphia cordifolia* Cav.	16	38880	Smith-Ramírez et al. 2014 and unpublished data
2000-2002/ 2015-2017	Northeast Chiloé (Senda Darwin)	*Amomyrtus meli* (Phil.) D. Legrand & Kausel	5	5200	This study
2000-2002/ 2015-2017	41.89°S, 73.67°W 30 m. a. s. l.	*Gaultheria ovata* DC. var. *ovata*	8	5740	This study

Tab. 1 continued

Year	Location	Plant species	Individuals per sampled plant	Observation time (minutes)	Reference study
2000-2002/ 2015-2017		*Myrceugenia planipes* (Hook & Arn.) O. Berg	6	5900	This study
2003	Osorno 40.58°S, 72.99°W 91 m. a. s. l.	*Eucryphia cordifolia* Cav.	14	1320	This study
2007	Northwest Chiloé (Guabún) 41.8°S, 74.02°W 131 m. a. s. l.	*Eucryphia cordifolia* Cav.	2	360	Smith-Ramírez et al. 2016
2017	Maulino forests (Los Queules) 35.9°S, 72.68°W 467 m. a. s. l.	*Laurelia sempervirens* (Ruiz & Pav.) Tul.	1	360	This study
		Gevuina avellana Molina	8	220	This study
		Luma apiculata (DC.) Burret	3	160	This study
2018	Villarrica 39.22°S, 72.21°W 318 m. a. s. l.	*Laurelia sempervirens* (Ruiz & Pav.) Tul.	3	200	This study

sempervirens, Los Queules) and a maximum of 16 individuals (*E. cordifolia* in Caulin, Chiloé Island). All observations were made over 20-minute between 10:00 and 18:00 h (GMT-3) (pollination activity occurs mostly within these hours in austral temperate forests), recording each insect that entered in an imaginary sampling quadrant of 8 to 30 contiguous flowers. Although we did not quantify the exact number of flowers visited when the individual entered the quadrant, no more than three flowers were usually visited. We then calculated the flower visit frequency of *A. aureorufa* as the visit number to the quadrant/flower number per minute. We conducted a total of 676 hours of observation on *E. cordifolia* flowers; mean observation time was 23.9 hours for the remaining 25 species, (Max: 126.4 hours in *M. ovata* var. *ovata* (Burret) Landrum; Min: 1.3 hours in *Ugni candollei* (Barnéoud) O. Berg.

Determination

During the first two years of this study, we collected some specimens of *A. aureorufa* to verify their identity (Fig. 2). We reviewed original descriptions and used the taxonomic keys of Philippi (1865) and Thompson (1999). *A. aureorufa* is a conspicuous hoverfly with dense bright orange pilosity on thorax and abdomen; orange fascia and antennae, black gena and venter, as well as a dark macula in the apex of the wings (Thompson, 1972). The specimens were deposited in the Luis E. Peña collection of the Universidad de Chile (MEUC), the Senda Darwin Collection (SDC), and the Chilean National Museum of Natural History, Santiago (Museo Nacional de Historia Natural de Santiago de Chile (MNHNCL)).

RESULTS

We observed *A. aureorufa* in 16 of the 19 study years in Caulín, always in low frequency (Fig. 3). Considering only the years it was found in *E. cordifolia* trees in Caulín, it represented 0.2% of abundance concerning other floral visitors. In Caulin, *A. aureorufa* was recorded with a mean annual frequency of 0.002 and a maximum frequency of 0.0097 flower visits/min (Fig. 3). In addition to *E. cordifolia*, we recorded *A. aureorufa* visiting flowers of *Myrceugenia planipes* (Hook. & Arn.) O.Berg (11 records in total), with a frequency of 0.0007 flowers/min. On average, frequency of flower visits was 2.86 times higher in *E. cordifolia* than in *M. planipes,* in north-central Chiloé Island. In the Osorno valley, which includes small forest fragments and isolated specimens of *E. cordifolia*, we only detected *A. aureorufa* twice in the fragmented forests close to large forest areas, corresponding to 0.002 flower visits/min. In the *E. cordifolia* trees sampled in Guabun (Northwest Chiloé), we found the highest flower visiting frequency in the upper canopy, 0.024 flower visits/min (8 records), which is 17.6 times higher than the frequency found in the understory, where only 0.0017 flower visits/min (two records) were observed (Smith-Ramírez et al. 2014). No individual of *A. aureorufa* was found in the understory of *E. cordifolia* trees located in the forest-agriculture transition in Guabun. In the study located at the northern extreme of the *A. aureorufa* distribution (Maulino forests), we found a total of 0.014 flower visits/min (five records) in *L. sempervirens*, but we did not find this fly species visiting *L. sempervirens* in the Villarica site. We did not detect *A. aureorufa* visits in any one of the other 25 plant species considered in this analysis.

DISCUSSION

The majority of woody species in SATF have open or bell-shaped flowers (Rodríguez et al. 2006), although they also have tubular flowers pollinated by hummingbirds, bees, and flies with long proboscides (Smith-Ramírez, 1993),

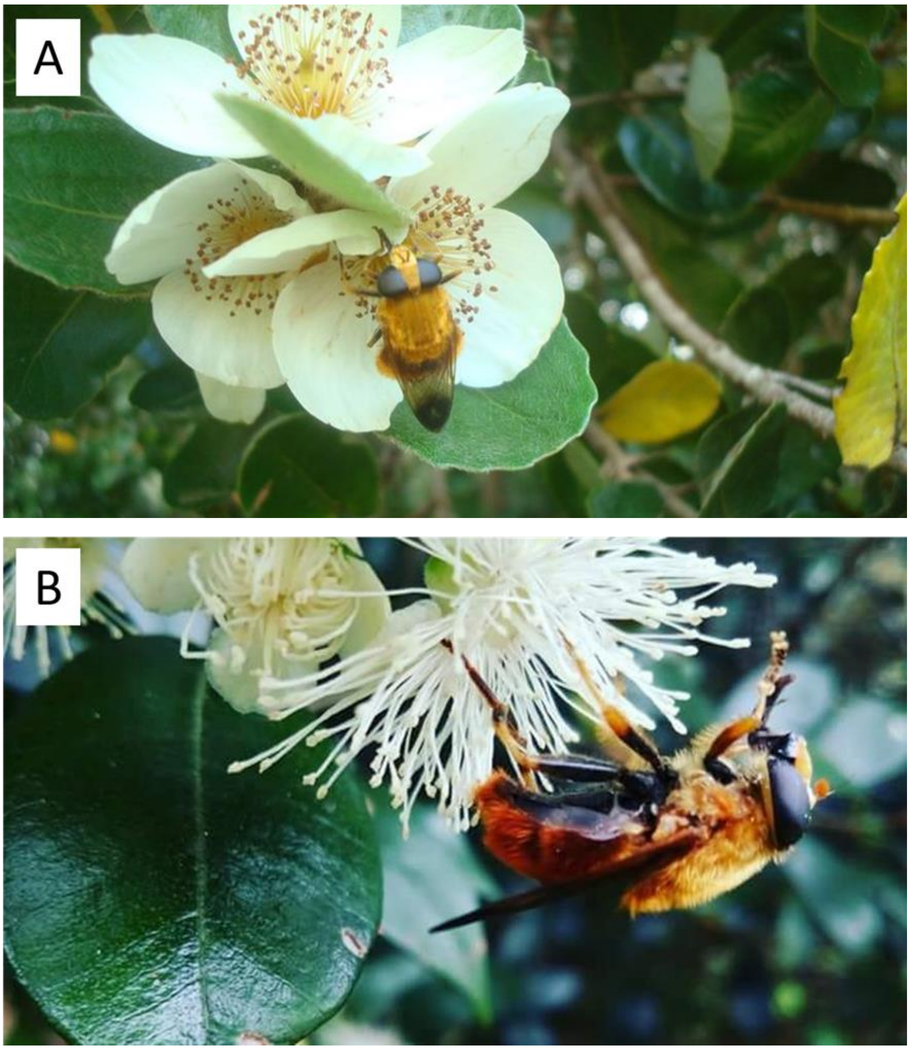

FIGURE 2. *Aneriophora aureorufa* on flowers of (A) *Eucryphia cordifolia* and (B) *Myrceugenia planipes*. Photographs by Rodrigo Barahona.

including also wind-pollinated flowers such as the southern beeches, *Nothofagus* Blume (Nothofagaceae Kuprian). The richness of woody species in these forests is not high compared to subtropical and tropical forests so that the 25 woody species with open and bell-shaped flowers studied in the southern distribution of *A. aureorufa* represent a non-negligible proportion of the plant diversity in SATF. In Los Queules, which corresponds to the northern distribution of *A. aureorufa* (where the plant species richness in higher), the only plant species that was found to be visited by *A. aureorufa* was *L. sempervirens*, of a total of 137 species studied by different authors (Lander et al. 2009; Medel et al. 2018; Menéndes, 2006; Murúa et al. 2010; Rivera-Hutinel et al. 2010). For this reason, we believe that there is evidence of a high specificity of *A. aureorufa* visiting *E. cordifolia*, secondarily *M. planipes*, and occasionally *L. sempervirens*. *M. planipes* only provides pollen, whereas *E. cordifolia* and *L. sempervirens* provide nectar and pollen rewards to floral visitors, which could explain the preference for *E. cordifolia.* However, we cannot rule out the possibility that our findings are partially a consequence of sampling effort. Many plant species were only sampled in one year, except *L. sempervirens* which was sampled in two years and *M. planipes*, *M. ovata* var. *ovata*, and *Amomyrtus meli* (Phil.) D. Legrand & Kausel in six years (Table 1). Previous studies have shown that pollinator networks (pollinator richness and plant-pollinator links) are difficult to detect completely, because they require an enormous sampling effort (Chacoff et al. 2012) and because networks vary significantly among years (Smith-Ramírez et al. 2014). In addition, our results could be biased by the height of the trees observed during sampling. The only study performed in the higher tree canopy (*E. cordifolia)* was Smith-Ramírez et al. (2016), detecting a higher flower visit frequency of *A. aureorufa* than other insect species.

E. cordifolia blooms in the austral summer (December to March) and *M. planipes* blooms from December to January. We assume the emergence of *A. aureorufa* occurs in December, coinciding with *E. cordifolia* and *M. planipes* blooms. However, in the northern distribution range insects generally emerge earlier, matching the bloom of *L. sempervirens* (which occurs during October and November). Currently, *E. cordifolia* is not present in the northern distribution of *A. aureorufa*, however, during Quaternary glaciations, the flora that is now in southern Chile (as in Osorno and Chiloé Island) occurred in the center of the country (where the Los Queules study site is) (Villagrán et al.

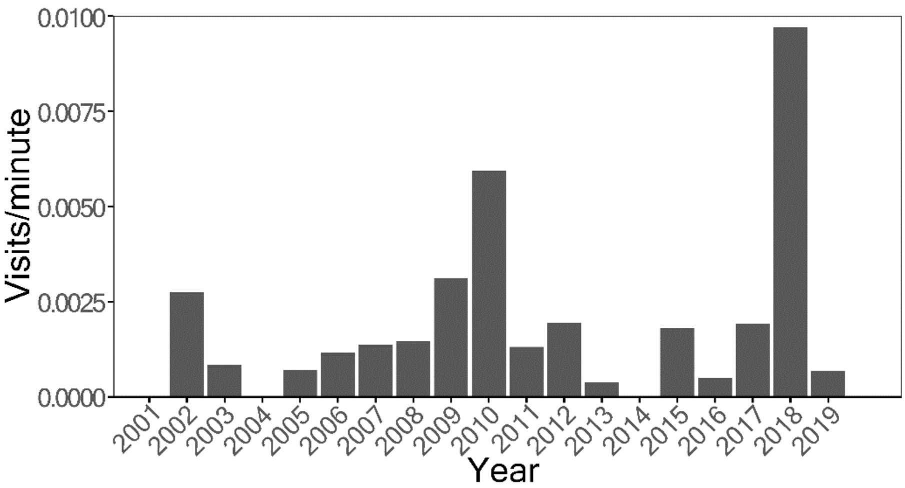

FIGURE 3. Visit number per minute of *Aneriophora aureorufa* on *Eucryphia cordifolia* flowers in Chiloé Island from 2001 to 2019. No sampling was performed in 2014.

2019), which could have produced a disengaged movement between partners of a mutualistic relationship.

A. aureorufa does not have a strongly specialized morphology regarding flowers visited, making it more flexible in terms of possible floral resources since it can visit both *E. cordifolia* and *L. sempervirens*. However, possibly some morphological fits may occur between the large body size of *A. aureorufa* and the big *E. cordifolia* flowers, with a diameter of 3-4.5 cm and radial symmetry. *M. planipes*, in contrast, has a diameter of around 2 cm with radial symmetry and *L. sempervirens* flowers are around 1.5 cm in diameter with bilateral symmetry. The non-tubular flowers from SATF are mostly small, except for *Corynabutilon vitifolium* (Cav.) Kearney and a rare tree, *G. keule*.

In all the locations where we observed *A. aureorufa*, we recorded the presence of old trees, especially in the old-growth forest in Guabun, where we recorded the highest flower visit frequency. We believe that old-growth forests are fundamental to the reproduction of this hoverfly because their larvae could have a saproxylic behavior, similar to other Eristalinae (Gilbert et al. 1994; Rotheray & McGowan, 2000). Old-growth forests with the presence of *L. sempervirens* are not common which could explain why *A. aureorufa* has not been observed visiting this species frequently.

We identified three previous studies that mentioned *A. aureorufa*: (1) Devoto (2006) associated this hoverfly with the small tree *Discaria chacaye* (G. Don) Tortosa in Laguna Tromen, in the Argentinean Andes close to the Chilean border at about 2000 m elevation; Devoto observed only one instance of *A. aureorufa* visiting this tree during a total of 3600 minutes of sampling. Unfortunately, there is no record of this sample to confirm the species identity. (2) Polidori et al. (2014) also observed *A. aureorufa* visiting *E. cordifolia* about 110 km southeast of our study site in Chiloé, and (3) the presence of *A. aureorufa* in the Argentinean border with Chile was recently confirmed in a camping site close to San Martin de Los Andes, but there were no plant species associated with this observation (López-García et al. 2019).

E. cordifolia is a Gondwanic species, belonging to the old family Cunoniaceae R. Br. Two representatives are found in Chile and at least four species have been recorded in east Australia. According to Thompson (1972), *A. aureorufa* is an ancient taxon that probably gave rise to *Criorrhina* Meigen, 1822, the phylogenetically closest genus (Thompson, 1972), which has similarities in genitalia to the Australian genus *Paratropidia* (Hull, 1949). Furthermore, there may be a relationship between *Aneriophora* and *Paratropidia* (Thompson, 1972). We propose that *E. cordifolia* and *A. aureorufa* could have an ancient Gondwanic relationship, maybe a parallel phylogeny; a means of testing a potential relationship between these genera would be to perform a phylogeny between the Eristalinae of the tribe Milesiini, which have various species related to *A. aureorufa*.

In terms of dependence in the mutualistic relationship, while *A. aureorufa* seems to depend on *E. cordifolia* and secondarily on *M. planipes*, the pollination of these emergent trees does not depend exclusively on this fly, since both trees attract more than 30 floral visitors' species per year (Smith-Ramírez et al. 2005).

The conservation status of *A. aureorufa* was classified as Least Concern by the Ministry of Environment of Chile using IUCN criteria (Barahona-Segovia et al. 2016). However, we believe this classification should be reconsidered, especially in the northern section of the SATF (Alaniz et al. 2018). Due to the prolonged observation period and the infrequent presence of *A. aureorufa*, we consider this species as rare in the forest-agriculture ecotones and fragmented forests, and almost absent in *E. cordifolia* trees isolated in pastures/prairies. Nevertheless, further studies are required to confirm whether its presence is also rare in continuous SATF forests. Information on the microhabitat type used by their larvae and on its phenology, is lacking. We only know *A. aureorufa* occurs from December to February (in Los Lagos Administrative Region) coincident with *E. cordifolia* flowering. We propose that *Eucryphia cordifolia* is an umbrella species, to conserve forest fragments. With this tree species it is possible to conserve *A. aureorufa*, and also a huge assemblage of other pollinators (Smith-Ramírez et al. 2014). *E. cordifolia* has been one of the most common tree species of SAFT, and is massively and continuously under logging pressure, mainly for wood fuel, disappearing in the northern part of its distribution (Alaniz et al. 2018).

We conclude that *A. aureorufa* presents one of the narrowest flower specializations described in the literature, it is a specialist of *E. cordifolia*-tree flowers in the central-southern temperate forests of South America, but not in the northern portion of its distribution where *E. cordifolia* is not present. Our data suggest that the persistence of *A. aureorufa* depends on the conservation of threatened Maulino forests in the north and old-growth *E. cordifolia* forests in the central-southern SATF, given that this hoverfly is highly dependent on old-growth forests.

ACKNOWLEDGEMENTS

We are grateful to all those who participated in the long-term studies on pollination over a period of 22 years. The English Grammar was reviewed by Susan Angus and Lafayette Eaton. We thank two anonymous reviewers. This study was funded by the Institute of Ecology and Biodiversity (IEB) PFB-23 and AFB 17008.

Funding: This work was supported by the Institute of Biodiversity and Ecology-Chile (IEB) [Grant numbers INCO-FP6, ICM 05-002, PFB-23, AFB17008]; Universidad de La Frontera [Grant number Project DI16-0060]; and CONICYT doctoral scholarship [Grant number 21160404] grant to R.M.B.-S.

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