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RESEARCH ARTICLE

Upper canopy pollinators of *Eucryphia cordifolia* Cav., a tree of South American temperate rain forest

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Abstract: Ecological processes in the upper canopy of temperate forests have been seldom studied because of the limited accessibility. Here, we present the results of the first survey of the pollinator assemblage and the frequency of insect visits to flowers in the upper branches of ulmo, *Eucryphia cordifolia* Cav., an emergent 30-40 m-tall tree in rainforests of Chiloé Island, Chile. We compared these findings with a survey of flower visitors restricted to lower branches of *E. cordifolia* 1- in the forest understory, 2- in lower branches in an agroforestry area. We found 10 species of pollinators in canopy, and eight, 12 and 15 species in understory, depending of tree locations. The main pollinators of *E. cordifolia* in the upper canopy differed significantly from the pollinator assemblage recorded in lower tree branches. We conclude that the pollinator assemblages of the temperate forest canopy and interior are still unknown.

Key words: *Bombus*, canopy studies, biodiversity in Chiloé Island, insect pollinators, ulmo.

Introduction

Studies of pollination biology in forest canopies are limited, because it is difficult to access the upper branches of trees that often exceed 30 m in height (Roubik 1993). The few existing studies have been conducted in the canopy of tropical forests, where access to the canopy has been implemented by means of tree climbing techniques or air walks; pollination studies in the canopy of temperate forests are notably lacking. Numerous studies of pollen vectors in temperate forests have relied on observations or collections made on low flowering branches, which are often located one to three meters from the ground level. In these studies, it has been found that around 180 species pollinate flowers, insects and birds, almost all of them natives (Smith-Ramírez 1998, Smith-Ramírez & Armesto 2003, Smith-Ramírez *et al.* 2005, Smith-Ramírez *et al.* 2014), which gives the impression that the biodiversity of pollinators in temperate forests is relatively known. The first objective of this study was to assess the species composition of pollinator assemblages and the frequency of visits to flowers in the crown branches of emergent *Eucryphia cordifolia* (Cunoniceae) trees in the canopy of an old-growth temperate rainforest in southern South America. The crown of this large evergreen broad-leaved tree often rises up to 30 m above the ground and extends for a radius of 10-15 m. A second goal of this study was to compare our findings with other studies of flower visitors focused on the lower branches of individuals of the same tree species in the understory. To our knowledge, this is the first report of pollinator diversity and flower visitation in the upper canopy of an austral temperate rainforest.

Material and methods

E. cordifolia Cav. is an evergreen broad-leaved tree from temperate rainforests. It occupies an emergent position in the forest canopy supporting a diverse array of climbers and epiphytes, including ferns, mosses and vascular plants (Díaz *et al*. 2010). This tree species has relatively large (5-6 cm in diameter), disk-shaped, symmetric white flowers, with many stamens, and offers abundant nectar and pollen rewards to pollinators, which are nearly all insects (Smith-Ramírez *et al*. 2005). Peak flowering of this species occurs in Chiloé forests from late January to early February (Smith-Ramírez & Armesto, 1994). This plant has a self-incompatible reproductive system and is strongly dependent on insect pollinator visits for setting fruits (Riveros, 1991).

The present study was conducted in a large patch (ca. 1000 ha) of old-growth rainforest in the northern part of Chiloé Island, in the locality Guabún in the Lacucycuy Peninsula (41˚ 38´ S, 74˚ 01´W). During three days in February 2007, during the peak of flowering season, we recorded the pollinator assemblage of *E. cordifolia* in the canopy of two individual trees that have an emergent position in the forest canopy at 30 m height. The trees were climbed using ropes and arborist techniques following the protocols described by the Tree Climbing Coalition USA (2006). Since it was difficult to choose and be acquainted with the study trees, we concentrated our work on two of them. To be acquainted with a tree means to get to know the branches that are strong enough to support the weight of researchers and to attach the climbing ropes. In addition, it was necessary for the climber to be able to position him or herself on the climbing rope in a way that allowed visual access to nearby flowering branches (sometimes not from the same tree that is climbing) and to detect and identify pollinators. Only after climbing several trees was it possible to know whether the conditions for sampling were adequate. The flowering branches studied were located approximately 23-25 meters above the ground in the forest canopy layer. We surveyed the pollinator visiting the flowers by sitting on a swing specially designed for conducting field observations in the canopy (Peña-Foxon & Díaz 2012). We completed 360 minutes of observations in total, 180 min in each *E. cordifolia* tree sampled. We compared species composition of the flower visitors and the frequency of visits to flowers in the canopy with simultaneous observations in the lower branches (c. two-three meters height) of two *E. cordifolia* trees in the same forest stand. In these trees we completed 240 observation minutes on flowering branches at two meters above the ground (120 min per tree). The survey of pollinators of *E. cordifolia* in the forest understory was made on trees different from those used for canopy sampling, because the emergent trees with flowers in the canopy do not have lower branches. The studied trees (canopy and understory sampling) were found within an area of a 400 m radius inside the forest. The sample was made on sunny days. Rainy weather precluded increasing the number of observation periods for the understory trees.

In addition, we compared the pollinator assemblages of canopy emergent *E. cordifolia* trees with *E. cordifolia* trees sampled in forest patch edges and isolated trees in an agroforestry landscape near the locality of Caulín, northern Chiloé Island (41° 49' S, 73° 37' W). This landscape mosaic of pastures and remnant forest patches is located about 22 km away from the forests of Guabún, where the canopy and understory pollinator studies were made. We reanalyzed pollinator data presented by Smith-Ramírez *et al.* (2014), who reported data collected two and five days before the present canopy study. Here, we reanalyzed data from 240 min of pollinator observations in each of two trees in forest patch edges and in two isolated remnant trees found within grazing pastures. The edge and isolated trees were about 400 m away from each other. The distance between the two edges and the two isolated remnant trees was about 15 to 25 m. All of these pollinator records, including those in the upper canopy study, were collected from February 18 to 26, 2007. The specimens were classified using a reference entomological collection based at Universidad Metropolitana de Ciencias de la Educación (UMCE), Santiago, Chile.

Pollinator observations were made by four people working simultaneously. The observations were divided into periods of 20 minutes each, with a pause of 10 to 60 minutes between sampling periods. These 20-minute periods were considered sampling units in subsequent analyses. During each observation period, the researcher focused on one quadrant, including 10 to 20 flowers in order to obtain information about pollinator frequency per flower number. We defined as pollinators all animal species that contacted the anthers and/or stigmata of *E. cordifolia* flowers. Due to the particular morphology of their flowers, an open corolla (5 cm across) with many short stamina it was easy to record contacts with the anthers and stigmata visually when insects were looking for nectar and pollen. However, it was not always possible to collect the insect flower visitors in the forest canopy due to the limited mobility of the researchers. Comparisons between frequencies of visits to flowers by different pollinators were analyzed using the student t-test, after data were log-transformed for normality.

Results

A total of 10 pollinator species with 31 individuals were recorded in the upper canopy, and eight species with 22 individuals in the understory of the Guabún rainforest during the sampling period (Table 1). All the pollinators were insects with the exception of a hummingbird, *Sephanoides sephaniodes* Lesson & Garnot which was recorded in the canopy. Only one of these pollinators (*Platynocera* sp. 1) was shared between the flowering branches in the two forest layers. The most frequent species visiting flowers in the upper canopy were *Aneriophora aureorufa* Philippi (Syrphidae) and *Platynocera* sp. 1 (Cerambycidae) (Table 1). In contrast, the most frequent flower visitor in the forest understory was a species belonging to the Mordellidae. During the entire sampling period, we recorded 31 visits to flowers in the forest canopy, and 20 visits to flowers in the understory. The frequency of visits to flowers standardized by observation period was similar for trees in the upper canopy and the understory (Student's t-test, P=0.15).

In the forest-pasture land mosaic, where we sampled at a height of 1.5-2.5 m, we found 15 pollinator species for trees in forest edges and 12 species in the case of isolated trees in open pastures. Four pollinator species were shared between trees in edges and trees in pastures (Table 1). The main flower visitors in both settings were the same, the honeybee *Apis mellifera* L. and the native bumblebee *Bombus dahlbomii* Guérin-Méneville. In total, we recorded 16 visits to *E. cordifolia* flowers in forest edges and 26 visits to flowers of isolated trees in pastures. The frequency of visits standardized by observation period was similar for trees in forest edges and in the middle of pastures (Student's t-test P=0.2).

Two pollinator species that visited flowers in the forest canopy (25 m) were shared with trees in forest edges and pastures; these species were the fly *A. aureorufa* and the bumblebee *B. dahlbomii*. At least one species was present both in the forest-pasture land mosaic and in the understory of old-growth forest in Guabún, which was Sarcophagidae sp. 5. Other species observed in these settings were impossible to collect for identification. The frequency of visits to flowers between the two areas studied (old-growth forest and agroforestry area) did not differ significantly (Student´s t P=0.09). More visits of introduced species (N=58) occurred in agroforestry areas than in old growth forest (N=1).

Table 1. Pollinators of *Eucryphia cordifolia* in four different habitats in Chiloé Island, Chile: upper canopy of an old-growth, evergreen temperate forest, lower branches in the understory of the same old-growth forest, branches up to 1.5-2.3 m for trees in forest patch edges in a forest-pasture land mosaic in Caulín, Chiloé, and isolated trees in pastures in the same area.

Pollinator species	**Order, family**	**Number of individuals /observation period X 100 (visit number)**	**Visits/flower/ minute X 100**
Upper canopy flowers			
Aneriophora aureorufa	Diptera, Syrphidae	2.35 (8)	0.118
Platynocera sp. 1	Coleoptera, Cerambycidae	2.35 (8)	0.118
Melanostoma fenestratus	Diptera, Syrphidae	1.18 (4)	0.059
Colletia aff. *seminitidus*	Hymenoptera, Colletidae	0.88 (3)	0.044
Bombus dalhbomi	Hymenoptera, Apidae	0.59 (2)	0.030
Sarcophagidae *sp.* 7	Diptera, Sarcophagidae	0.59 (2)	0.030
Platynocera sp. 2	Coleoptera, Cerambycidae	0.29 (1)	0.015
Hemiptera 1	Hemiptera	0.29 (1)	0.015
Lauxanidae 1	Diptera, Lauxanidae	0.29 (1)	0.015
Sephanoides sephaniodes	Ave, Trochilidae	0.29 (1)	0.015
Forest understory flowers			
Mordella sp 1	Coleoptera Mordellidae	4.44 (8)	0.222
Staphilinidae 1	Coleoptera, Staphilinidae	1.67 (3)	0.084
Staphilinidae 2	Coleoptera, Staphilinidae	1.67 (3)	0.084
Sarcophagidae sp. 5	Diptera, Sarcophagidae	1.67 (3)	0.084
Platynocera 1	Hymenoptera, Cerambycidae	1.11 (2)	0.056
*Eristalis tenax**	Diptera, Syrphidae	0.56 (1)	0.028
Lauxanidae 1	Diptera, Lauxanidae	0.56 (1)	0.028
Unknown species 1	Diptera, Tachinidae	0.56 (1)	0.028
Forest edge			
*Apis mellifera**	Hymenoptera, Apidae	9.79(47)	0.490
Bombus dalhbomi	Hymenoptera, Apidae	1.01 (5)	0.052
Sarcophagidae sp. 1	Diptera, Sarcophagidae	0.63(3)	0.032
*Vespula germanica**	Hymenoptera, Vespidae	0.63(3)	0.032
Lauxanidae sp. 3	Diptera, Lauxanidae	0.63(3)	0.032
Corynura atrovirens	Hymenoptera, Halictidae	0.42(2)	0.021
Cadeguala occidentalis	Hymenoptera, Colletidae	0.21(1)	0.011
Lypha erigonopsidis	Diptera, Tachinidae	0.21(1)	0.011
Sarcophagidae sp. 3	Diptera, Sarcophagidae	0.21(1)	0.011

Sarcophagidae sp. 4	Diptera, Sarcophagidae	0.21(1)	0.011
Chauliognathus sp.	Coleoptera, Cantharidae	0.21(1)	0.011
Trichophthalma barbarossa	Diptera, Nemestrinidae	0.21(1)	0.011
Trichophthalma herbsti	Diptera, Nemestrinidae	0.21(1)	0.011
Aneriophora aureorufa	Diptera, Syrphidae	0.21(1)	0.011
Unknown species 2	Diptera, Syrphidae	0.21(1)	0.011
Isolated trees in pasture			
Bombus dalhbomi	Hymenoptera, Apidae	2.5(12)	0.125
*Apis mellifera**	Hymenoptera, Apidae	1.45(7)	0.073
Aneriophora aureorufa	Diptera, Syrphidae	0.63(3)	0.032
Corynura atrovirens	Hymenoptera, Halictidae	0.63(3)	0.032
Trichophthalma conmutata	Diptera, Nemestrinidae	0.42(2)	0.021
Corynura lepida	Hymenoptera, Halictidae	0.21(1)	0.011
Corynura patagonica	Hymenoptera, Halictidae	0.21(1)	0.011
Eristalis elegans	Diptera, Syrphidae	0.21(1)	0.011
Melanostoma chalconotus	Diptera, Syrphidae	0.21(1)	0.011
Trichophthalma barbarossa	Diptera, Nemestrinidae	0.21(1)	0.011
Sarcophagidae sp. 5	Diptera, Sarcophagidae	0.21(1)	0.011
*Vespula germanica**	Hymenoptera, Vespidae	0.21(1)	0.011

*Introduced species

Discussion

Despite our limited sample size, we believe this first effort to study pollinator assemblages at 25 m height in the forest canopy, by using climbing techniques, provides important data to expand our knowledge of pollinator species composition in the temperate rain forests of Chiloé Island. This study makes it possible, for the first time, to compare pollinators in the upper canopy with pollinators that visit flowers on lower branches.

One of the most remarkable results from the present study was the record of *Colletia* aff. *seminitidus* Spinola in the upper canopy of the old-growth forest of Guabún. This is a very conspicuous bee, which had not been recorded previously in the course of our 18- year study of the pollinator assemblages visiting flowers in lower branches of *E. cordifolia* and other plant species in northern Chiloé Island (Smith-Ramírez *et al*. 2005; Smith-Ramírez *et al*. 2014). This addition to the known pollinator assemblage of the canopy tree *E. cordifolia cordifolia* is relevant, because nearly 150 pollinator species or morpho-species have already been described to pollinate *E. cordifolia* flowers, one of the largest, richest pollinator assemblages for any forest tree in this area (Smith-Ramírez *et al*. 2014). Another outstanding result from the canopy study is the dominance of *A. aureorufa* in the pollinator assemblage of upper branches, and the presence of a species of the Mordellidae in the assemblage of flower visitors of the old-growth forest understory. During 15 years of pollinator studies in the forest-pasture land mosaic of Caulín and other similar locations in northern Chiloé Island (Senda Darwin Biological Station, about 8 km from Caulín), the most important flower visitors of *E. cordifolia* and 12 other forest species have always been strongly conservative, primarily the honeybee *A. mellifera* and the bumblebee *B. dahlbomii*, which together accounted for 42 to 58 percent of the frequency of visits to flowers (Smith-Ramírez *et al*. 2005). The absence of honeybees in the canopy and understory of the old-growth forest in Guabún was surprising because many colonies are brought to the island every year during the peak flowering period of *E. cordifolia* and other forest trees. Therefore, these insects are expected to be widespread in northern Chiloé, a region well known for its commercial production of *E. cordifolia* honey. It is likely that honeybees are missing from the old-growth forest, because the food habitat of this species comprises mainly trees on forest edges and in open areas without a closed canopy, as documented by Smith-Ramírez *et al*. (2005). The pollinator assemblages described here might represent the situation restricted to large patches of old-growth forests without major human impact, or areas far from human-dominated landscapes. In fact, 200 km north of Chiloé Island, in the foothills of the Andes, pollinator faunas of indigenous temperate forests were characterized by a low abundance of honeybees, while at lower elevations, in small forest patches and isolated trees in pastures interspersed in a large area of farm and pastureland, the abundance of honeybees was much higher (Smith-Ramírez unpublished data). Less frequent upper canopy flower visitors differ greatly from understory flower visitors, but such variability in species composition of pollinators also occurs when comparing *E. cordifolia* trees from different individuals and years in Chiloé (Smith-Ramírez *et al*. 2014).

From the results of this study, we cannot ascertain whether different pollinator species use different vertical strata along *E. cordifolia* trees (e.g., flowers in the upper canopy versus understory branches when present) because we did not sample systematically along the height of the tree and the sample size is still limited. Such differentiation of pollinator assemblages along the height of the tree has been proposed for some pollinator groups in tall tropical forests (Roubik 1993). The present study provides strong evidence that our current knowledge of the pollinator assemblage composition and diversity in temperate forests of southern South America is still incomplete and restricted to lower layers of the forests. Future studies assessing tree pollinator diversity should focus particularly on the remnants of old-growth forest and the forest canopy. In addition, the absence of introduced species in the canopy of old-growth rain forests is remarkable.

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