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First evidence of insect attraction by a Southern Hemisphere Splachnaceae: The case of *Tayloria dubyi* Broth. in the Reserve Biosphere Cape Horn, Chile.

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With 3 figures and 1 table

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Abstract: The moss *Tayloria dubyi* (Splachnaceae) is endemic to the subantarctic Magallanes ecoregion where it grows exclusively on bird dung and perhaps only on feces of the goose *Chloephaga picta*, a unique habitat among Splachnaceae. Some species of Splachnaceae from the Northern Hemisphere are known to recruit coprophilous flies as a vector to disperse their spores by releasing intense odors mimicking fresh dung or decaying corpses. The flies land on the capsule, and may get in contact with the protruding mass of spores that stick to the insect body. The dispersal strategy relies on the spores falling off when the insect reaches fresh droppings or carrion. Germination is thought to be rapid and a new population is quickly established over the entire substrate. The objectives of this investigation were to determine whether the coprophilous *T. dubyi* attracts flies and to assess the taxonomic diversity of the flies visiting this moss. For this, fly traps were set up above mature sporophyte bearing populations in two peatlands on Navarino Island. We captured 64 flies belonging to the Muscidae (*Palpibracus chilensis*), Tachinidae (*Dasyuromyia* sp) and Sarcophagidae (not identified to species) above sporophytes of *T. dubyi*, whereas no flies were captured in control traps set up above *Sphagnum* mats nearby.

Key words: Diptera, entomophily, Splachnaceae, subantarctic Magallanic ecoregion, *Tayloria dubyi*.

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Introduction

Among seedless plants entomophily is known only from some species the moss family Splachnaceae (Koponen 1990). The insect-mediated dispersal syndrome comprises various morphological and chemical innovations designed to attract insects feeding or ovipositing on dung and carrion. The spores of entomophilous Splachnaceae are sticky, and adhere to the bodies of visiting insects as they walk over the protruding mass of sticky spores. The dispersal strategy relies on the flies reaching fresh droppings soon after visiting the moss. Spores would fall off, germinate and develop an extensive mat quickly covering the vacant substrate (Marino et al. 2009). Not all Splachnaceae rely on insects to disperse their spores, as nearly half of the species are anemophilous or wind dispersed (Koponen 1990; Goffinet et al. 2004). Entomophily has been demonstrated thus far for several species of *Tetraplodon*, *Splachnum* and *Tayloria* in boreal and alpine habitats in Europe and North America (Koponen 1990; Marino et al. 2009). Although several Southern Hemisphere taxa exhibit an entomophilous syndrome and a coprophilous habitat, empirical evidence for insect-mediated spore dispersal is lacking (Koponen & Koponen 1977, 1990; Goffinet et al. 2006). In the Northern Hemisphere, entomophilous species are restricted to either carnivore or herbivore dung, and this specialization results from them attracting distinct vectors (e.g., Koponen & Koponen 1977; Marino et al. 2009): species growing on carnivore dung attract a fly fauna much more representative of flies associated with carrion, whereas those colonizing herbivore dung attract relatively few carrion flies (Marino 1991; Marino et al. 2009). Coprophilous Splachnaceae select their vector using visual and olfactory cues, and in particular distinct odors that mimic decomposing organic material. Since the insect distinguish between substrate types, distribution of spores by the flies is non random and these mosses tend to exhibit a strong specificity to either carnivore or herbivore dung (Marino et al. 2009). The flies that are recruited belong to a variety of families. Koponen & Koponen (1977) captured coprophilous flies from four families (Sepsidae, Scatophagidae, Muscidae and Sarcophagidae) using traps baited with sporophytes of *Splachnum ampullaceum* Hedw. and *S. luteum* Hedw., *S. vasculosum* Hedw. and *Tetraplodon mnioides* (Sw. ex Hedw.) Bruch & Schimp. The majority of flies trapped were Muscidae and Sepsidae. Marino (1991) captured flies on *S ampullaceum* and *S. luteum*, *T. mnioides* and *T. angustatus* (Hedw.) Bruch & Schimp. and found spores on flies from the above families as well on species of Anthomyiidae, Caliphoridae, Muscidae, Fanniidae and Scathophagidae.

The subantarctic forests of the Magallanes region, in the extreme South of Chile, which is considered a global "ecosystem of highest ecological importance" (Goffinet et al. 2006), harbor five species of Splachnaceae: *Tetraplodon fuegiensis* (Hedw.) Bruch & Schimp. and four species of *Tayloria* (namely, *T. dubyi* Broth., *T. magellanica* (Brid.) Mitt., *T. mirabilis* (Cardot) Broth. and *T. stenophysata* (Herzog) A.Kop. *Tayloria dubyi* is a rather uncommon endemic species occurring in *Sphagnum*-bogs (Fig. 1). It grows exclusively on bird dung and perhaps only on feces of the goose *Chloephaga picta* (Gmelin), a unique habitat among Splachnaceae (Jofre et al. 2010). The green leafy stems of *T. dubyi* rarely exceed two cm in height and form dense clumps often less than two cm in diameter. Following sexual reproduction they

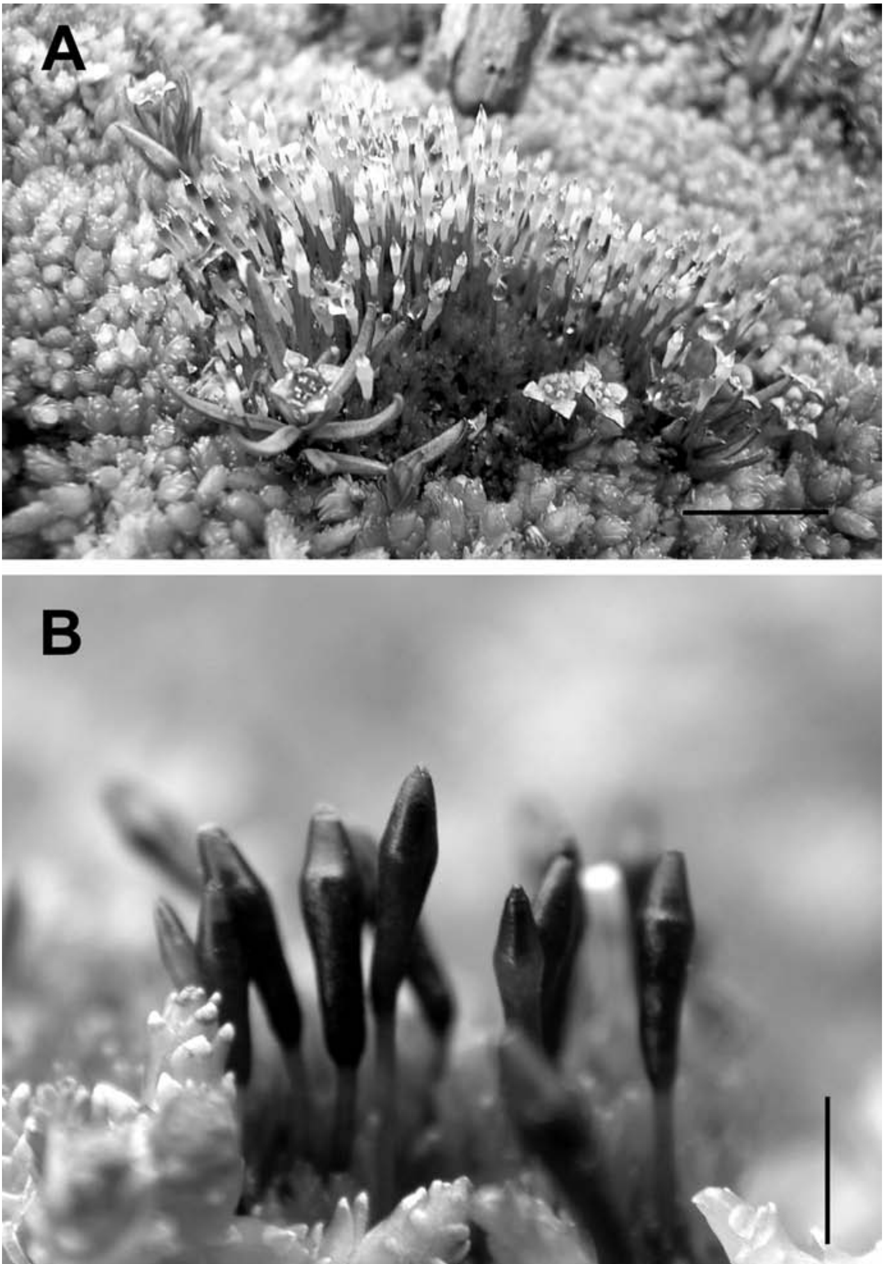

Fig. 1. *Tayloria dubyi* growing exclusively on bird dung and perhaps only on feces of the goose *Chloephaga picta*. (A) Immature sporophytes and (B) detail of mature sporophytes. Bar in A = 0.9 cm and bar in B = 0,25 cm.

develop highly contrasted dark reddish to purple sporophytes that produce sticky orange spores less than 10mm in diameter (Jofre et al. 2010). The sporophytes release a strong odor when mature (Jofre pers. observation). The color of the capsule, the small size and the aggregated exposure of the sticky spores and the substrate suggest that this species relies on insects to disperse its spore. However, empirical evidence from trapping experiments was lacking.

The objectives of this investigation were: 1) to determine whether *Tayloria dubyi*, a species endemic to the Magallanes region, attracts flies, 2) to assess the taxonomic diversity of the flies visiting this moss.

Materials and methods

AREA OF STUDY: *Tayloria dubyi* is known from the canal zone of Aysen, the islands of the Reserve Biosphere Cape Horn (RBCH) and the western margin of Tierra del Fuego (Matteri 1985; Goffinet et al. 2006; Jofre 2010; Fig. 2). On Navarino Island, *T. dubyi* has been observed growing on feces of the goose *Chloephaga picta* in peatlands in the sector on the southern outskirts of Windhond Bay, and along the northern coastline between the subantarctic and trans-andean zones of the RBCH (Rozzi et al. 2006; Jofre 2010).

The study sites were located on the north coast of Navarino Island (55°S), in the RBCH in the region of Magallanes and Chilean Antarctic, Chile (Fig. 2). This zone is characterized by a trans-andean climate with steppe vegetation and is located east of an isothermal tundra zone that is extremely rainy (Pisano 1983). The mean annual temperature is 6°C and annual precipitation amounts to 467 mm. The peatlands are immersed in a mosaic of evergreen forests dominated by the southern beech *Nothofagus betuloides* (Mirb.) Oerst and mixed forests of *N. antarctica* (G.Forster) Oerst and the deciduous *N. pumilio* (Poepp & Endl.) Krasser (Rozzi et al. 2004).

STUDY SITES: Populations of *T. dubyi* were sampled in two sites. The first, called "Mejillones" (54°53'56"S; 67°57'55,2"W) was located about 25 km west of the city of Puerto Williams and one km east of Mejillones Bay, at an elevation of 40 m above sea level (Fig. 2). The peatland was dominated by *Sphagnum magellanicum* Brid. and *S. fimbriatum* Wilson, covering an area 80 m long and 19 m wide. The second site, called "Omora Park" (54°56'37"S; 67°38'49"W) was located about 2 km west of the city of Puerto Williams, alongside the freshwater lagoon of the Omora Ethnobotanical Park, at an elevation of 127 m above sea level (Fig. 2). This peatland was 50 m long and 22 m wide. In both sites we performed a census of the total populations of *T. dubyi*. At Mejillones we found only 22 populations, 10 of which were used in experiments to trap flies. In the site Omora Park, we found only 12 populations of *T. dubyi*, six of which were used in fly trapping experiments.

FLY TRAPPING EXPERIMENTS: To test the fly attraction by *T. dubyi*, we set up traps above mature, sporophyte bearing populations and placed control traps above *Sphagnum* at least 2 m away from the nearest populations of *T. dubyi*. A distance of two meters was chosen after preliminary assays determined the maximum radius of fly attraction by the odor of *T. dubyi* to be about one meter. In Mejillones we installed 20 traps: 10 above populations of *T. dubyi* and 10 control traps above *S. magellanicum* or *S. fimbriatum*. In Omora Park we installed six traps above populations of *T. dubyi* and the same number of control traps above *S. magellanicum*. Each trap was assigned a number using biodegradable experimental flagging.

Fly traps were constructed with 1L plastic beverage bottles, which were cut in half (Fig.3). The lower portion was inverted and the upper portion was placed narrow end first within it, creating a funnel that led to an open chamber into which the flies could enter but from which they could not easily escape. Each trap was supported above the moss population by wires, placing the lower rim 2 cm above the moss sporophytes (Fig. 3). This design was effective because flies that visit mosses depart in a vertical ascending flight, which takes them directly into the trap (see Marino 1991). Flies were trapped for 5 consecutive days each month (from October 2007–April 2008). The traps were checked daily and captured flies were anesthetized with acetone and collected for pinning.

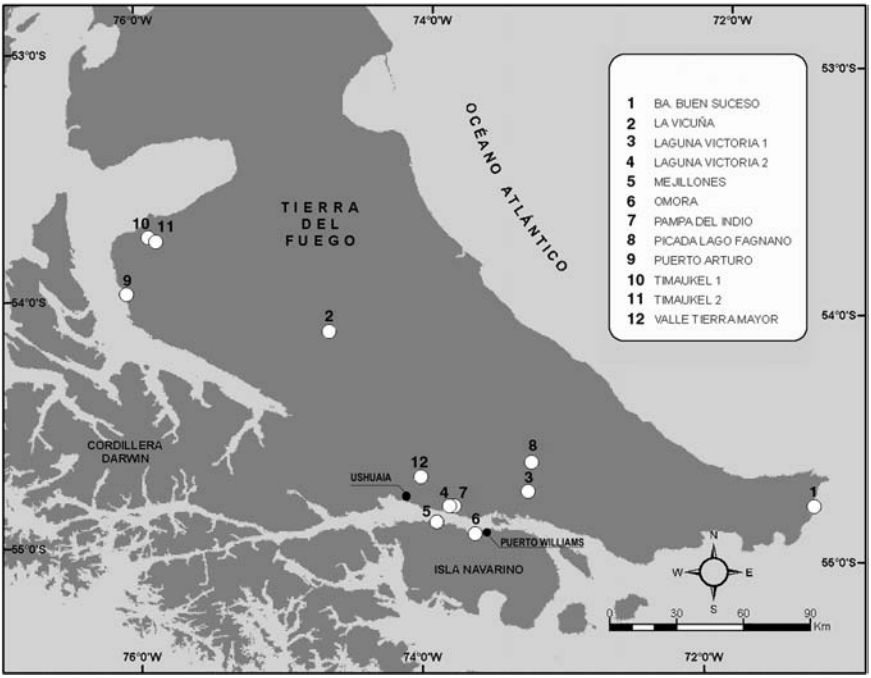

Fig. 2. Map of the southernmost region of Chile showing the study sites: Mejillones and Omora Park (5 and 6 number, respectively). The map also shows the sites where *Tayloria dubyi* was collected by Matteri (1985) in Tierra del Fuego Island.

STATISTICAL ANALYSIS: Data were analyzed statistically using ANOVA and Duncan's test with the software packages of Statistica (7.0) and MVSP (3.12).

Results

FLY CAPTURE: A total of 64 individual flies were captured in the traps placed above populations of *T. dubyi*; 39 individuals (61%) were captured at the Mejillones site and 25 individuals (39%) were taken at the Omora Park site. No flies were captured in control traps (Table 1). Significant differences in the number of flies captured in Mejillones occurred between months (ANOVA; df = 2, F = 3.55, P = 0.04) as 77% (N = 39) of flies were trapped in December (Duncan's Test: P = 0.02). By contrast, the differences observed in the total number of flies captured each month at the Omora Park site were not significant (ANOVA; df = 2, F = 2.75, P = 0.096) (Table 1).

FLY DIVERSITY AND TAXONOMIC IDENTITY: Traps baited with Splachnaceae captured 3 families of flies (Muscidae, Tachinidae and Sarcophagidae). The majority (41 individuals; 64% of all captured flies) of flies trapped were Muscidae [*Palpibracus chilensis* (Bigot 1885)] approximately evenly divided between the Mejillones and Omora Park sites. Tachinidae (*Dasyuromyia* sp.) were next in abundance (14 indivi-

Fig. 3. Model of the trap used to catch flies that visited sporophytes of *Tayloria dubyi*. This trap was constructed using recycled 1 litre plastic bottles.

duals; 21% of all captured flies) and Sarcophagidae ranked third in abundance (9 individuals; 15% of all captured flies). Most flies were captured between December and January.

Discussion

The sporophyte of *Tayloria dubyi* is of a deep reddish-purple color and releases strong odors that resemble those of decomposing organic matter. These characters are thought to be essential components of a syndrome associated with insect-mediated dispersal of the spores (Koponen 1977). The trapping experiments presented here provide unequivocal evidence that *T. dubyi* attracts flies, which belong to only 3 families (Muscidae, Tachinidae and Sarcophagidae).

Entomophilous Splachnaceae are highly specialized for attracting insects, and for ensuring contact between the spore mass and the visiting fly. The syndrome for insect mediated spore dispersal includes brightly colored sporophytes, reduced sporangial mass with small, thin-walled sticky spores, and an enlarged sterile region below the sporangium producing volatile compounds and in some cases facilitating landing of the insect (Koponen 1977; Marino et al. 2009). *Tayloria dubyi* is among

Table 1. Total and mean values of flies captured per month during October 2007 and April 2008 in Mejillones and Omora Park study sites (SD = standard deviation).

	Mejillones			Omora Park		
	Traps over *T. dubyi*		Control	Traps over *T. dubyi*		Control
Month	**Total**	**Mean±SD**	**Total**	**Total**	**Mean±SD**	**Total**
October	0	0	0	0	0	0
November	0	0	0	0	0	0
December	30	3±4.1	0	22	3.6±5	0
January	6	0.6±1.1	0	2	0.3±0.5	0
February	3	0.3±0.6	0	1	0.2±0.4	0
March	0	0	0	0	0	0
April	0	0	0	0	0	0

the smallest of the moss species that exhibit these features. However, the deep purple color of the sporophytes contrasts sharply with the green vegetative stems and the pinkish-red *Sphagnum magellanicum* among which it grows, and may hence serve as an effective visual cue. The neck of the capsule of *T. dubyi* is not enlarged but is much longer than the sporogenous region.

The odor released by the capsule approximates, both in quality and intensity, the smell of decomposing shellfish. Whether color and odors of the sporophyte accomplish distinct but complementary functions in attracting and guiding the insect to the spore mass remains to be tested. The odor blend emitted by the apophysis of *T. dubyi* includes indole, phenol, para-cresol and para-cresol methyl ether compounds (R.A.Raguso unpubl. data), compounds that are similar to those commonly found in herbivore feces (Jürgens et al. 2006). Odors seemed to be emitted only when ambient temperatures exceeded 10°C, mainly at the end of December when most sporophytes were mature. This temperature may represent a threshold for fly activity (Jofre et al. 2010).

Seasonal variation in insect recruitment is shaped first by the maturation of the sporophytes and then also by characteristics of the habitat and daily weather: the sporophytes of *T. dubyi* mature in December and the species occurs in cold temperate unforested peatlands exposed high winds, limiting insect activity (Jofre et al. 2010). The number of flies captured on *T. dubyi* ranged from three to four flies per day (Mejillones and Omora Park site, respectively). This low total number of flies captured may reflect that, in general, the Patagonian peatlands are subject to strong winds and low temperatures that limit fly activity in general. In Newfoundland, Canada, a region that, like Patagonia, also experiences windy, cool and wet summers, Marino et al. (2009) trapped more flies per day (seven to eight flies/day) on *Splachnum ampullaceum*. In the same way, other studies indicate that the number of flies captured in Northern Hemisphere could be higher than those observed on Navarino Island. For example, Bequaert (1921) noted that *S. rubrum* attracts the greatest number of flies on sunny days, with 30 visits in 30 minutes at one field Arctic site. Koponen & Koponen (1977) captured 92 flies per day above *S. ampullaceum*, *S. luteum*, *S. vas-*

culosum and *T. mnioides* in Finland. On the other hand, Troilo & Cameron (1981) captured a mean of 8.4 flies per hour above *S. ampullaceum* in 22 days of study in Michigan, North America. Later, Marino (1991) in Alberta, Canada captured more than 1,000 flies above *S. ampullaceum*, *S. luteum*, *T. angustatus* and *T. mnioides* in 10 days of study.

Flies captured above *T. dubyi* sporophytes belong to the Muscidae (*Palpibracus chilensis*), Tachinidae (*Dasyuromyia* sp) and Sarcophagidae (unidentified genus). Koponen & Koponen (1977), Cameron & Wyatt (1986) and Marino (1991), also trapped flies from various lineages on Splachnaceae although representing a much greater diversity of fly families. For example, Koponen & Koponen (1977) trapped members of the Sepsidae, Scathophagidae, Muscidae and Sarcophagidae. The majority (77%) of these were *Pyrellia* and *Neomyia* spp. (as *Orthellia*) (Muscidae) and sepsid flies. The breadth of vectors recruited was further broadened by Marino (1991) who also captured species of Anthomyidae (*Pegoplata patellans* Pand.), Fanniidae (*Fannia spathiophora* Mall.) Muscidae (*Eudasyphora cyanocolor* Zett.), Calliphoridae (*Phormia regina* Meig. and *Calliphora vomitoria* L.) and Scathophagidae (*Scatophaga suilla* Fab.) above populations of *Tetraplodon angustatus*, *T. mnioides*, *Splachnum luteum*, and *S. ampullaceum*. This information indicates that the number of captures, diversity of families and species of flies that visit Splachnaceae species in the Northern Hemisphere is broad and diverse compared with *T. dubyi* in the Southern Hemisphere.

Species of Splachnaceae associated with carnivore dung attract a fly fauna much more representive of flies associated with carrion, whereas those associated with herbivore dung attract relatively few carrion flies (Marino et al. 2009). In *Tayloria dubyi* most captured flies were *Palpibracus chilensis* (Muscidae Azeliinae, Reinwardtiini), a species that has been reported previously from southern Chile (Soares & De Carvalho 2005; Couri & Penny 2006). *Palpibracus* is restricted to Chile and Argentina, with 19 species (Soares & De Carvalho 2005; Couri & Penny 2006). The second largest group of flies captured belonged to *Dasyuromyia* (Tachinidae, Dexiinae, Dexiini). This genus includes 8 species, restricted to Chile and Argentina (Guimarães 1971). We also captured Sarcophagidae flies. Many Muscidae and Sarcophagidae (as well as Fanniidae, Anthomyiidae and Scathophagidae) are associated with dung, and use this resource either as a breeding site (females visit it to oviposit or larviposit, and then the larval development occurs on this substrate) or as food, feeding directly on the dung (coprophagy) or feeding on the fungi growing on dung (saprophagy if they eat fungi it should be called mycophagy; saprophagy referes to feeing on dead organic material). All the species listed by Marino (1991) have coprophilous and saprophagous adults that use dung as a breeding site, whereas their larvae vary in their feeding habits (some are saprophagous, others are facultative/obligate carnivores) (Skidmore 1985). With regard to *Palpibracus chilensis*, information about adult and larval feeding habits and adult breeding habits is lacking. *Brachygasterina* is the sister-group to *Palpibracus* (Soares & De Carvalho 2005) and is represented in our sample by one species, *B. valdiviensis* that breeds on decaying flesh (fish, rat and chicken; Pamplona & Couri 2000). Members of the Reinwardtiini have been recorded breeding on a variety of media: dung, rotting vegetable matter, fungi, garbage, vertebrate and invertebrate carrion and birds' nests (Ferrar 1987).

On the other hand, nearly all species of Tachinidae are parasitoids (in the larval stages) and the female uses its available energy (after copulation) to locate a host and oviposit/larviposit on it. The hosts are usually other arthropods, mostly other insects (Orthoptera, Mantodea, Hemiptera, Lepidoptera, Coleoptera, etc.) (Guimarães 1977; Stireman et al. 2006). While the larvae are carnivorous (within their hosts), the adults of Tachinidae are known to feed on floral nectar (Larson et al. 2001) and may also derive nutrients from rotting feces (Stireman et al. 2006). In Patagonian Chile and Argentina, *Dasyuromyia* adults (males and females) have been collected visiting flowers of *Chrysanthemum* (Townsend 1936). Additionally, *Dasyuromyia* species in Chile and Argentina have been reported as parasitoids of scarabeid beetles (*Oryctomorpus bimaculatus* Guerin) in decaying wood of *Nothofagus obliqua* (Mirb.) Oerst (Cortés 1986). In both study sites (Mejillones and Omora Park) there was much decaying wood of *Nothofagus* species close to our traps. The *Dasyuromyia* flies captured in our traps may have been searching for larval hosts or sources of adult nutrition.

Finally, although we could not verify that spores of *Tayloria dubyi* are dispersed by flies, we have shown that the sporophytes of *T. dubyi* effectively attract flies whose anatomy and behavior are suitable for entomophilous dispersal between goose dung in the peat bog habitats of this moss. Whether insects actually disperse spores is likely but fundamental empirical evidence consisting of spores recovered from trapped insects is still lacking. Future trapping experiments should determine the relative contributions of sporophyte odor and color to fly attraction, and whether flies leave *T. dubyi* sporophytes carrying spores.

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