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Differences in arthropods found in flowers versus trapped in plant resins on *Haplopappus platylepis* Phil. (Asteraceae): Can the plant discriminate between pollinators and herbivores?

Cristian A. Villagra · Alvaro Astudillo Meza · Alejandro Urzúa

Abstract Plants produce secondary metabolites related to ecologically relevant processes. These compounds include surface secretions such as latex, mucilage and resins that help plants face abiotic and biotic environmental threats such as drought, nutrient deficiency, extreme temperatures and UV radiation, as well as herbivory, pathogenic microorganisms and other natural enemies. We studied the resinous coating found on involucral bracts of *Haplopappus platylepis* Phil. (Asteraceae). This plant belongs to a speciose genus widely distributed in South America (Lane and Hartman in Am J Bot 83:356, 1996). *H. platylepis* is characterized by resinous fragrant leaves. In this species, resins cover the involucral bracts as well as young leaves and are also secreted on reproductive stalks in smaller amounts. We carried out chemical analysis and natural history observations in order to identify whether arthropods caught in inflorescence resin differed from the ones freely visiting floral disks. Regarding bracteal adhesive's chemistry, we identified a mixture of diterpenoids and flavonoids; these compounds form a dense surface resin layer, especially over inflorescence's bracts. In relation to associated arthropods, we found a marked difference in the main organisms captured by bracteal resin compared to insects we observed foraging on disk florets; *Arthrobracus* (Coleoptera: Melyridae) and *Linepithema* (Hymenoptera: Formicidae) were the predominant insects "trapped in resin", while *Diadasia* (Hymenoptera: Apidae) was the most frequent "floral visitor". We propose that bracteal resin of *H. platylepis* may function as a selective trap for non-mutualistic insects reaching reproductive structures of this plant and discuss other multiple possible roles for this secretion, including protocarnivory.

Keywords Constitutive resistance · Terpenoids · Larcenist · *Diadasia chilensis* · *Lioptilodes friasi*

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Introduction

In spite of being sessile organisms, plants are able to respond to certain abiotic and biotic factors of their habitat by producing a diverse group of secondary metabolites. Related to this, many plants secrete sticky substances such as latex, resins and mucilages (reviewed by Adler and Irwin 2005; Knudsen et al. 2006). Usually adhesive mixtures are concentrated over plant structures susceptible to herbivory and abiotic stress, especially flowers and seeds (Miller et al. 2005). Depending on their chemical composition, these secretions may accomplish several crucial functions for plant survival and reproduction. Viscous coatings are related to plant protection against abiotic stresses such as drought, nutrient deficiency, extreme temperature and UV radiation, mostly when viscid mixture includes resinous terpenoids (e.g., Hoffmann et al. 1984; Zavala and Ravetta 2002). For example, shrubs and herbs from xeric habitats such as creosote bushes (Zygophyllaceae) and *Holocarpha* (Asteraceae) herbs produce leaf terpenoid resins associated to their tolerance to dry

conditions and high UV radiation (reviewed by Langenheim 2003). Additionally, sticky surface compounds, such as flavonoids and terpenoids, are often linked with plant interactions with other organisms such as pathogens, herbivores and pollinators. For instance, resiniferous bractlets in *Dalechampia* (Euphorbiaceae) produce triterpenes in aggregations in their inflorescences (Armbruster 1996). This mixture of compounds functions as a chemical defense against infectious microorganisms (Armbruster 1996) and may also serve as a reward for specialized pollinators (Armbruster et al. 2009).

Plant sticky exudates of different chemical nature are also capable of catching organic particles like pollen, anemochoric seeds and even small arthropods. In the case of insect-trapping secretions, the mixture may lure animals attracted to its shinning appearance or scent. Moreover, secretion's toxic compounds may accelerate the death of trapped animals. These exudates are known to cause insect suffocation by tracheal obstruction and starvation by inability to move (Adlassnig et al. 2010). For example, sticky latex in lettuce inflorescences, *Lactuca sativa* L. (Asteraceae), traps the entire body of aphids (Dussourd 1995), gluing the insect mouthparts. Thus, this latex is considered as a chemo-mechanical defense against these herbivores (Dussourd 1995; Konno 2011).

Furthermore, if soluble compounds derived from trapped organisms are taken up by the plant, then adhesive traps may contribute to improve plant nutrient supply (known as "carnivorous" or "insectivorous" plants sensu Darwin 1875). This can be achieved directly from decaying corpses trapped in the viscous layer in cases when plants secrete proteolytic enzymes aiding the digestion of nutrients (i.e., Tökés et al. 1974). Also, even if plants do not release enzymes together with the sticky secretion (known as "protocarnivorous", reviewed by Albert et al. 1992), nutrient uptake can be achieved indirectly by obtaining N from the feces of specialized Hemiptera, residents of sticky plants that feed on the trapped insect carrion (Ellis and Midgley 1996; Voigt and Gorb 2008a, b).

Protocarnivorous attributes, such as adhesive coatings without morphological adaptations for carnivory, have received less attention than more charismatic cases of plant insectivory (Chase et al. 2009). Due to this, several relevant issues on the ecology and evolution of this kind of plant–arthropod interaction are still unclear: for instance, the prevalence of this nutritional adaptation in plants is not known (Ellison and Gotelli 2001). Also, there is a need for better taxonomic resolution of the captured prey; this would help to understand the degrees of ecological specialization on these plants (Ellison and Gotelli 2009). Moreover, the possible multiple ecological functions of protocarnivorous adhesive traps are largely unknown, due to lack of studies on chemical composition of the viscid

secretions and their properties regarding biotic and abiotic factors (reviewed by Adlassnig et al. 2010).

Plant surface secretions may correspond to a relevant trait for plant survival and reproduction. Many of their ecological functions may depend on exudate chemical composition and its interaction with plant-associated organisms. In this work, we studied the subshrub *Haplopappus platylepis* Phil. (Asteraceae), endemic in central Chile. This plant produces a resinous coating copiously secreted over the involucrum of the flower head, completely covering the surface of the capitulum bracts with a layer of adhesive resin of whitish sparkling luster, capable of capturing various groups of arthropods. Our goal was to study possible ecological functions for the involucral resin of *H. platylepis*. Specifically, we question whether this resin coating may correspond to a passive and selective trap for insects reaching the inflorescence. If so, is this resin capable of trapping non-mutualistic visitors such as herbivores or parasites more frequently than positive visitors such as pollinator candidates? For this, we first made field surveys and collections of both the arthropods found on floral heads, and those found dead in the bracteal resin. We then used analytical approaches to identify the main chemical compounds present in the floral resin. Furthermore, we discuss the potential impact on plant reproductive success of different arthropods we found as "floral visitors" and also those we found "trapped in resin". Finally, we briefly review multiple potential functions for the sticky bracteal adhesive.

Materials and methods

Study site

We carried out our study at Bioparque Puquén, Los Molles (32°14′S, 71°31′W 12 m.a.s.l.), Petorca Province, Valparaiso Region, Chile. This location is characterized by low thermal oscillation with an annual average of 14 °C, 450 mm annual precipitation and average humidity of 75 %. In this site, *H. platylepis* populations are usually found in open areas surrounded by a varied community of endemic plant species.

Study organism and methods

Haplopappus platylepis (Fig. 1A) is a perennial, endemic subshrub from the dry "coastal steppe matorral" ecosystem of coastal central Chile (Gajardo 1994). During austral autumn–winter (April–August), *H. platylepis* remains as a flat rosette of bald lanceolate leaves with no adherent properties. In spring (September–November), the plant produces a group of three to seven reproductive stalked
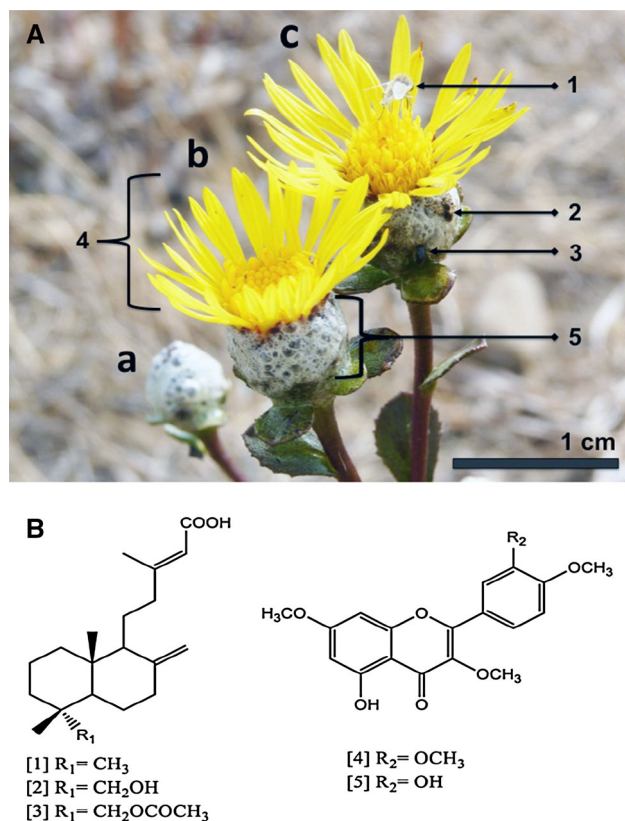
Fig. 1 A Photograph showing part of *H. platylepis* capitula ontogeny; *a*: young buds fully protected by resinous bracts, *b*: just opened inflorescence displaying ligulate and tubular flowers in the inflorescence disk, *c*: mature flower, note: beginning of senescence of ligulate flowers and level of development of tubular flowers. Together with the floral parts are both "floral visitors" (*1*) and insects "trapped in resin" (*2*, *3*). The resinous exudate is not found on reproductive parts of inflorescence structures (*4*), but is profusely produced over bracts (*5*). The *bar* indicates 1 cm. B Compound structures of ent-labdane diterpenes and flavonol constituents of the resinous exudates of *H. platylepis*

sprouts per plant, each bearing freely distributed small rounded leaves and one terminal racemose inflorescence. Floral head buds are fully covered by an adhesive secretion when the capitulum opens at the beginning of summer (December). This viscid layer is water-insoluble, transparent-white and shiny. Involucral bracts resemble reproductive stalk leaves but emphasize the production of the sticky coating. This secretion is also found covering leaves, with a relatively thin layer in comparison with bracts (authors' personal observation) (Fig. 1A). At capitulum anthesis, involucrum leaves retract on top allowing ligulate and disk florets to open free from exudate. Therefore, if visitors reach floral heads via the top, they are able to access floral resources with no threat from the stickiness of resinous coating. Capitula remain open for 2 weeks, and plants continue blooming with new floral units until the end of the summer (March). Fertilized florets form stacks of

cypselae seeds with few pappi bristles that aid in their dispersal. We observed that while the adhesive coating in dead and dried-up floral heads can persist, it becomes partially heat-degraded by summer temperature of the dry central Chilean climate. Therefore, resinous cover in buds and young leaves may also protect plant's organs against desiccation, elevated temperatures and radiation (Rhoades 1977; Zavala and Ravetta 2002), as various authors have reported for other resinous plant species growing in arid habitats (Hoffmann et al. 1984; Langenheim 2003).

Chemical analyses

We recorded IR-FT spectra in a Bruker IFS66V and NMR spectra in a Bruker 400 UltraShield spectrometer in $CDCl_3$. In order to identify the different compounds in the resin exudates, we extracted head buds by dipping the fresh plant material in cold CH_2Cl_2 for 30 s (following Tojo et al. 1999). This procedure assures the total and selective extraction of the resin. We obtained the CH_2Cl_2 extract after filtration of the suspension; we eliminated the solvent by evaporation. We studied the resinous exudate by IR (film) and 1H-NMR spectroscopy. We employed thin layer chromatography (TLC) with Merck silica gel chromatoplates (0.2 mm) using CH_2Cl_2 and CH_2Cl_2–MeOH (97:3) as developing systems. We visualized terpenoids by spraying the chromatoplates with *p*-anysaldehyde/H_2SO_4 and heating at 105 °C. For flavonoids, we used natural product-polyethylene glycol reagent and visualized them at UV-365 nm (Wagner and Bladt 1996). Moreover, we fractionated part of the resinous exudate of *H. platylepis* (5 g) by column chromatography (CC) over silica gel, using CH_2Cl_2 with gradually increasing concentrations of MeOH. We monitored the fractions via TLC on silica gel using CH_2Cl_2:MeOH (95:5) to obtain the crude compounds. For the final purification with CH_2Cl_2:MeOH (97:3), we used preparative TLC (PTLC) on pre-coated silica gel plates (60 F254, Merck, 1.0 mm thick, 20 × 20 cm).

Insect visitors

To study the different arthropods associated with natural populations of *H. platylepis* capitula, we collected all animals caught on bracteal resin and also made observations on the arthropods visiting flower heads in the field. In the first case, we inspected one involucral bract from different plants (*n* = 242) and collected and preserved resin-trapped arthropods in ethanol (90 %). In the second case, we observed and quantified the insects visiting floral disks of *H. platylepis*, considering both those accessing this structure by walking up the inflorescence and those that reached the floral disk by flying and landing on it (Corsi

Table 1 Arthropod species identity detailed to the maximum taxonomic resolution possible

No.	Genus	Order	Family	FV	TR
1	*Lycosa* sp.	Araneae	Lycosidae	1	8
2	*Arthrobrachus nigromaculatus*	Coleoptera	Meliridae	0	158
2	*Arthrobrachus* sp. (small)	Coleoptera	Meliridae	5	180
3	*Hippodamia variegata*	Coleoptera	Coccinelidae	0	2
4	*Dioxyna chilensis*	Diptera	Tephritidae	58	52
5	*Geron* sp.	Diptera	Bombyliidae	56	0
6	*Calliphora* sp.	Diptera	Calliphoridae	22	0
7	*Drosophila* sp.	Diptera	Drosophiidae	3	0
8	*Uroleucon* sp.	Hemiptera	Aphidae	0	4
9	*Diadasia chilensis*	Hymenoptera	Apidae	898	0
10	*Apis mellifera*	Hymenoptera	Apidae	86	0
11	*Caenohalictus* sp.	Hymenoptera	Halictidae	10	0
12	*Chilicola vernalis*	Hymenoptera	Colletidae	70	1
13	*Megachile saulcyi*	Hymenoptera	Megachilidae	8	0
14	*Vespula germanica*	Hymenoptera	Vespidae	41	0
15	*Linepithema humile*	Hymenoptera	Formicidae	0	168
16	*Tatochila mercedis mercedis*	Lepidoptera	Pieridae	2	0
17	*Auca delessei*	Lepidoptera	Nymphalidae	4	0
18	*Proeulia* sp.	Lepidoptera	Tortricidae	14	4
19	*Lioptilodes friasi*	Lepidoptera	Pterophoridae	5	0
			Total	1,283	577

No. represents genera classification used (in bold letters). For 11 of these animals, we also provide species identity. "FV" correspond to Floral Visitors and "TR" means Trapped in Resin groups. The presence of each taxon in these groups is represented by crude amounts found in each survey

and Bottega 1999). After landing on the capitulum, these visitors spent most of the time collecting pollen and feeding on nectar from florets. We surveyed foraging visits from 10:00 to 17:00 at each site. In total, we completed 35 h of observations. Additionally, we collected two individuals of each arthropod species found during field observations for identification.

All specimens were identified with the aid of taxonomists and reference collections from the Entomology Institute at the Universidad Metropolitana de Ciencias de la Educación (UMCE, Santiago) and the Universidad de Tarapacá (Arica, Chile). Although we were able to identify more than half of all arthropods to the species level, all analyses were done at the genus level, since this was the finest taxonomic resolution common to all taxa (see Table 1).

We compared the proportional abundances of different arthropod genera using overall chi-square followed by a multiple proportion Scheffé post hoc test (Zar 1999). The groups compared corresponded to (1) "floral visitors", defined as all genera visiting florets of floral disks and (2) "trapped in resin", representing the genera found trapped in involucral bract resinous coating. We contrasted these two groups for the relative abundance of each genus of invertebrate identified, using a z-test for two proportions. Finally, we compared the similarity of these groups using the Jaccard similarity index (JSI) (Jaccard 1901). This index is based on the presence–absence relationship between the number of species in common in two communities and its relation to the total number of species recorded (Kent and Coker 1992). JSI is expressed as follows:

$$JSI = [a/(a + b + c)] * 100$$

where a is the number of genera common to both arthropod communities, b is the number of genera unique to one of the communities (in our case, "trapped in resin") and c is the number of genera unique to the other (in our case, "floral visitors"). The index is expressed as a percentage, which reflects the percent of similarity between the communities.

Results

Chemical compounds of the resinous exudate

We identified five compounds in the resinous exudates, belonging to two groups: ent-labdane diterpenoids and flavonoids. In the first group, we identified ent-8(17), 13-labdadien-15-oic acid (copalic acid) (1), *ent*-18 hydroxy-8(17),13-labdadien-15-oic acid (2) and *ent*-18 acetoxy-8(17),13-labdadien-15-oic acid (3). In the second, we identified the flavonols 5-hydroxy-3,7,3′,4′-tetrametoxyflavone
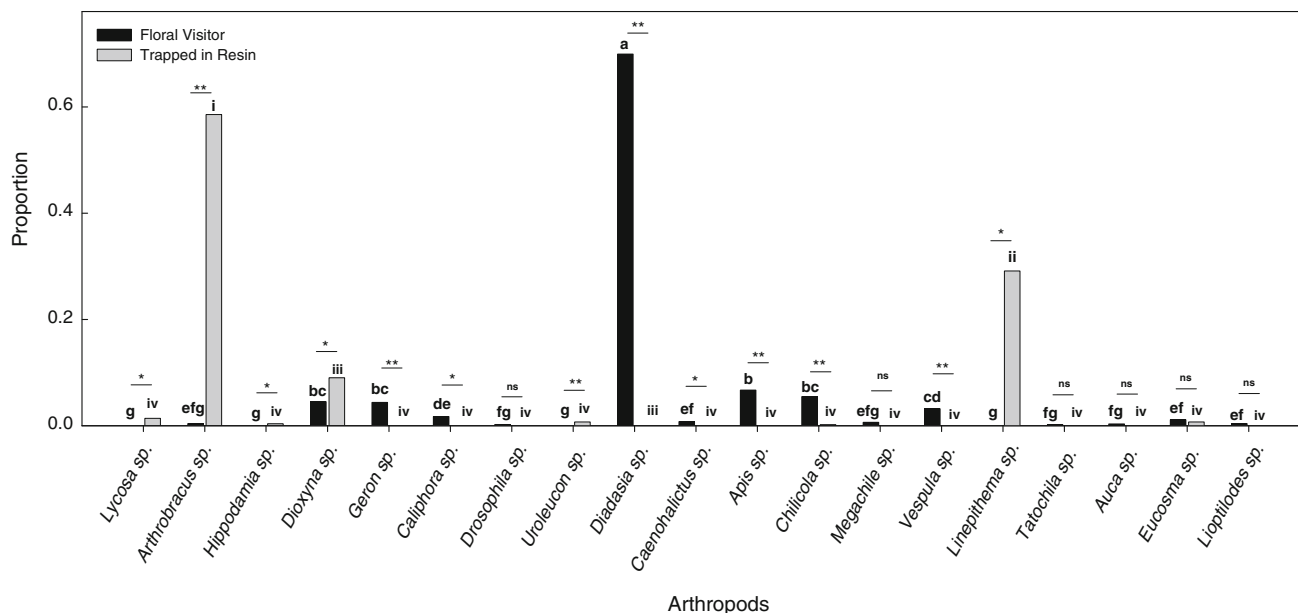
Fig. 2 Relative abundances of different arthropods found either as "floral visitors" (*solid bars*) or "trapped in the resin" (*gray bars*). The Y-axis represents the proportion of each kind in relation to the total individuals each group; the X-axis corresponds to different arthropod taxa found on floral heads. *Different letters* correspond to statistically significant differences at $p < 0.05$ within each group ("floral visitor" or "trapped in resin") obtained after overall chi-square followed by a multiple proportion comparison post hoc test. *Asterisks* represent statistical differences between groups based on a two-proportion z-test

(4) and 5,3′-dihydroxy-3,7,4′-trimethoxyflavone (ayanin) (5) (Fig. 1B).

Insects

Considering both "floral visitors" and "trapped in resin" surveys together, we found individuals belonging to 19 invertebrate genera; 18 of these were insects and one was a spider (see Table 1 for details). The Jaccard similarity index between "floral visitors" versus "trapped in resin" arthropod genera was 26.32 % ($n = 19$; $p = 0.05$). This percentage indicates a significant difference in species composition between these groups (following Real 1999).

We found statistically significant differences in the proportions of "floral visitors" genera ($\chi^2 = 10,976$, $N = 1,283$, $df = 18$; $p < 0.001$). *Diadasia* (Apididae) bees were by far the most frequent visitors (Fig. 2), corresponding to six times more frequent than visits by honey bees, which was the closest genus in proportion of visits (Scheffé post hoc test: diff = 41.7310; SE = 0.799; $q = 52.1873$; $p < 0.05$). The remaining inflorescence visitors were few individuals per genus (Fig. 2).

We also found statistically significant differences in the proportions for "trapped in resin" genera ($\chi^2 = 4,206$, $N = 577$, $df = 18$; $p < 0.001$). This group was predominantly composed of *Arthrobrachus* (Coleoptera: Melyridae) followed by *Linepithema* (Hymenoptera: Formicidae)

ants (Fig. 2). The number of beetles caught in resin doubled the number of ants found in the same survey (Scheffé post hoc test: diff = 17.252; SE = 1.192; $q = 14.472$; $p < 0.05$). The remaining genera were just few specimens we recovered from the bracteal glue (Fig. 2). Besides these genera, we seldom saw other insects stuck in the resin, outside our surveyed plants, such as *Epiclines gayi* (Coleoptera: Cleridae), small grasshoppers and two kinds of true bugs (Heteroptera: Lygaeidae). However, due to the small incidence of these insects, we can only consider their resin adherence as accidental.

Discussion

Based on our natural history observations, we found that "trapped in resin" group was not a random sample of the inflorescence-visiting arthropod community, but comprised a couple of recurrent genera: *Arthrobrachus* (Coleoptera: Melyridae) and *Linepithema* (Hymenoptera: Formicidae). In other cases of associations, researchers describe this ant to tend herbivorous insects such as homopterans in a mutualistic fashion, often with negative consequences for the host plant (Oliver et al. 2008); however, for *H. platylepis,* we did not observe such association. On the other hand, we documented a diverse group of insect genera visiting floral structures, which we never found entrapped in involucral bracts, mainly bees.

Regarding chemical composition of the resinous mixture, we identified several diterpenoids and flavonoids in the viscous mixture with known antibacterial and antimicotic properties. These compounds may also prevent dehydration of floral organs. All these results considered, we suggest that *H. platylepis* resin may correspond to an insectivorous trap for certain genera, such as ants and beetles, but may also accomplish other roles in relation to the plant's ecology.

On the multiple functions of bracteal resin

Resinous secretions are associated with multiple functions in the plant ecological context. Among the functions proposed for *Haplopappus* resins are resistance against water and temperature stress together with antiherbivory effects (Hoffmann et al. 1984; Urzúa et al. 2000; Urzúa 2004; Urzúa et al. 2004). Resin in *H. platylepis* may also function as a selective insect-trapping mechanism that may deter some plant visitors.

We found insects properly visiting involucral floral disks, most of them corresponding to bee genera (Table 1). These have been previously described as the main pollinators of *Haplopappus* (Urzúa et al. 2007; Klingenberg 2007).

Notwithstanding, the efficiency of such "floral visitors" as true pollen vectors remains to be determined (Waser 1996). Most insects we found being able to access floral heads (i.e., bees and butterflies) belonged to genera known to be good pollinators (Herrera 1989, 1990) and were rarely seen in the "trapped in resin" group. Meanwhile the main victims of sticky resin, ants and beetles, are usually reported as poor pollinators, among other reasons, due to their relatively short travel distance between food sources is considered (Kevan 1983). Thus, comparing all arthropod genera found, it seems that bracteal resin selectively traps insect genera with lesser pollen transfer potential. All possible reproductive consequences remain to be tested in future research.

Concerning the potential relationship between bracteal resin and not-trapped floral disk visitors, it is possible that certain characteristics of resinous coating may also help attracting visitors to floral heads by the shiny nature of these compounds as it has been proposed for other systems; moreover, resinous exudates may also secrete volatiles (not evaluated in this study) able to enhance floral head attractiveness to potential pollinators. Future experiments will cover these aspects of the interaction. Furthermore, in other plants, authors have found that resin itself may correspond to a reward for pollinators; for example, resin use for nest construction has been reported in several bee species, largely in the tropics (reviewed by Armbruster 1984). However, in our case study, we did not observe bees, or any arthropod, collecting resin from the calyx of *H. platylepis* floral heads.

In addition, plant sticky surface may play a role in the relationship of the plant with its herbivore's predators. Concerning this, the relationship could have different sings in terms of reproductive success. In some cases, sticky plant traps may enhance predator's attraction toward plant and promote its foraging on trapped herbivores (Krimmel and Pearse 2013). Contrastingly, other studies have reported that predatory insects are also affected by traps, and this resulted in a decrease of their predation rates due to a reduction in foraging efficiency and residence time on sticky plant species (Gassmann and Hare 2005). In our work, we rarely saw spiders trapped in resin and never walking over floral disk. Thus, its presence on *H. platylepis* seems incidental, rather than an ecological pattern.

Regarding other possible attributes for bracteal coating, recent studies have reported antibacterial properties. In fact, potential biomedical applications have been studied for several of the chemical compounds found in these exudates (Urzúa et al. 2012). For example bioassays with copalic acid demonstrated antichagasic, antibacterial and antitumor effects without cytotoxic consequences for humans (Ohsaki et al. 1994; Leandro et al. 2012). Furthermore, a derivative of ayanin, ayanin diacetate, is also considered as a selective anticancerigenous drug (Marrero et al. 2012). From the plant's point of view, the antifungal and antibacterial function of these chemicals may be related to the protection of developing seeds or even decelerate the decomposition of trapped insects (Wink 1988), protecting developing seeds from fungal degradation promoted by trapped dead insects and may even extend the availability of these carcasses for opportunistic predators to feed on.

Sticky insectivorous plants

As a final remark, we ask whether the presence of insect-trapping plant exudate in *H. platylepis* allows us to consider this species as a sticky carnivorous plant. Since early days, naturalists have suggested that plant species with surface viscous coatings may obtain additional nutrients from the degradation of the organisms that die trapped in these adhesive substances (Darwin 1875; Kerner 1878; Adlassnig et al. 2010). Several of these plants secrete proteolytic enzymes together with the viscid exudate, allowing faster degradation and the following uptake of corpse-derived nutrients. Other plants, such as many resinous species like *H. platylepis*, lack the proper enzymatic machinery and are considered "protocarnivorous" (Darnowski et al. 2006; Chase et al. 2009). However, some protocarnivorous plants are capable of obtaining nutrients from captured arthropods indirectly with the aid of

predatory insects able to walk on the sticky traps and feed on carcasses, fertilizing the plant with their feces. This phenomenon, known as "digestive mutualism" allows plants to absorb nitrogen from fecal fertilization thanks to cuticular gaps present in their leaves (Spomer 1999). For example, several Hemiptera species are capable of living in viscid traps from species that are not considered carnivorous plants (reviewed by Adlassnig et al. 2010). In other cases, such as the South African perennial shrub *Roridula gorgonias* and mirid bugs of the genus *Pameridea* (Hemiptera: Miridae), the association established is highly mutualistic (Ellis and Midgley 1996; Voigt and Gorb 2008a, b). Thus, in these situations, plants may be considered true carnivores. Additionally, considering the kind and frequency of prey captured, it is predicted that carnivorous plants with more sophisticated traps should be more selective and predictable than those species with less elaborated insect-trapping systems (Ellison and Gotelli 2009). Several insectivorous plants capture a diverse range of prey (Albert et al. 1992); however, for many specialized ones, the insects trapped are usually ants and flies (Ellison and Gotelli 2009; Adlassnig et al. 2010). In the case of *H. platylepis*, we demonstrated that the insects captured were not a random sample of the available insects visiting inflorescences. The main species we found dead in resin were beetles and ants, thus in terms of "prey specificity" this plant resembles a carnivorous species.

We do not have any evidence of enzymatic activity in *H. platylepis*' exudates nor have we further evidence of any resident insect feeding on trapped corpses and defecating over involucral bracts. Therefore, with the available information, we can only propose *H. platylepis* as a protocarnivorous plant (Aldenius et al. 1983). To the best of our knowledge, this is the first proposed protocarnivorous *Haplopappus* species. Future work will address additional ecological questions raised from this study.

To this point, *H. platylepis*' resin seems to be related with selective insect trapping together with previously reported antimicroorganism function for the chemical compounds we detected in the bracteal viscous mixture. As proposed by Armbruster (1996), multiple ecological functions of secondary floral metabolites may arise as exaptations (Gould and Vrba 1982). This idea is less popular than trade-offs among those who work on floral chemical ecology (but see Langenheim 2003); however, it is worth mentioning it as a possible explanation, capable of connecting multiple historical origins with extant ecological interactions on floral traits (Armbruster 1997; Armbruster et al. 1997, 2009). Comparative studies of chemical composition and insect communities, together with phylogeographical research would be desirable to determine the origins of the rare and profuse resinous exudation found in the involucral bracts of this plant species. In the case of the genus *Haplopappus*, mixtures of diterpenic acids in combination with small amounts of flavonoids have been previously documented in the resinous exudates of other species (Tojo et al. 1999; Urzúa 2004; Urzúa et al. 2006). Furthermore, among the flavonoids detected in *H. platylepis,* we found ayanin, which has been previously reported in *H. chrysanthemifolius*, a shrub found in sympatry with our study plant (Faini et al. 1999). In these other species, the resinous exudates are distributed evenly in vegetative and reproductive structures, and the ecological role proposed for these compounds are antimicroorganism and antidesiccation functions (McLaughlin and Hoffmann 1982; Urzúa et al. 2007). In the case of *H. platylepis*, these secretions are mainly concentrated over involucral bracts; thus, if this species may correspond to a derived group in *Haplopappus*, protocarnivory and antiherbivory may rise as exaptation over the initial antimicrobial function through the ecological history of plant–arthropod interactions in this lineage. To answer these questions, a phylogenetic approach is needed.

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