



The role of sterile apices of *Puya chilensis* (Bromeliaceae) on the nectar-feeding behavior of passeriform birds in central Chile

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ABSTRACT

The factors affecting the behavior of non-specialized nectar-feeding passerines have received little attention in the literature on plant-pollinator interactions. *Puya chilensis* (Bromeliaceae) has sterile branch apices that project outward from the inflorescence. In this study, we evaluate the functional role of sterile apices as support systems for bird foraging behavior. We recorded bird visitation and flower probing in the presence and absence of sterile branches during the spring seasons of 2021 and 2024. The results revealed that experimental plants with excised branches received fewer bird visits and flower probeings than control plants, indicating that sterile branches play an important role in the nectar-feeding behavior of passerine birds in *P. chilensis*.

1. Introduction

The concept of pollination syndrome refers to the combination of floral traits (e.g., color, phenology, morphology, scent, rewards, size) associated with attracting and utilizing a specific type of pollinator responsible for pollen transfer (Faegri and van der Pijl, 1979; Rosas-Guerrero et al., 2014). One of the most studied syndromes is ornithophily, primarily attributed to selection imposed by hummingbird pollinators on flower phenotypes (Ollerton, 2024). Generally, ornithophilous plants invest significant resources in producing abundant nectar, which serves as the primary reward for birds. Additionally, these plants tend to develop larger flowers that effectively accommodate bird foraging (Cronk and Ojeda, 2008). As diurnal animals, birds rely on vision as their main sensory modality while foraging (Ollerton, 2024), capable of perceiving colors, particularly those in the long-wavelength end of the visible light spectrum (Stiles, 1976). Thus, red-toned flowers are often perceived as attractive to birds, especially when the flower's wavelength contrasts with the surrounding vegetation (Schaefer and Ruxton, 2011). While these floral characteristics have been extensively studied, the concept of syndrome has been debated from various perspectives, leading to a more pluralistic view on the role of bird pollination in floral design evolution (e.g., Waser et al., 1996; Ollerton, 1998; Fenster et al., 2004). While the birds involved in the ornithophily syndrome may access flowers by perching or hovering, perching birds are supposed to have less specialized adaptations than

hovering birds to collect nectar. Perching birds rely mostly on structural features of plants, such as stems, pods, pendulous bracts, leaf stalks, adjacent branches, flower buds, and terminal inflorescences of plants for nectar-feeding. Most evidence for the perching strategy comes from studies carried out in the Old World. For example, sunbirds have been extensively described to employ diverse plant perches for their foraging activities (e.g., Gill and Wolf, 1978; Evans, 1996; Johnson, 1996; Ford and Johnson, 2008; Liu et al., 2013; van der Niet et al., 2015, but see Wester, 2014). This observation, together with the prevalent hovering foraging behavior shown by hummingbirds in the Neotropics, led to the generalization that hovering and perching characterize foraging in the New and Old World, respectively (see reviews in Padyšáková and Janeček, 2016; Ollerton, 2024). However, there is an increasing number of reports on bird hovering in the Old World (e.g., Geerts and Pauw, 2009; Janeček et al., 2011; Wester, 2013, 2014; Padyšáková and Janeček, 2016; van der Niet, 2024), and mixed pollination by hovering hummingbirds and perching passerines seems to be more common than previously thought in America (e.g., Cruden and Toledo, 1977; Sazima et al., 1993).

In Bromeliaceae species, hummingbirds have been reported as the most important pollinators (Canela and Sazima, 2005), with ca. 50–60% of bromeliads showing floral syndromes compatible with pollination by hummingbirds (Kessler et al., 2020). In Chile, the genus *Puya* (Bromeliaceae) consists of 11 taxa, divided into 4 species, 2 subspecies, 4 varieties, and 1 hybrid taxon, which highlights its diversity (Zizka et al.,

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2013). In this regard, a subgroup of *Puya* species belongs to the subgenus *Puya*, which is characterized by having a compound inflorescence with sterile branches that protrude in different directions from the main inflorescence axis. In addition to this morphological trait, species of this subgenus produce large volumes of highly dilute nectar, and are mainly pollinated by passerine species (Scogin and Freeman, 1984; González-Gómez et al., 2004; Hornung-Leoni et al., 2013). The remaining taxa belong to the subgenus *Puyopsis*, which, unlike *Puya*, lack sterile branches (Scogin and Freeman, 1984; Hornung-Leoni and Sosa, 2008; Schulte et al., 2010), produce smaller and more concentrated nectar volumes, and are pollinated mainly by hummingbirds (Hornung-Leoni et al., 2013).

Puya chilensis (subgenus *Puya*) inhabits ecosystems of northern and central Chile. Its single stem and inflorescence emerge conspicuously from the shrub cover, providing food and shelter for local fauna, including both vertebrates and invertebrates. During its flowering period, it produces a large volume of nectar that sustains various bird species, which, while feeding, accumulate pollen on their beak and heads. This observation led to the suggestion that the reproduction of *P. chilensis* depends on passerine pollination (Torres-Mura, 2006). The first observation for a potential role of the sterile branches in the inflorescence of *P. chilensis* dates back to 1898, when the German naturalist Federico Johow highlighted their potential as bird feeding platforms (Johow, 1910). Since then, *P. chilensis* has been cited, but not demonstrated, to provide perching opportunities for passerine birds (Westerkamp, 1990), and quantitative information is restricted to casual natural history observations. In this study, we examine whether the sterile apices of *P. chilensis* play a functional role in facilitating the foraging behavior of bird pollinators. More specifically, we address the following questions: (i) Do sterile apices of *P. chilensis* influence the attraction and arrival of avian pollinators to the inflorescence? (ii) How important are sterile apices for flower inspection and nectar-feeding by birds in *Puya chilensis*? To answer these questions, we set up a field experiment and recorded the identity, visitation, and nectar-feeding rate of birds in the Austral spring season of 2021 and 2024.

2. Materials and methods

2.1. Study site and field procedure

This study was carried out in a 0.016 ha plot located in a coastal site of the Coquimbo Region, Chile (32°01'55.0" S, 71°31'03.0" W). The study site belongs to the xeric-oceanic Mediterranean bioclimate zone characterized by a pronounced interannual variability in precipitation that can lead to prolonged drought periods, directly affecting the local vegetation (Di Castri and Hajek, 1976; Luebert and Plischoff, 2006; Armesto et al., 2007). The predominant vegetation is of a coastal Mediterranean desert scrub with *Bahia ambrosioides* (Asteraceae) and *Puya chilensis* (Boraginaceae) as the most representative species. The landscape also includes typical Mediterranean sclerophyllous species such as *Peumus boldus* (Monimiaceae), *Lithraea caustica* (Anacardiaceae), *Cryptocarya alba* (Lauraceae), and *Azara celastrina* (Salicaceae). The endangered shrub *Pouteria splendens* (Sapotaceae) is often found associated with coastal rocks in the complex landscape (Luebert and Plischoff, 2006), and cacti species delimit the terrestrial-intertidal interphase (e.g., *Eulychnia castanea*, *Echinopsis litoralis*, and *Eriosyce chilensis*).

In 2021, sampling was conducted on 37 plants (17 individuals with apices and 20 individuals without apices), while in 2024, 42 plants were included (20 individuals with apices and 22 individuals without apices), totaling 79 individuals (37 as part of the control group and 42 of the experimental group). The plants included in this study were those feasible to be studied and quantified, avoiding damage to the vegetation surrounding *P. chilensis* and minimizing general disturbance to the natural system. Once mapped, the chosen plants were randomly assigned to control or experimental categories. In general, plants tended to show spatial distributions more aggregated than expected by a

random process, probably reflecting underlying conditions for recruitment and growth (Fig. 1).

To examine whether sterile apices influence bird visitation and feeding rate (i.e., flower probings) at inflorescences, all the sterile branches of experimental plants were removed using pruning shears (see Fig. 2A and B). Regarding bird observations, we considered a bird visitation when birds landed on any part of the plant inflorescence. Repeated visits by the same bird after leaving a plant were defined as independent recordings. A flower probing was considered when birds introduced their head into flowers. When the same bird probed multiple flowers during a visit, each probing was recorded in order to subsequently estimate the species' feeding rate.

Data were collected in the spring austral season, during five consecutive days in October 2021, and nine days in October 2024. Observations were performed with 10 × 42 binoculars by five observers with prior field experience and expertise in bird identification. The observers were located ca. 10 m from the plant, from 8:00 to 19:00, and always on sunny days. In the first sampling season, the total observation time per plant was 180 min, totaling 6660 min (111 h). Three plants had to be excluded from analyses in 2021. In 2024, the average observation time per spike was 393 min, totaling 16,500 min (275 h).

2.2. Statistical analyses

To evaluate the overall effect of sterile branch removal on bird visitation rate and feeding rate, we assessed the fit of mixed-effects GLM models with Gaussian distribution and identity link function, using treatment as a fixed effect and year as a random effect. Total flower number in inflorescence was included in rate estimates to avoid potential confounding effects associated with variation in the availability of flowers. In this way, bird visitation and feeding rate (flowers probed at inflorescences) were estimated on a per-flower basis. Because the identity of the species accounting for most of the visits and flower probings changed between 2021 and 2024 (Fig. 3), we examined the extent of variation in bird behaviour between years. To this end, we performed separate one-way ANOVAs for 2021 and 2024. Likewise, an indirect measure of foraging efficiency per species was calculated by dividing the number of flowers probed per visit. All analyses were conducted in R v.4.1.1 (R Core Team, 2025).

3. Results

3.1. Interannual variation in overall bird visitation to *Puya chilensis*

During 2021 and 2024, a total of 485 bird visits to *P. chilensis* individuals were recorded. Of these, 66.4% ($n = 322$) occurred in 2021, while only 163 visits (33.6%) were observed in 2024. This difference resulted from a decrease in bird activity and probably from a shift in the composition of the pollinator assemblage. For instance, the White-crested Elaenia (*Elaenia albiceps*) and the Giant Hummingbird (*Patagona gigas*) were present during 2021 only (Fig. 3). There was also a turnover in the importance of visitor species across years. In 2021, the most frequent species visiting plants were the Grey-hooded Sierra Finch (*Phrygilus gayi*, 56.8% of visits), followed by the Austral Blackbird (*Curaeus curaeus*, 11.8% of visits) and the Diuca Finch (*Diuca diuca*, 10.9% of visits). In contrast, during 2024, the most common species were the Rufous-collared Sparrow (*Zonotrichia capensis*) and the Diuca (*Diuca diuca*), which accounted for 41.7% and 26.4% of visits, respectively (Fig. 3). Although the total number of visits in 2021 was three-fold higher than in 2024, some species increased substantially in their visits during 2024. For example, while *Z. capensis* had a low representation in 2021, it was the main visitor in 2024. On the contrary, *P. gayi*, a species that dominated the visits in 2021, was almost absent in 2024 (Fig. 3), indicating that the composition of the species assemblage visiting *P. chilensis* was variable across years.

Regarding visits to plants, most species visited inflorescences with

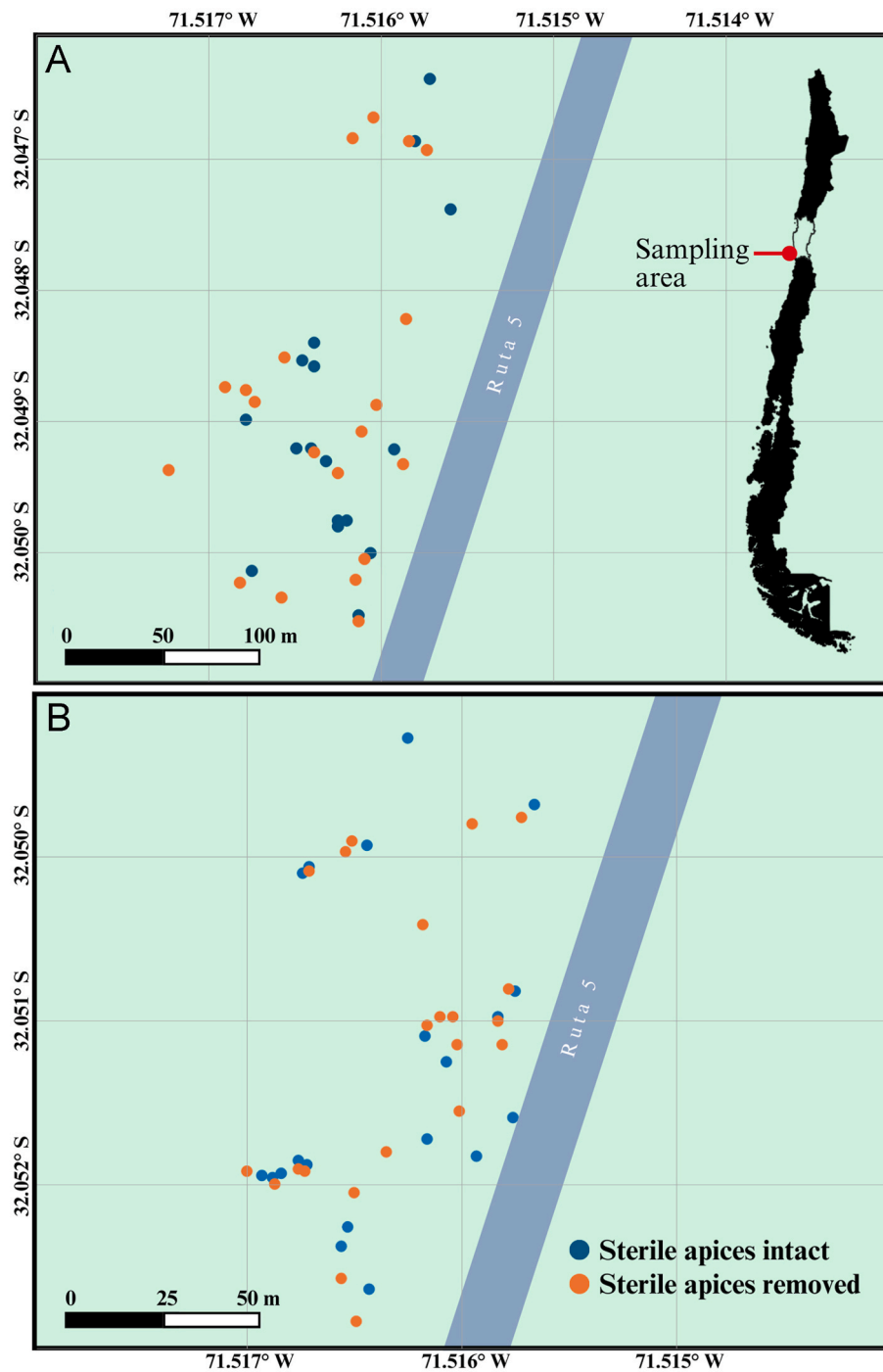


Fig. 1. Maps illustrating the spatial distribution of control (blue dots) and experimental (orange dots) plants in the study site during 2021 and 2024. The spatial distribution of control and experimental plants was examined separately using Ripley's K function and subsequent tests for complete spatial randomness (CSR) using 99 random simulations. In the four situations here examined, the observed K -values lay above random expectations, albeit within point-wise envelopes in most distances (see Baddeley et al., 2014), suggesting that the observed plant distributions are more aggregated than expected by a random process. (A) In 2021, control plants had a spatial pattern within the limit of CSR ($P = 0.05$), with a maximum deviation found at a 29.7-m radius. In contrast, plants in the experimental group did not differ from randomness ($P = 0.22$). (B) In 2024, control plants differed from CSR expectations ($P = 0.03$), with a maximum deviation found at 17.9 m radius. Experimental plants did not differ from random expectations ($P = 0.01$), with a maximum deviation occurring at a 29-m radius.

sterile apices intact (control) than inflorescences with apices removed (experimental). An interesting exception was *P. gayi* and *Turdus falcklandii* in 2021 and 2024, respectively, as they were the only species that made more visits to plants in the treatment group. On the other hand, when analyzing the number of flowers probed during visits, a preference for inflorescences in the control group was also evident (Fig. 3). In total, 1446 probed flowers were recorded in 2021, of which 841 (58.2%)

corresponded to the control group and 605 (41.8%) to the treatment group. In 2024, the difference was even more pronounced. From a total of 185 flowers probed, 154 (83.2%) corresponded to the control group and only 31 (16.8%) to the treatment group.

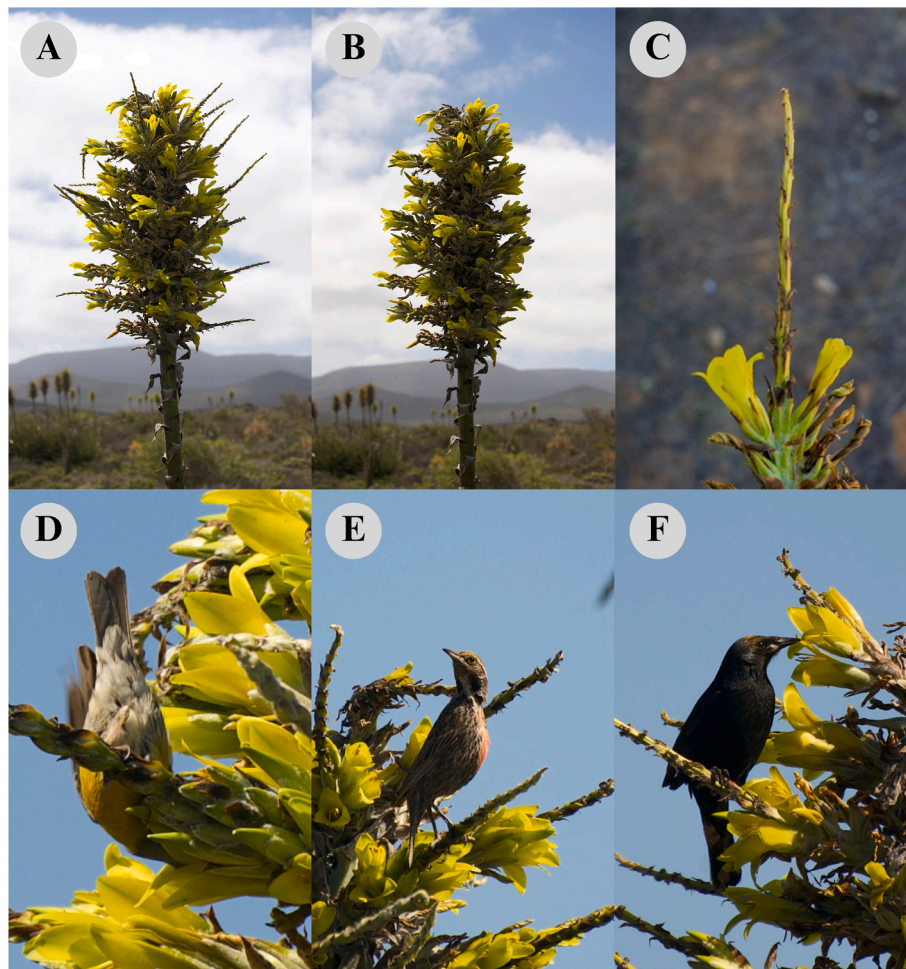


Fig. 2. Pictures showing plants before (A) and after (B) the experimental removal of sterile apices of *P. chilensis*. (C) Detail of a sterile branch. (D–F) Passerine birds perched on sterile apices: (D) *Phrygilus gayi* (Grey-hooded Sierra Finch), (E) *Leistes loyca* (Long-tailed Meadowlark), and (F) *Curaeus curaeus* (Austral Blackbird).

3.2. Effects of sterile apex removal on visitation rate, feeding rate, and foraging efficiency

GLM effects revealed that birds tended to visit plants with excised branches at a lower rate than control plants (estimate = -0.58 , SE = 0.32 , $P = 0.070$). Likewise, the feeding rate was lower in experimental than control plants (estimate = -3.52 , SE = 1.63 , $P = 0.030$), indicating that branch removal influenced the two parameters of bird behavior studied here. More detailed analyses on a per-year basis revealed that plants did not differ in the number of visits received in 2021 ($F_{1,35} = 1.14$, $P = 0.292$), but control plants received a significantly higher visitation rate than experimental plants in 2024 ($F_{1,40} = 0.61$, $P = 0.006$) (Fig. 4A). Regarding feeding rate, birds tended to forage less on experimental than control plants in 2021 ($F_{1,35} = 3.70$, $P = 0.063$), and this effect was amplified in 2024 ($F_{1,40} = 7.46$, $P = 0.009$) (Fig. 4B), confirming that birds reduced their visits and feeding rate in the absence of sterile branches in comparison to control plants. These effects translated into an overall reduction in the efficiency of birds at foraging (Fig. 5). Except for *L. loyca* in 2021 and *D. diuca* in 2024, all species reduced the number of flowers probed by visit in experimental plants in comparison to controls, which suggests that sterile branches play an important role in the economy of foraging.

4. Discussion

4.1. The role of sterile apices as support systems

Our results indicate that the experimental removal of sterile apices in *P. chilensis* led to an overall reduction in bird visitation and feeding rates in comparison to control plants. This effect was more pronounced in 2024 than in 2021, probably due to variation in the pollinator bird assemblage, as species differed in their responses to perch removal. In the experimental plants, birds primarily perched on the tip of the inflorescence while feeding on the uppermost flowers, and spent more time and energy finding and maintaining a stable position to access the nectar through the floral entrance. This behaviour contrasts with that observed in control plants, where the sterile apices provided physical support that enabled birds to obtain a broader visual perspective and jump from one perch to another in the inflorescence, reaching multiple flowers without having to constantly reposition their feet (Pyke, 1981), thereby granting them greater flexibility during the feeding process (van der Niet, 2024). Unlike flowers borne on flexible stems that tend to bend or break under the weight of a bird (Paton and Ford, 1977), the rigid architecture of sterile branches (Fig. 2C) allows larger and heavier birds to access the floral resources effectively. In the *Puya*–bird system studied here, the structural support provided by sterile apices appeared to be highly effective, as suggested by the low number of broken apices. A visual inspection of 1065 apices in 35 plants revealed only 72 broken structures, corresponding to 6.8% of the total. This low percentage suggests that apices are sufficiently rigid to support the weight of *C.*

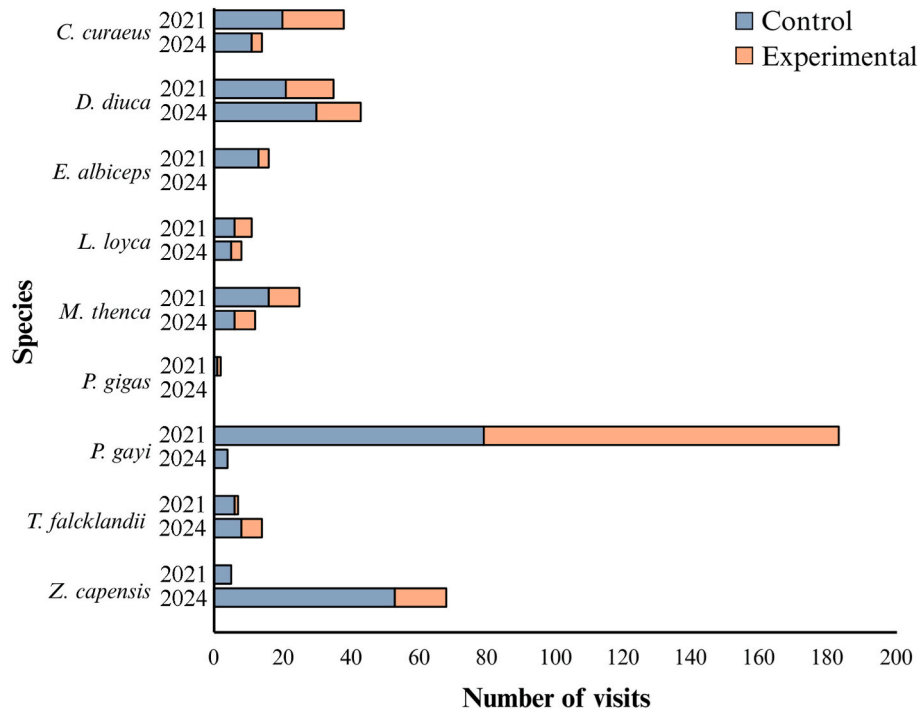


Fig. 3. Number of bird visits to control and experimental plants by species and year. Blue bars indicate visits to control plants (with sterile apices intact), and orange bars are visits to experimental plants (with sterile apices excised).

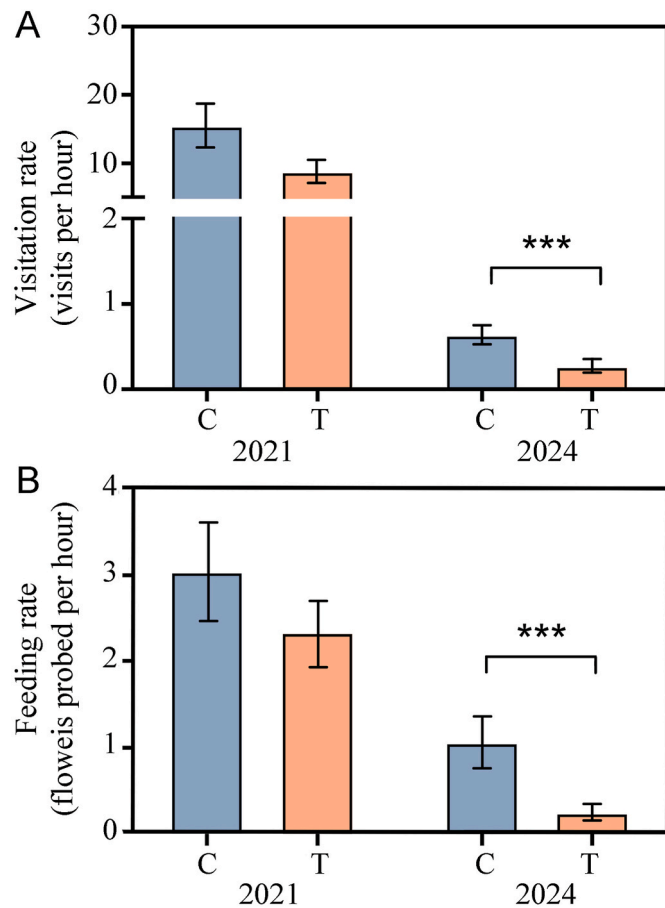


Fig. 4. Within-year contrasts of bird behavior between control (C) and experimental plants (T). Values for visitation rate (A) and feeding rate (B) were standardized by the number of flowers opened at each inflorescence.

curaeus (110 g), *M. thenca* (77 g), and *T. falcklandii* (100 g), the heaviest nectar-feeding passeriform species present in the local assemblage. This pattern of structural adaptation has also been documented in other ornithophilous plant species. For instance, in the genus *Erica*, bird-pollinated species have thicker stems than species pollinated by insects or wind (Siegfried et al., 1985). Similar adaptations have been reported in the Iridaceae family (Goldblatt and Manning, 2006) and in the genus *Satyrium* (Orchidaceae; Johnson, 1996), where robust stem structures facilitate bird perching.

The functional role played by sterile apices in *P. chilensis* raises the question of the distribution and function of apices in other *Puya* species. In this regard, two hypotheses have been proposed. The first one states that sterile apices are currently under passerine-mediated selection concerning their current role as support systems. This hypothesis can be traced back to the seminal field observations performed by Johow (1910). Our results provide partial support for Johow's hypothesis as plants with apices removed were much less visited and flowers less probed than control plants. More study is needed to confirm that apices promote bird pollination and influence plant reproductive success. The second hypothesis states that sterile apices in *Puya* evolved once in an ancestral species and became retained in a subset of species (the subgenus *Puya*), being lost multiple times along evolutionary history (Jabaily and Sytsma, 2010). The absence of sterile apices in species of the subgenus *Puyopsis* relates to the more prevalent hummingbird visitation at present, suggesting that the architectural modification of inflorescences was accompanied by a concomitant change in the identity of bird visitors. Indeed, among the recorded visitors to *P. chilensis*, the giant hummingbird *P. gigas*, a specialized nectarivore species, had a negligible importance in comparison to passeriform species (see Figs. 3 and 5A). The observation that non-specialized nectar-feeding passeriform species account for most visits in *P. chilensis* is consistent with assertions that the historical relationship between birds and flowers may involve not only specialized bird species, such as hummingbirds, sunbirds, and honeycreepers, but also more generalist passeriforms that lack of specialized traits for nectar consumption (Ollerton, 2024).

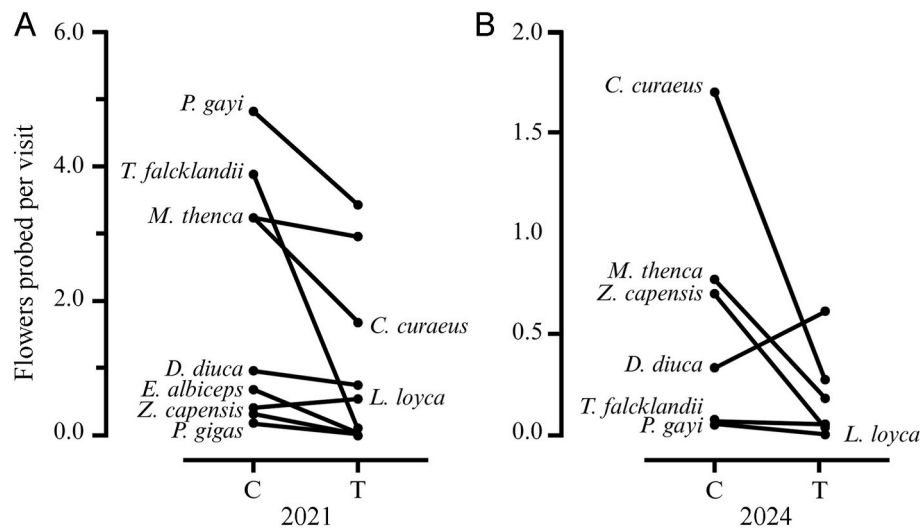


Fig. 5. Pattern of change in bird foraging efficiency (number of flowers probed by visit) in the presence (C) and absence (T) of sterile apices in 2021 (A) and 2024 (B). For clarity, only the mean values per species are shown per category.

4.2. The temporal variation in the bird assemblage

Temporal shifts in the composition of pollinator bird assemblages have been documented extensively in the Neotropics (e.g., Waser, 1979; Pyke, 1988; Vaughton, 1990, 1992; Fenster and Dudash, 2001; Price et al., 2005). However, this information is almost entirely restricted to hummingbird assemblages, and data on passeriform generalist pollinators remain scarce (Zych et al., 2019). In this study, the preference shown by passerine birds for plants with intact sterile apices was stronger in 2024 than in 2021. It is interesting to note that the year 2021 was the second driest on record in continental Chile since 1961, with 64.8 mm precipitation near the study site, which represented a 43% deficit concerning normal conditions. This stringent environmental condition may have imposed birds an urgency to access the nectar to hydrate and meet nutritional demands, turning birds less selective and at the same time more efficient at feeding on plants (1.97 and 1.05 flowers probed per visit on the average in control and experimental plants, respectively; Fig. 5), using indistinctly plants with apices removed or intact. In contrast, the year 2024 was characterized by abundant rainfall in the study site (207.8 mm), and the precipitation level remained within normal limits. Under these conditions, passeriform birds would not experience the same physiological stress than in dry years, choosing plants with sterile apices intact, that ensure a low energetic cost while collecting nectar, and relaxing the demand to be an efficient nectar consumer (0.57 and 0.17 flowers probed per visit on the average in control and experimental plants, respectively; Fig. 5). If this interpretation is correct, the usage of structural features of plants by passeriform birds may be contingent on climate characteristics, being a behavior that is mainly expressed during favorable years when desiccation does not imply a severe risk for survival.

4.3. Limitations and projections of this study

Previous studies on the feeding strategies in birds indicate that the preference shown for some perches and not others depends on several factors, such as season and the stage of the reproductive cycle (Morrison, 1980), the sex involved, as males and females may exhibit different preferences when feeding on nectar (Austin, 1976), and the nature of the perch involved (Anderson et al., 2005). This variability highlights the importance of considering a broader range of ecological and behavioral variables in future research. Since this study was carried out in a single site during a limited number of days each year, studies that increase the number of sampled populations across spatial contexts may help to

elucidate the mechanisms shaping the dynamics of *P. chilensis*–Passeriform bird interactions. Furthermore, increasing the temporal scale of sampling will permit tracking the change in climatic conditions, variation in resource availability, and the way passeriform birds contribute to plant reproductive success in changing environments. In this regard, several questions arise, for example: What is the ultimate impact of sterile apices on seed production in *P. chilensis*? Does the presence of sterile apices favor cross-pollination and offspring genetic variability? Are sterile apices evolving under passeriform-mediated selection? Although the present study represents the first quantitative approach aimed at examining the functional role and relevance of sterile apices in the system, future research will help to understand further details and the ecological and evolutionary consequences of this passeriform-plant interaction in central Chile.

CRediT authorship contribution statement

Natalia Ugas-Bravo: Writing – review & editing, Writing – original draft, Validation, Software, Investigation, Data curation. **Pilar Guerrero:** Investigation, Data curation. **Rodrigo Medel:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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