Potential effects of artificial feeders on hummingbirds-plant interactions: are generalizations yet possible?

Efectos potenciales de los bebederos artificiales en la interacción colibrí-planta: ¿es posible hacer generalizaciones?

María Angela Echeverry-Galvis [1*], Nicolás Téllez-Colmenares [2], Laura Ramírez-Uribe [3], Juan Sebastián Cortes-Cano [1], Felipe A. Estela [3] & Alejandro Rico-Guevara [2,4]

[1]Departamento de Ecología y Territorio, Pontificia Universidad Javeriana. Bogotá, Colombia
[2]Centro de investigación Colibrí Gorriazul. Fusagasugá, Colombia
[3]Facultad de Ingeniería y Ciencias, Pontificia Universidad Javeriana. Cali, Colombia
[4]Department of Biology, University of Washington. Seattle, WA, Estados Unidos

* ma.echeverryg@javeriana.edu.co

DOI: 10.59517/oc.e576

Recibido
31 de julio de 2022
Aceptado
27 de enero de 2024
Publicado
22 de febrero de 2024

ISSN 1794-0915

Citación
Echeverry-Galvis, M.A., N. Téllez-Colmenares, L. Ramírez-Uribe, J.S. Cortés-Cano, F.A. Estela & A. Rico-Guevara. 2024. Potential effects of artificial feeders on hummingbirds-plant interactions: are generalizations yet possible?. Ornitología Colombiana 25:2-18 https://doi.org/10.59517/oc.e576

Abstract

Human influence on ecosystems and species interactions has frequently been observed by ornithologists. This is most evident where food is provided to wildlife, such as around hummingbird feeders. This artificial contribution of resources raises questions about its impact on aspects like pollination, floral visits, and movement within and among landscapes. Through a systematic literature review, we compiled hypothetical changes and effects that the presence of artificial feeders could have on pollinator-plant relationships. We found 26 articles discussing the role of feeders in plant-animal interaction dynamics, categorizing potential impacts as positive, negative, or neutral (no impact). We found that scientific output on this topic is limited, and that determining clear impacts of feeders was challenging. Several researchers also note that feeder effects and interactions in plant-pollinator relationships could be species-specific, rendering generalizations inappropriate. We conclude that the supporting literature is insufficient and inconclusive, underscoring the need for rigorous studies to assess how feeders might influence reproductive biology, hummingbird spatial distribution, and ecosystem processes modification. Additionally, we performed a systematic Google® search to identify widely disseminated pages that provide the information that ultimately reaches the general public and thus becomes the accepted common knowledge. From the first 40 pages on this topic, we examined the sources used to support the information, revealing a dearth of verifiable sources such as scientific papers. We deem it essential to advocate that the dissemination of public domain information regarding the use of feeders should be substantiated by concrete ornithological studies.

Key words: Food supplementation, hummingbird feeders, mutualisms, plant-animal relation, pollination

Resumen

La influencia humana en los ecosistemas y las interacciones entre especies han sido observadas en variados estudios ornitológicos. Este fenómeno es evidente en áreas donde se proveen alimentos a diferentes comunidades de fauna, como en los comederos de colibríes. Esta suplementación artificial de recursos plantea preguntas sobre su impacto en aspectos como la polinización, visitas florales y movilidad de los colibríes. A partir de una revisión sistemática de literatura se realizó la identificación de los posibles cambios y/o efectos que la presencia de bebederos artificiales podría tener sobre la relación polinizador-planta. Se identificaron 26 artículos que mencionan temas sobre bebederos y su rol en la interacción planta-animal, catalogando los posibles impactos como positivos, negativos o neutros (sin impacto). Se encontró una baja producción científica sobre el tema, donde no fue posible determinar si hay un impacto claro a causa de los bebederos. Adicionalmente, varios investigadores afirman que algunos de los efectos e interacciones de los bebederos en la relación planta-animal podrían estar asociados a un efecto especie-específico, por lo que las generalizaciones son inadecuadas. La literatura de soporte es insuficiente y no concluyente, resaltando la necesidad de estudios rigurosos para evaluar cómo los comederos pueden afectar la biología reproductiva, la distribución espacial y los procesos ecosistémicos de los colibríes a diferentes escalas y aspectos como la biología reproductiva, la distribución espacial de los colibríes y sobre la modificación de procesos ecosistémicos. Complementariamente, se hizo una búsqueda por Google® para identificar páginas de difusión masiva que den información al público en general; de los resultados se tomaron las 40 primeras páginas y sobre ellas se indagó con relación a las fuentes que sustentaban la información planteada, encontrando un vacío de fuentes verificables, como artículos científicos. Consideramos fundamental impulsar la idea de que la divulgación de información de dominio público debe de ser en mayor medida sustentada por datos y estudios ornitológicos concretos.

Palabras clave: relación planta-animal, polinización, suplementación de alimento, mutualismo, bebederos

Introduction

The mutualistic relationships between hummingbirds and flowers are fundamental for both success and survival, while also providing ecosystem services such as crop pollination (Bascompte 2009, Losapio *et al.* 2021). Anthropogenic modifications of ecosystems are a central factor affecting biodiversity and the interactions between species, such as mutualistic interactions. The continuous processes of urbanization, deforestation, and agricultural expansion have been particularly significant in changing natural communities, both in their composition and distribution (Loreau *et al.* 2022), effects that will be exacerbated due to climate change (Velásquez *et al.* 2013). However, over the past decades there has been a noticeable increase in positive attitudes toward nature within human societies. For example, more people have moved into rural areas, and outdoor activities such as nature-based tourism and birdwatching (Kellert 1985, Horn & Johansen 2013, Jaung & Carrasco 2022, Vimal 2022) have been increasingly emphasized for their positive impact on human health and well-being (Kim *et al.* 1997, White *et al.* 2019). Consequently, the popularity of birdwatching and bird photography has soared, with their success heavily relying on attracting and interacting with wildlife (*e.g.*, Kellert 1985, Sekercioglu 2002, Glowinski 2008, Jones 2011), often using supplementary feeding (Goddard *et al.* 2013, Baicichi *et al.* 2015). Feeders allow closer observation of species that otherwise will be difficult to find or photograph, such as hummingbirds, facilitating nature tourism (Keniger *et al.* 2013). However, to date there is a lot of debate as to what is the ecological role of this supplemented food supply.

Luring wildlife is achieved through various types of attractors, such as seeds, fruits, and artificial nectar (Prescott *et al.* 2000, Sonne *et al.* 2016). Feeders may mitigate mortality caused by temporal resource scarcity, and their presence could enhance reproductive success (Robb *et al.* 2008), as well as alter reproductive temporal patterns by extending breeding seasons due to the enhanced availability of food sources (Schoech & Hahn 2007). Given the decline of bird populations worldwide for various species, feeders may increase the number of individuals, as long as the high availability of supplemental food remains constant (Sherman 1913, Wilson 2001, Wethington & Russell 2003).

Considering these advantages, besides research, it is estimated that a third of households in Europe, and a fifth in North America and Australia, have bird seed feeders (Fuller *et al.* 2008). The economic investment in feeders and wild bird food is substantial, in the United States alone, more than five billion dollars were spent on bird food in 2011 (U.S. Fish and Wildlife Service, & U.S. Census Bureau 2018). Determining the precise connection between the cost and the amount of supplemented food is difficult, however, Glue (2003) suggests that as of 2003, households in the United Kingdom provided more than 60,000 tons of seeds at feeders yearly (Glue 2003), with no national estimate regarding sugar use for nectar feeders.

One type of commonly used feeder provides artificial nectar for birds; these feeders come in a variety of shapes and arrangements, offering food for various birds such as tanagers, orioles, and other songbirds, as well as woodpeckers in the Americas (*e.g.*, Teixeira *et al.* 2012) and for hummingbirds and other avian nectarivores (Hewes *et al.* 2022, Rico-Guevara pers. obs.). Additionally, insects, mainly Apidae, and bats (Chiroptera) have been observed visiting artificial nectar feeders (Rico-Guevara pers. obs., Maguiña & Muchhala 2017). While hummingbird feeders have gained popularity (Sonne *et al.* 2016), research on their potential long-term effects on bird ecology at different scales, from individuals to populations and communities, remains limited (Jones 2011). To date, the effects of food supplementation remain understudied globally, with limited experimental research on tropical species (Scheuerlein & Gwinner 2002, Class & Moore 2013). Artificial feeders have been extensively used as research tools across various disciplines from behavior and ecology (Brodin & Clark 2008, Robb *et al.* 2008, Jones 2011), to biomechanics and fluid dynamics (*e.g.*, Stromberg & Johnsen 1990, Ballantyne *et al.* 2011, Rico-Guevara *et al.* 2019).

Hummingbird feeders have arisen concerns about health and sanitation due to multiple individuals visiting the same feeding point, potentially increasing infection rates by fungi and bacteria (Galbraith *et al.* 2017). One persistent myth is that feeders could promote diabetes in birds, but this has been falsified (Chen & Welch 2014). Despite these concerns, one aspect attracting most attention is the potential impact of feeders on the mutualistic plant-animal relationships between avian nectarivores and the plants they visit, where the birds obtain nectar, an energetically-rich and predictably-replenishable resource, while the adjacent plants might encounter enhanced or reduced pollination services (Stiles 1978, Stiles 1981, Rico-Guevara *et al.* 2021). On the other hand, feeders might offer energetic advantages as hummingbirds can avoid costly hovering, might have access to more nectar than what they can drink in one meal, and extract the liquid more rapidly leading to faster licking rates (Ewald & Williams 1982, Rico-Guevara *et al.* 2015), thus decreasing the handling time in obtaining a given amount of energetic reward (Gass & Roberts 1992). True (1995) estimated a nectar intake equivalent to making 2000 - 5000 floral visits per day when visiting a single feeder in the northern United States. However, this statement lacks other ecological and biological variables and information, such as the number of visits per individual, intake rate per visit, flower-beak match, species-specific interactions, sugar concentration and volume of floral rewards, and foraging strategy, among others. Unlike feeders, the bill-corolla fit at flowers determines the bill tip-nectar surface distance, which may increase as the nectar chamber depletes deep inside the corolla (Rico-Guevara *et al.* 2021). Additionally, visiting various floral resources scattered in the landscape demands time and energy in searching and traveling (Tello-Ramos *et al.* 2019, Sargent *et al.* 2021). Conversely, feeders are fixed, usually reliable, resources that are commonly clumped together (McCaffrey & Wethington 2008). The time and energy savings associated with feeders could allow increased investment in breeding activities, for example courtship; some hummingbirds perform displays in proximity to artificial feeders (Rico-Guevara *et al.* 2022).

Several important aspects of the effects of supplemental feeding remain little explored: (1) is it a low-cost resource, could it endow hummingbirds with more energy for reproduction and recruitment of new individuals to the local population –a cross-generational effect–, (2) if the local abundance of hummingbirds increases due to feeders, individuals that cannot actively feed on them would seek resources close by wildflowers and thus enhance pollination rates of nearby plants–as a spillover effect–, (3) if hummingbirds visit feeders much more than the plants in the surrounding areas, pollination will be diminished –a short-distance effect, and (4) the possibility of distorting migration patterns (latitudinal, altitudinal, among mountains, islands, etc.), where hummingbirds that would otherwise migrate, decide to stay in a place with feeders, breaking the temporal link with other possible hummingbird-pollinated plants in other parts of their geographic ranges –a long-distance effect.

The introduction of artificial feeders raises significant questions about potential interference with ecological and evolutionary processes, particularly flower visits and pollination. Without ignoring the unanswered questions regarding the kind of impacts feeders could have, our literature review focused on studies evaluating the second outlined effect in the previous paragraph, on the possible effects of feeders on plant-pollinator relationships at the community level for plants and hummingbirds. We aimed to evaluate if possible generalization can be made regarding the negative or positive impact of hummingbird feeders on the ecological role of pollination in the ecosystems, based on a literature survey, while contrasting the science-based information with community dissemination by open access internet resources.

Methods

We performed surveys on five search engines (Scopus, Web of Science, Scielo, Redalyc, and GoogleScholar) covering English, Spanish, and Portuguese literature. The entire databases of each search engine were utilized without time limitation, employing search equations in the three languages (Table 1). A total of 973 original publications were retrieved, encompassing the use of hummingbird feeders in diverse areas of knowledge, such as engineering (mimetics, aerodynamics, aviation), neurobiology (association experiments), cognition (mathematical processing in animals), and robotics (movement). Papers unrelated to the plant-pollinator interaction were excluded, along with taxonomic studies within the natural sciences (*e.g.*, capturing hummingbirds in feeders for sampling).

After the first filter, 209 references were left. A second filter looked for specific information in the abstract on hummingbird-plant relationships, pollination, hummingbird feeders, and metabolic information regarding hummingbirds and plants interactions, after which ten additional references were removed. Four researchers determined, independently, whether the manuscript contained information on hummingbird feeders concerning the plant-animal interactions, defining them as relevant or not to the scope of the review. In those cases where only one of the evaluators was in opposition to the other three, a majority decision was made (there were no instances in which two researchers were in favor and two against including a given article).

From this last filter, 60 references were chosen for a complete review. Out of them, 29 had generic information about food supplementation for birds (including the use of drinkers/waterers in other nectar-feeding species in locations such as Australia), and others were undergraduate thesis works that were removed from the dataset. This led to a final group of 26 references (Fig. 1) (Supplementary Table 1). Bibliometric data of each study (year, authors, journal, among others), country of research, ecosystem, or habitat (if not found in the manuscript, it was assigned based on Google Earth temporal images), and central question or objective of the work were determined, along with the duration and methods used. Lastly, the main results, conclusions, and recommendations were identified and tabulated.

Table 1. Search equations adjusted to the specifications of each search engine.

Search engine	Search equations	Results
WoS	ALL FIELDS: (hummingbird), Refined by: ALL FIELDS: (artificial). Timespan: All years. Indexes: SCI-EXPANDED, SSCI, A&HCI, ESCI.	165
Scopus	TITLE-ABS-KEY (hummingbird) AND (artificial)	297
GoogleScholar	Hummingbird AND feeder AND trop*	444
Scielo y Redalyc	Palabras claves: Bebederos artificiales AND Aves	67

Due to the limited sample size in the literature survey, we grouped research papers into six main topics based on their primary objectives: 1) natural history description, 2) landscape relationships, 3) biotic interactions, 4) diseases, 5) diet preferences (including works in which there is an evaluation of the presence or absence of feeders on pollen loads in hummingbirds), as well as research in which records of flower visits are considered in feeders vicinity, and 6) behavior. Following the classification, we recorded whether they referred to the feeders' effects as positive, negative or neutral.

Internet public information.- Aside from the literature search, an open search was carried out on Google®, using four-word combinations like those utilized in the literature search engines, with two combinations specifically focused on the plant-animal relationship ("hummingbird feeder effects", "Efectos bebederos colibríes", "Hummingbird feeders & plants" and "Comederos de colibríes y plantas"). The first ten results from each combination were selected, encompassing official and institutional pages, bird tourism companies, universities, regional authorities, specialized blogs in avifauna, or companies dealing with objects related to bird feeding items. From the 40 websites identified (Supplementary Table 2), only twelve provided relevant information on the influence of hummingbird feeders on plant-pollinator interactions. For these web pages, we evaluated

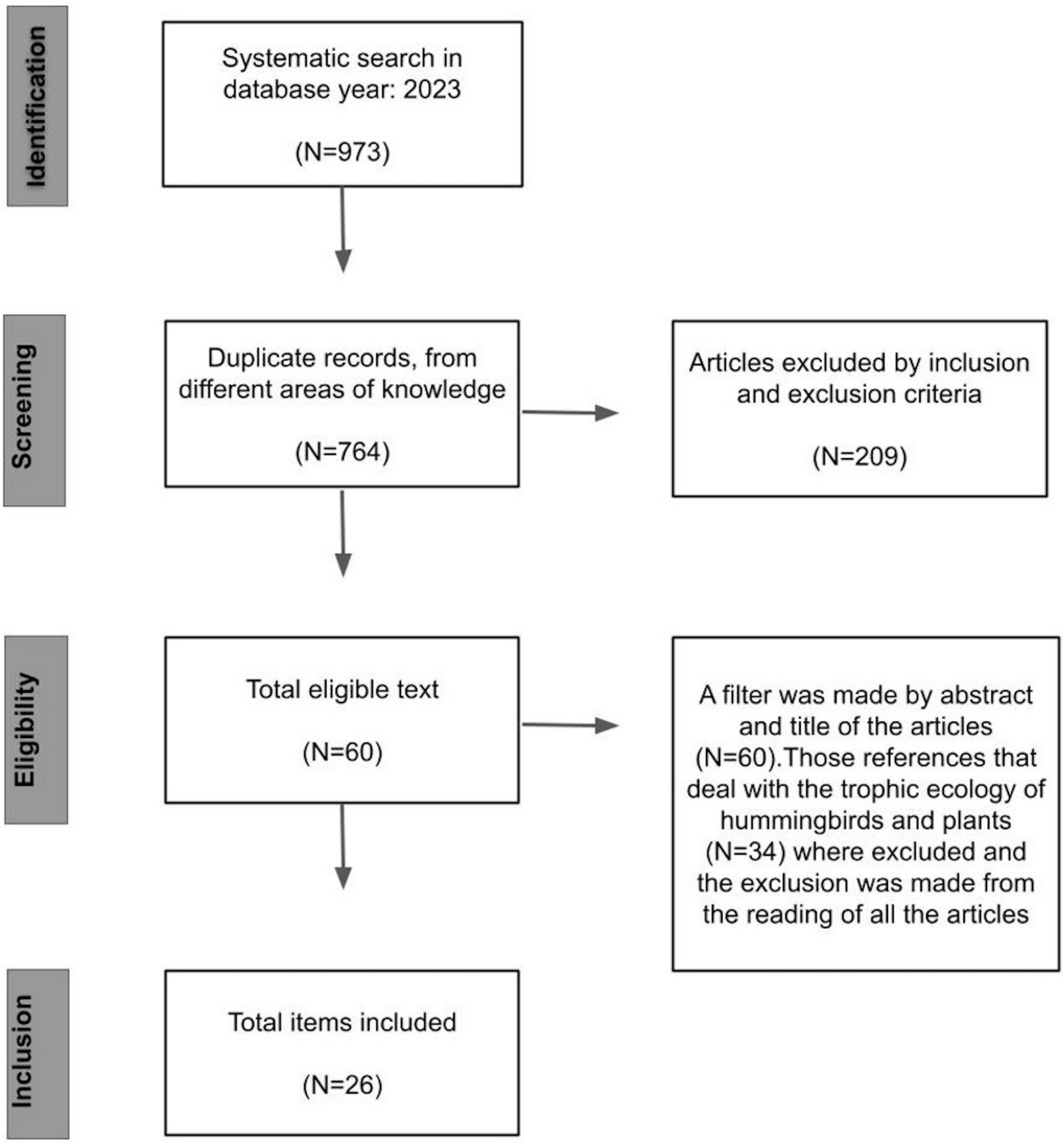

Figure 1. Process of systematic review for the inclusion and exclusion of references found in the literature survey based exclusively in the five search engines.

whether they depicted feeders as having a neutral, positive, or negative impact on the plant-animal relationship. The results from this Internet search were kept separate from those obtained from scientific databases. Similar to the grouping done for the scientific literature, the web pages were also classified into the same general categories.

Results and discussion

A small number of studies were found dealing with evaluating plant-animal relationships around feeders (Table 1, Supplementary Table 1). We find the low number of studies worldwide worrisome. Based on the proposed search equations, only 26 manuscripts were identified regarding the use of hummingbird feeders and their impacts on this mutualistic plant-animal relationship, which is surprising since feeders have been around for over a century (Sherman 1913). Additionally, there appears to be a general lack of awareness of this literature in sources of information available to the general public; among the first 40 web pages providing information on hummingbird-plant interactions and feeders on the Internet, only nine of them refer to scientific literature (Supplementary Table 2).

The results of our literature survey revealed that México and the United States had six research articles each. Brazil followed closely with four references, all published after 2012, exploring aspects beyond animal -plant interactions, including behavioral changes associated with feeders, conspecific displacement, and nectar preferences (Fig. 2). Questions regarding the use of feeders and their implications in ecological interactions are relatively recent, with the earliest study dating back to 1981, with annual increases in the last 20 years, without surpassing four studies published in 2008. In Colombia, studies were mostly done around Cundinamarca and Valle del Cauca, where the use of feeders appears to be more widespread and popular for attracting hummingbirds, either for aesthetic purposes or as sites for birdwatchers. We found one article encompassing all of the Americas, which investigated people's perceptions of the relationship between feeders and hummingbirds and their potential impact on pollination (Dunn & Tessaglia 1994).

Out of the 26 manuscripts reviewed, 11% represent accessible publications in languages other than English. Among these studies, 36% focus on interactions observed in tropical mountain forests, ranging from humid montane forests to areas adjacent to paramo, with examples in pine vegetation (Mexico) or oak forests (cloud forests). The next category comprises 24% of studies conducted in temperate forests, both in the northern and southern regions, while the remaining investigations pertain to diverse habitats such as dry forests, the Atlantic Forest, urban and peri-urban areas, or regions characterized by a mosaic of native vegetation and cultivated areas. Throughout these studies, a total of 89 hummingbird species and 91 plant species were examined, with the most extensive hummingbird community comprising 37 species (Schondube & Martinez Del Rio 2003).

Behavior and preferences.- Hummingbird aggressive behavior is evident at both flowers and feeders. However, relative to feeders offering nectar with the natural concentration of sugar in flowers, those presenting higher concentrations produce higher aggressive interaction rates and are visited by larger individuals (Lanna *et al.* 2017). The larger (heavier) the species, the greater the aggression at feeders, except for trapliner species such as *Phaetornis* spp., which are not identified as aggressive at the feeders or in natural nectar sources (Lanna *et al.* 2017, Téllez-Colmenares 2018). Among the examined studies, species exhibiting aggressive behaviors while feeding on flowers tend to display a minor increase in aggressive behavior at feeders (Lanna *et al.* 2017). On the other hand, species with little or no defensive or aggressive tendencies near flowers may or may not exhibit aggression at feeders. As a result, the aggressive behavior of territorial species observed in their natural habitat appears to be consistent with their behavior at artificial feeders (Lanna *et al.* 2017).

The use of feeders is closely linked to the feeding preferences of individual hummingbird species. The specific holes for drinking nectar within the feeder can influence access to specific species, favoring or limiting certain groups (Maglianesi *et al.* 2015, Rico-Guevara pers. obs.). Nectar concentrations ranging from 20-30% are generally preferred by most species within a hummingbird community (Blem *et al.* 2000, Tello-Ramos *et al.* 2019, Téllez-Colmenares & Rico-Guevara 2023), with some species capable of detecting variations within this range of approximately 1% (Blem *et al.* 2000). Additionally, hummingbirds can recognize feeders that provide a higher reward and exhibit fewer errors, utilizing visual recognition, including UV color combinations (Pyke 2016, Téllez-Colmenares 2018, Téllez-Colmenares & Rico-Guevara 2023). This has allowed preference experiments offering a selection of different concentrations and/or different locations, to detect if there are advanced learning spatial processes, recollection of visited resources, and how

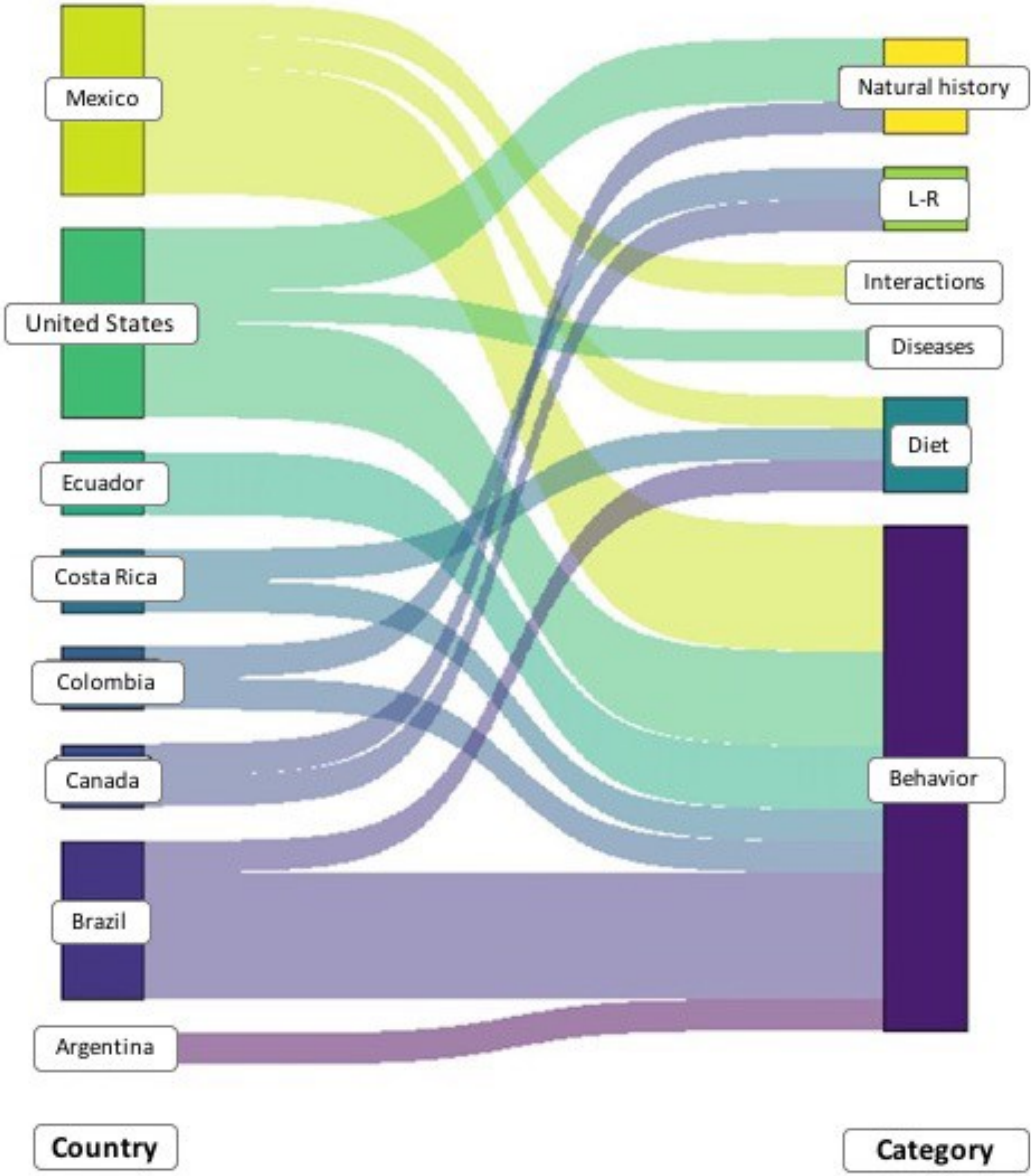

Figure 2. Relationship between the country of research (to the left) and the hummingbird topics divided in six categories (see methods section) (to the right) (L-R= Landscape-Relationship), discussed within 60 scientific papers, prior to the final exclusion filter.

this could modify flower visitation and pollination (*e.g.*, Blem *et al*. 2000, Sonne *et al.* 2016, Lanna *et al.* 2017).

Diversity and abundance.- The presence of feeders also induces shifts in the abundance of individuals at different spatial scales. Some studies have reported no significant correlation between bird abundance and the presence of feeders beyond 75 meters (Torres *et al*. 2008). However, in closer proximity to the feeders, there is a notable increase in the number of individuals (Torres *et al*. 2008). Sonne *et al*. (2016) observed a rise in hummingbird abundance up to 100 meters from the feeder location, but no discernible differences were detected in the birds' ability to function as pollen vectors, as indicated by the number of pollen grains in the loads of hummingbirds foraging in areas with or without feeders. It has been suggested that the increased presence of hummingbirds in the vicinity of feeders, within a 100 meter range, could lead to an augmented visitation rate to more plants, generating a "spillover" effect over local floral resources (Sonne *et al*. 2016). In a study by Avalos *et al*. (2012), out of 183 individual hummingbirds examined, more than 50% had either no or only a few pollen grains when visiting feeders. Nonetheless, few studies have considered species-specific conditions, such as the functional coupling between the corolla and the beaks of hummingbirds, which determine the benefits for both the plants and the nectarivores under natural conditions (Rico-Guevara *et al*. 2021, Avalos 2012).

Energetic surplus.- The presence of artificial feeders in the landscape may not deter hummingbirds from their natural resources; on the contrary, it may provide them with access to rapid bursts of energy (Brockmeyer & Schaefer 2012). In situations where the regular food supply of hummingbirds has been affected by environmental changes, such as urbanization (Nuñez-Rosas & Arizmendi 2019), these artificial resources can be advantageous, where in heavily transformed matrices or urban areas, only a few private gardens offer floral resources with adequate energetic rewards (Pyke 1981, Arizmendi *et al*. 2008, McCaffrey & Wethington 2008). Consequently, hummingbird feeders and bird-friendly gardens/backyards could potentially serve to initiate or restore historical energetic landscapes (Arizmendi *et al*. 2008).

Hummingbirds may visit feeders as their main source of energy, which could lead to a reduction or elimination of their pollination contributions if they become overly dependent on the feeders when local flowers are unavailable (Chalcoff *et al*. 2008, Nuñez-Rosas & Arizmendi 2019). It has been shown that the frequency of visits to specific plant species in the presence of feeders varies across different seasons. In Canada, a long-term study conducted over seven sampling bouts of 10 days each throughout the year revealed that hummingbirds captured in proximity to feeders had none or very low pollen loads compared to those caught in areas without feeders, suggesting a possible range of effect of up to 3 kilometers (Hurly & Oseen 1999). However, this effect may be influenced by season and the abundance of wildflowers, with hummingbirds near feeders exhibiting null pollen loads more frequently during the dry season in Costa Rica (Avalos *et al*. 2012). Similar observations have been made where feeders account for up to 59% of all visits compared to a wide range of flowers based on direct observations of flower patches versus feeders (Inouye *et al*. 1991, McCaffrey & Wethington 2008); however, this percentage decreases during the flowering peaks of all nearby species (Inouye *et al*. 1991, McCaffrey & Wethington 2008). These findings underscore how hummingbirds make foraging decisions, suggesting that individuals continuously evaluate environmental information while considering the available wild resources and the artificial alternatives, along with their own morphological constraints, such as bill-corolla matching and nectar extraction mechanisms in both natural and artificial conditions (Rico-Guevara & Rubega 2011, Rico-Guevara *et al*. 2015, Rico-Guevara *et al*. 2023).

Several studies highlight the importance of elucidating species-specific relationships when studying the effects of feeders on plant-animal interaction. In one of two plant species evaluated in detail in Valle del Cauca, Colombia, proximity to hummingbird feeders had no association with the number of seeds produced, while in the other plant species, proximity to feeders was correlated with lower seed production (Ramírez-Burbano *et al*. 2022). For 22 months, Ramírez-Burbano *et al*. (2022) studied 20 species of hummingbirds and 55 species of plants, with monthly sampling in areas where feeders were located. Surveys included measurement of nectar production for all flowers, hummingbird visitation frequencies (by video recording), determination of monthly abundance, and other variables. They found that 76% of plant visits can be considered legitimate, that is, where there is a coupling between beak and corolla (or resource source) that would allow efficient resource extraction (Wolf *et al.* 1972) and corresponding pollination benefits (Rico-Guevara *et al.* 2021), while the morphological match between hummingbird's beaks and feeders only occurred in 23% of the visits (Ramírez-Burbano *et al.* 2022). Based on such data, they concluded that the plant-hummingbird interaction networks were not altered in the presence of artificial feeders, even when morphological coupling metrics between resources and hummingbirds were considered.

In the context of community-level interactions, a study compared the microbial and fungal diversity of feeders with that present in floral resources (Lee *et al.* 2019). The results revealed significant differences in microbial communities, with greater abundance and richness observed in feeders, particularly with higher bacterial turnover across a three-day period, although no significant variation was noted in fungal diversity (Lee *et al.* 2019). This variability was associated with a decline in the frequency of hummingbird visitation over time, indicating the possible existence of a mechanism for detecting 'old nectars' (Lee *et al.* 2019), perhaps because nectar fermentation might produce volatiles that hummingbirds would perceive (Goldsmith & Goldsmith 1982, Kim *et al.* 2021). Additionally, in relation to phoretic mites, which disembark from the hummingbird's beak and move towards the nectar source during the visit, deposition rates increased with sugar concentration in feeders (Márquez-Luna *et al.* 2016). This calls attention for deeper community-wide analysis of the possible effects of feeders on symbiotic relations, including when in the day pollen is available and stigmas are receptive in each plant species. Feeders with higher sugar concentrations received more visits and more floral mites, which could potentially be transferred to wildflowers or other feeders (Márquez-Luna *et al.* 2016), resulting in an infection cycle.

Hummingbirds seem to increase their activity in the vicinity of feeders (Baum & Grant 2001) and species richness seems also influenced by the availability of nectar (Montgomerie & Gass 1981). The number of individuals at the feeders decreases when there is a high number of flowers in the environment and vice versa (Inouye *et al.* 1991, Arizmendi *et al.* 2008, McCaffrey & Wethington 2008). Furthermore, preference for feeders might change over short temporal scales, for example, throughout the day when the amount of nectar in the flowers decreases, whether because of natural production rhythms or due to progressive nectar depletion by visitors foraging (McCaffrey & Wethington 2008). Such mixed visiting between flowers and feeders may originate from the fact that sugary water in feeders, with a concentration of 20% (suggested for feeders, and whose main component is sucrose), does not satisfy all the energetic and nutritional requirements, and individuals must consume other components present in plant nectar such as glucose and fructose (Baker & Baker 1983). More so, when hummingbirds break down sucrose into glucose and fructose with sucrase enzyme (Martínez del Río 1990). In addition, hummingbirds frequently visit the feeders at hours when plant nectar should be scarce (McCaffrey & Wethington 2008, Téllez-Colmenares per. obs.).

Arizmendi *et al.* (2007, 2008) found that in some cases pollination rate of plants close to the feeders decreased. While the decrease in visitation rate can pose a challenge at the ecosystem level, it might be compensated by the high population density and diversity of pollinator species present (Arizmendi *et al.* 1996). It is important to interpret the findings from these three studies with caution, as the authors note that the observed strong effects are species-specific. For some species, the installation of feeders in undisturbed habitats is likely to attract additional individuals from a distance, diverting them away from areas they would naturally inhabit (Arizmendi *et al.* 2007).

Some hummingbird species are opportunistic rather than specialists, so they exhibit adaptability to disturbed areas (*e.g.*, Ramírez-Burbano *et al.* 2022). Several researchers (Savard *et al.* 2000; Arizmendi *et al.* 2008; Fuller *et al.* 2008) suggest that the use of artificial feeders can influence species distributions, potentially leading to increased richness and/or species displacement. A well-documented case in North America is the range expansion of Anna's hummingbird (*Calypte anna*) which has colonized northern territories and experienced population growth across its range, likely influenced by anthropogenic factors such as feeder availability, introduction of *Eucalyptus*, food resources in urban gardens, suitable nesting sites, and warmer urban environments (Greig *et al.* 2017, Battey 2019, English *et al.* 2021). In environments with significant human intervention, feeders can effectively modify habitat quality and availability, enabling access to food resources for species that might otherwise be unable to inhabit such areas (Fuller *et al.* 2008) to support individual and population survival (Rodríguez-Ramírez 2020). Despite the possible relevance of feeders in conservation efforts, there is still a knowledge gap regarding ecological parameters such as the drinking rate of hummingbirds at feeders, their energy budgets, foraging strategies (Rico-Guevara *et al.* 2021), commuting patterns (Sargent *et al.* 2021), and how these systems compare to natural environments. An important step in this direction is the study by Ramírez -Burbano *et al.* (2022), which examines network interactions with and without food supplementation.

Other effects.- Beyond the literature survey, we identified other potential negative effects of using feeders, including hummingbird feeders. For instance, the presence of feeders can lead to a temporary loss of certain exploratory foraging behaviors in hummingbirds due to the reliable food source (Brittingham & Temple 1992). The spread of disease is another concern associated with feeders, with studies indicating that the number of individuals, feeder type, and habitat can influence the risk (Fischer *et al.* 1997, Süld *et al.* 2014), enhanced by poor feeder sanitation. Additionally, feeders can increase the risk of predation on hummingbirds by birds of prey (Dunn & Tessaglia 1994), praying mantises (Nyffeler *et al.* 2017), and cats (Lepczyk *et al.* 2003). Collisions with windows in proximity to the feeders have also been reported as a threat to hummingbirds (Klem *et al.* 2004). Furthermore, the establishment of feeders within urban or peri-urban landscapes may attract invasive species, leading to increased competition and potential displacement of various native bird species (Chace & Walsh 2006, Parsons *et al.* 2006). These negative consequences of feeders underscore the importance of considering their potential impacts on hummingbird populations and ecosystems.

Eighteen of the articles we surveyed point to neutral effects of feeders, followed by 10 identifying negative effects, 7 with positive, and 10 identifying multiple effects based on species identity (Table 2). The most common topic evaluated in the plant-hummingbird interaction has been that regarding preference and additional energetic resources (Table 2).

It is noteworthy that although we intended to limit this review to studies on the interaction between plants and hummingbirds, some also include evaluations of other nectarivores. For example, some songbirds (Icteridae, Parulidae, Tyrannidae) usually visit feeders with a higher concentration of sugars (Teixeira *et al.* 2012), without having clear mutualistic relationships with wild plants. This is the case with some bat species that are not known to pollinate but do visit feeders (Maguiña & Muchhala 2017), or *Glossophaga* bats which are pollinators (Rojas-Sandoval *et al.* 2008). In cases where bats do pollinate wild plants and visit feeders, no difference was identified in the pollen load of bats depending on the presence of the feeder that these mammals also used in a four-month investigation (Maguiña & Muchhala 2017).

Internet public information.- We considered 12 of the 40 initial results from websites, which indicated some effect on plant-animal interactions (Table 3). These websites were no more than 10 years old, four a product of professional blogger interpretations, seven belonging to public or private entities, and one a university website. Of the 12 websites mentioning plant -pollinator interaction, only three are written in Spanish (which are easily translatable with the online service of different web search engines. However, this does not imply the translation is accurate).

Three websites refer to neutral impact (two with scientific literature support) (Table 2 and Supplementary Table 2), one site called for caution

Table 2. Summary of the positive, negative, or neutral effects linked in 26 manuscripts and twelve websites on the plant-animal relationship in the framework of the use of artificial hummingbird feeders.

Topic	Effect			# Manuscripts that mention an effect (*)	# Websites that mention an effect (^)
	Positive	Neutral	Negative		
Pollination/ visits	x			4 (6, 9, 10, 15)	
		x		4 (5, 15, 19, 22)	1 (2)
			x	6 (6, 7, 11, 12, 13, 23)	5 (1, 5, 19, 33, 34)
	Not defined			2 (3, 16)	
Abundance/ diversity/ behavior	x			1 (6)	
		x		6 (1, 8, 14, 17, 19, 20)	1 (2)
			x	2 (6, 12)	
Preferences/ Extra resource-energy (+:supplement; -:Dependence)	x			2 (10, 15)	5 (5, 8, 9, 14, 27)
		x		5 (1, 5, 14, 15, 20)	2 (15, 23)
			x	1 (21)	1 (33)
	Not defined			5 (4, 15, 18, 24, 25)	

*numbers in parentheses refer to Supplementary Table 1, ^numbers in parentheses refer to Supplementary Table 2

with both positive and negative effects shown, but with no evidence in the literature to support the claims. Four other websites portray a positive effect, all of which were characterized as feeders' providers of which only one had accessible literature support. Another four websites identify negative impacts (Table 2), one with independent scientific support and another one as a general reference from a bird guide.

One webpage called for caution regarding sugar metabolism in hummingbirds (HummingWorld 2022) a concern which has been shown to be unfounded since 2014 (Chen & Welch 2014) and was further tested by Latorre-Valencia (2020) showing that hummingbirds drinking from feeders had a lower blood glucose concentration than those who fed on wild resources.

Remaining open questions.- Hummingbirds are highly diverse, with over 350 species (Clements et *al.* 2022, Remsen *et al.* 2022). Concurrently, hummingbird-pollinated plants encompass approximately 1340 species, spread across more than 404 genera in 68 botanical families (Arizmendi & Rodríguez-Flores 2012, Serrano-Serrano *et al.* 2017, Abrahamczyk & Steudel 2022). Given the vast number of interactions involved and their potential outcomes, comprehensively defining all of them as positive, negative, or neutral poses an immeasurable task. We therefore would like to highlight open questions which may contribute to decision-making tools for the use, or abstention, of feeders.

(1) What is the influence of landscape on the intensity of hummingbird feeder usage, and how might this influence benefits or harms? Hummingbird species exhibit variations in their movement patterns and mobility investments (Brittingham & Temple 1992, Morneau *et al.* 1999, Sargent *et al.* 2021). As human-induced land use changes lead to fragmented environments, the mobility of certain hummingbird species may be constrained (Savard *et al.* 2000, Fuller *et al.* 2008, Hadley & Betts 2009). In such cases, locations with available feeders could serve as stepping-stones for hummingbirds, facilitating local movements and even migration, thereby aiding gene flow between plant populations (*e.g.,* Torres-Vanegas *et al.* 2019) across different patches or landscape types. Although these concepts are starting to be explored (Restrepo-Zuleta 2017), further and more extensive research is needed to gain a comprehensive understanding of these dynamics.

(2) Feeders as means of attraction for restoration. As feeders could act as energy boosters for birds, is it pertinent to use feeders as a first stage of attraction,

Table 3. Twelve resulting websites, official pages, institutional pages, avitourism companies, universities, state websites, blogs specialized in avifauna or companies that distribute objects related to the feeding of summary birds where possible effects of feeders on the plant-hummingbird relationship (Google® search engine).

ID (sensu Annex 2)	Website general topic	Year	Website type	Link
1	Feeders effects on pollination	2012	Blog	https://fieldstudies.org/2012/02/whats-the-impact-of-hummingbird-feeders/#:~:text=Supplementing%20hummingbirds%20with%20food%20seems,it%20on%
2	Birds abundance and pollination	2013	Blog	https://jeffollerton.co.uk/2015/10/01/how-do-artificial-nectar-feeders-affect-hummingbird-abundance-and-pollination-of-nearby-plants-a-new-study-in-the-journal
5	Feeders: pros and cons.	2013	Blog	https://www.birdphotos.com/photos/node/8351
8	Generalities	2015	Private/public entity	https://www.nps.gov/articles/hummingbirds.htm
9	Attracting hummingbirds	NA	Private/public entity	https://www.audubon.org/news/hummingbird-feeding-faqs
14	Feeders use	2020	Private/public entity	https://www.biologiatropical.org/blog/como-atraer-de-manera-responsable-a-nuestros-vecinos-voladores-y-
15	Feeders use	2019	Private/public entity	https://www.avesdebarrio.seo.org/2019/02/14/26893/
19	Generalities	2017	University website	https://asociacioncolombianadeornitologia.org/wp-content/uploads/2017/10/MemoriasNectarivoras.pdf
23	Feeders: pros and cons.	2017	Private/public entity	https://feederwatch.org/blog/flowers-vs-feeders-hummers-buzz-native-nectar/
27	Feeders use	2014	Private/public entity	https://extension.tennessee.edu/publications/documents/w305.pdf
33	Generalities	2018	Private/public entity	https://www.avesbogota.org/wp-content/uploads/2019/02/Libro_Colibr%C3%
34	Nectar recipe	NA	Blog	https://www.hummingworlds.com/es/receta-de-nectar-casero-para-colibries/

allowing interactions in potential areas for restoration along with the implementation of native flower gardens? Hummingbird feeders can create interactions in areas with limited pollinator communities, especially in ecosystems with historical transformations. Providing supplementary food through feeders attracts and sustains hummingbirds, promoting pollination activity and potentially enhancing pollination services in human-altered landscapes and urban areas. They are also beneficial in urban environments where pollinators are scarce, as demonstrated by M del C Arizmendi and colleagues' work in Mexico.

(3) Seed production changes. Under species-specific interactions, what is the effect on seed production of hummingbird-pollinated plants, when feeders are closer or further away? Although hummingbirds can be key pollinators for many plants, what is the proportion of fertilization that is generated from a possible reduction in visits? This raises a trade-off between the quality and quantity of pollination, and how it may be influenced by feeder use. For instance, Tejada-Valencia (2020) found that feeders could reduce the number of fruits and seeds up to 500 meters away, and van Duuren (2012) suggested that one in every four surveyed plant species might be affected in terms of seed production by the presence of feeders, although these two studies were exploratory. Further investigations in this area are warranted to better understand the implications of feeders on seed production and the interactions between plants and pollinators (Rico-Guevara *et al.* 2021).

(4) Feeder design. If interactions are specific, would it be fitting to design new feeders that enable for a better integration of such artificial elements into specific wild settings? For example, a feeder shape that provides a closer match between bill morphology

and feeder geometry (Ibarra *et al.* 2015, Maglianesi *et al.* 2015). Similarly, could a specific concentration of sugar solution benefit one species more than another? If super concentrated nectar is available, trapliners can access to the feeders without being excluded. For example, *Phaethornis* hummingbirds will readily drink a solution with 60% sugar solution, but other species do not drink nectar with such a high concentration (Téllez-Colmenares 2018, Téllez-Colmenares & Rico-Guevara 2023).

(5) Variation of interactions across gradients. Do behavioral patterns and plant-pollinator-feeder associations occur in the same way across latitudinal or altitudinal gradients? How do associations change depend on the community structure, total offer, seasonality of the plants, and life history of each species? If the relationships between natural settings and artificial feeders are not only species-specific, but rather ensemble-specific, which are the critical aspects determining the stability of the resulting network?

(6) Effect on survival and/or reproduction of hummingbirds. Could food supplementation lead to greater success in survival? Do hummingbirds that visit feeders live longer than those that do not? Or is it possible to establish whether hummingbirds that have the extra energy from feeders have more clutches, and/or more surviving offspring, and/or offspring of better quality (*e.g.*, heavier chicks)?

(7) Plant phenology for pollinator interactions. It is necessary to better understand the local flowering phenology, resource distribution, and patterns of nectar production and concentration, then compare their seasonality (or lack of) with feeder offerings. Given that some hummingbirds change the visitation frequency to feeders depending on wildflower resources, long-term data are needed to determine whether the novel resource could indeed temporarily supplement the diet and evolve into a new stable ecological situation.

In conclusion, despite the widespread use of feeders, the effects of their use on the relationship between hummingbirds and the plants they pollinate remain largely unknown. The limited scope of studies conducted on both hummingbird and plant species suggests that the effects may vary depending on the specific species involved. Importantly, the absence of definitive scientific evidence has led to contrasting messages in mass media and online platforms, leading to potential polarization on the topic. Therefore, we emphasize the need for (1) generating unbiased and informative content online, accurately representing the current knowledge, and identifying gaps in information; (2) approaching widely distributed information without scientific support with caution, and (3) promoting further scientific research in the themes identified in this study as the key areas of uncertainty. Achieving a balance and advancing in-depth research will be crucial in understanding the overall impact of feeder use across ecological levels.

This manuscript is available in its full length in Spanish at: https://doi.org/10.59517/oc.e576

Literature cited

Abrahamczyk, S. & B. Steudel. 2022. Why are some hummingbird-pollinated plant clades so species-rich? American Journal of Botany 109(7):1059–1062. https://doi.org/10.1002/ajb2.16018

Arizmendi, M.C. & C.I. Rodríguez-Flores. 2012. ¿How many plant species do hummingbirds visit? Ornitología Neotropical 23(Supplement):49–54. https://sora.unm.edu/node/133579

Arizmendi, M.C., C.A. Dominguez & R. Dirzo. 1996. The role of an avian nectar robber and of hummingbird pollinators in the reproduction of two plant species. Functional Ecology 10(1): 119–127. https://doi.org/10.2307/2390270

Arizmendi, M.C., C. Monterrubio-Solís, L. Juarez, I. Flórez-Moreno & E. López-Saut. 2007. Effect of the presence of nectar feeders on the breeding success of *Salvia mexicana* and *Salvia fulgens* in a suburban park near México City. Biological Conservation 136(1):155–158. https://doi.org/10.1016/j.biocon.2006.11.016

Arizmendi, M.C., E. López-Saut, C. Monterrubio-Solís, L. Juárez, I. Flores-Moreno & C. Rodríguez-Flores. 2008. Efecto de la presencia de bebederos artificiales sobre la diversidad y abundancia de los colibríes y el éxito reproductivo de dos especies de plantas en un parque suburbano de la ciudad de México. Ornitología Neotropical 19:491–500. https://sora.unm.edu/node/133507

Avalos, G. 2012. What's the impact of hummingbird feeders? The School for Field Studies bog. https://fieldstudies.org/2012/02/whats-the-impact-of-hummingbird-feeders/

Avalos, G., A. Soto & W. Alfaro. 2012. Effect of artificial feeders on pollen loads of the hummingbirds of Cerro de La Muerte, Costa Rica. Revista de Biologia Tropical 60 (1):65–73. https://doi.org/10.15517/rbt.v60i1.2362

Baicichi, P., M.A. Barker & C.L. Henderson. 2015. Feeding Wild Birds in America. Texas A & M University Press.

Baker, H. & I. Baker. 1983. Floral nectar constituents in relation to pollinator type. In U. S. Van Nost. Reinhold (Ed.), Jones CE, Little RJ (Handbook, pp. 117–141).

Ballantyne, R., J. Packer & L.A. Sutherland. 2011. Visitors' memories of wildlife tourism: Implications for the design of powerful interpretive experiences. Tourism Management 32(4):770–779. https://doi.org/10.1016/j.tourman.2010.06.012

Bascompte, J. 2009. Mutualistic networks. Frontiers in Ecology and the Environment 7(8):429–436. https://doi.org/10.1890/080026

Battey, C.J. 2019. Ecological release of the Anna's Hummingbird during a northern range expansion. American Naturalist 194(3):306–315. https://doi.org/10.1086/704249

Baum, K.A. & W.E. Grant. 2001. Hummingbird foraging behavior in different patch types: Simulation of alternative strategies. Ecological Modelling 137(2–3):201–209. https://doi.org/10.1016/S0304-3800(00)00436-1

Blem, C.R., L.B. Blem, J. Felix & J. Van Gelder. 2000. Rufous Hummingbird sucrose preference: Precision of selection varies with concentration. Condor 102(1):235–238. https://doi.org/10.2307/1370432

Brittingham, M.C & Temple, S.A. 1992. Use of winter feeders by Black-Capped Chickadees. The Journal of Wildlife Management 56(1):103–110. https://doi.org/10.2307/3808797

Brockmeyer, T. & H.M. Schaefer. 2012. Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds? Basic and Applied Ecology 13(3):294–300. https://doi.org/10.1016/j.baae.2012.02.005

Brodin, A. & Clark, C.W. 2008. Energy Storage and Expenditure. In D. W. Stephens, J. S. Brown, & R. C. Ydenberg (Eds.), Foraging (Stephen, D, pp. 221–270). University of Chicago Press. https://doi.org/10.7208/9780226772653-009

Chace, J.F. & J.J. Walsh. 2006. Urban effects on native avifauna: A review. Landscape and Urban Planning 74 (1):46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Chalcoff, V.R., M.A. Aien & L. Galetto. 2008. Sugar preferences of the green-backed firecrown hummingbird (*Sephanoides sephaniodes*): A field experiment. Auk 125(1):60–66. https://doi.org/10.1525/auk.2008.125.1.60

Chen, C.C.W. & K.C. Welch. 2014. Hummingbirds can fuel expensive hovering flight completely with either exogenous glucose or fructose. Functional Ecology 28 (3):589–600. https://doi.org/10.1111/1365-2435.12202

Class, A.M. & I.T. Moore. 2013. Effects of food supplementation on a tropical bird. Oecologia 173(2):355–362. https://doi.org/10.1007/S00442-013-2636-5

Clements, J.F., T.S. Schulenberg, M.J. Iliff, S.M. Billerman, T.A. Fredericks, J.A. Gerbracht, D. Lepage, B.L. Sullivan & C.L. Wood. 2022. The eBird/Clements checklist of Birds of the World: v2022. https://www.birds.cornell.edu/clementschecklist/download/

Dunn, E.H. & D.L. Tessaglia. 1994. Predation of Birds at Feeders in Winter. Journal of Field Onrithology 65(1):8–16. http://www.jstor.org/stable/4513887

Duuren, I.V. 2012. Hummingbird-pollination in the rainforest of Un poco del Chocó Do artificial hummingbird feeders interfere with pollination? (Issue August) Hageschool Hasdenbosch, Germany.

English, S.G., C.A. Bishop, S. Wilson & A.C. Smith. 2021. Current contrasting population trends among North American hummingbirds. Scientific Reports 11(1):1–9. https://doi.org/10.1038/s41598-021-97889-x

Ewald, P.W. & W.A. Williams. 1982. Function of the Bill and Tongue in Nectar Uptake by Hummingbirds. Auk99 (3):573–576. https://doi.org/10.1093/auk/99.3.573

Fischer, J.R., D.E. Stallknecht, M.P. Luttrell, A.A. Dhondt, & K.A. Converse. 1997. Mycoplasmal Conjunctivitis in Wild Songbirds: The Spread of a New Contagious Disease in a Mobile Host Population. Emerging Infectious Diseases 3(1):69–72. https://doi.org/10.3201/eid0301.970110

Fuller, R.A., P.H. Warren, P.R. Armsworth, O. Barbosa & K.J. Gaston. 2008. Garden bird feeding predicts the structure of urban avian assemblages. Diversity and Distributions 14(1):131–137. https://doi.org/10.1111/j.1472-4642.2007.00439.x

Galbraith, J.A., M.C. Stanley, D.N. Jones & J.R. Beggs. 2017. Experimental feeding regime influences urban bird disease dynamics. Journal of Avian Biology 48(5):700–713. https://doi.org/10.1111/jav.01076

Gass, C.L. & W.M. Roberts. 1992. The Problem of Temporal Scale in Optimization: Three Contrasting Views of Hummingbird Visits to Flowers. The American Naturalist 140(5):829–853. https://doi.org/10.1086/285443

Glowinski, S. 2008. Bird-watching, Ecotourism, and Economic Development: A Review of the EvidencE. Applied Research in Economic Development 5(3):65–77. http://ocean.otr.usm.edu/~w301497/teaching/archives_teaching/ghy350_spring2010/temp_docs_350/glowinski_2008v5n3.pdf

Glue, D. 2003. Variety at Winter Bird Tables. Bird Populations 7:212–215.

Goddard, M.A., A.J. Dougill & T.G. Benton. 2013. Why garden for wildlife? Social and ecological drivers, Motivations and barriers for biodiversity management in residential landscapes. Ecological Economics 86:258–273. https://doi.org/10.1016/j.ecolecon.2012.07.016

Goldsmith, K.M. & T.H. Goldsmith. 1982. Sense of Smell in the Black-Chinned Hummingbird. The Condor 84(2):237–238. https://doi.org/10.2307/1367678

Greig, E.I., E.M. Wood & D.N. Bonter. 2017. Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. Proceedings of the Royal Society B: Biological Sciences 284(1852):1–9. https://doi.org/10.1098/rspb.2017.0256

Hadley, A.S. & M.G. Betts. 2009. Tropical deforestation alters hummingbird movement patterns. Biology Letters 5(2):207–210. https://doi.org/10.1098/rsbl.2008.0691

Hewes, A., D. Cuban, D. Groom, A. Sargent, D. Beltrán & A. Rico-Guevara. 2022. Variable evidence for convergence in morphology and function across avian nectarivores. Journal of Morphology 289(12):1483–1504. https://doi.org/10.1002/jmor.21513

Horn, D.J. & S.M. Johansen. 2013. A comparison of bird-feeding practices in the United States and Canada. Wildlife Society Bulletin 37(2):293–300. https://doi.org/10.1002/wsb.281

HummingWorlds. 2022, July 30. Receta de néctar casero para colibríes. https://www.hummingworlds.com/es/receta-de-nectar-casero-para-colibries/

Hurly, A.T. & M.D. Oseen. 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. Animal Behaviour 58(1):59–66. https://doi.org/10.1006/anbe.1999.1130

Ibarra, V., M. Araya-Salas, Y.P. Tang, C. Park, A. Hyde, T.F. Wright & W. Tang. 2015. An RFID based smart feeder for hummingbirds. Sensors 15(12):31751–31761. https://doi.org/10.3390/s151229886

Inouye, D.W., W.A. Calder & N.M. Waser. 1991. The effect of floral abundance on feeder censuses of hummingbird populations. The Condor 93(2):279–285. https://doi.org/10.2307/1368943

Jaung, W. & L.R. Carrasco. 2022. A big-data analysis of human-nature relations in newspaper coverage. Geoforum 128:11–20. https://doi.org/10.1016/j.geoforum.2021.11.017

Jones, D. 2011. An appetite for connection: Why we need to understand the effect and value of feeding wild birds. Emu 111(2):i–vii. https://doi.org/10.1071/MUv111n2_ED

Kellert, S.R. 1985. Birdwatching in American society. Leisure Sciences 7(3):343–360. https://doi.org/10.1080/01490408509512129

Keniger, L.E., K.J. Gaston, K.N Irvine & R.A. Fuller., 2013. What are the benefits of interacting with nature? International Journal of Environmental Research and Public Health 10(3):913–935. https://doi.org/10.3390/ijerph10030913

Kim, A.Y., D.T. Rankin & E.E.W Rankin. 2021. What is that smell? Hummingbirds avoid foraging on resources with defensive insect compounds. Behavioral Ecology and Sociobiology, 75(9):132. https://doi.org/10.1007/s00265-021-03067-4

Kim, S., D. Scott & J. Crompton. 1997. An exploration of the relationships among social psychological involvement, behavioral involvement, commitment, and future intentions in the context of birdwatching. Leisure Research 29(3):320–341. https://doi.org/10.1080/00222216.1997.11949799

Klem, D., D.C. Keck, K.L. Marty, A.J. Miller Ball, E.E. Niciu & C.T. Platt. 2004. Effects of window angling, feeder placement, and scavengers on avian mortality at plate glass. Wilson Bulletin 116(1):69–73. https://doi.org/10.1676/0043-5643(2004)116[0069:EOWAFP]2.0.CO;2

Kummer, J.A. & E.M. Bayne. 2015. Bird feeders and their effects on bird-window collisions at residential houses. Avian Conservation and Ecology 10(2):6. https://doi.org/10.5751/ace-00787-100206

Lanna, L.L., C.S. de Azevedo, R.M. Claudino, R. Oliveira & Y. Antonini. 2017. Feeding behavior by hummingbirds (Aves: Trochilidae) in artificial food patches in an Atlantic forest remnant in Southeastern Brazil. Zoologia 34:1–9. https://doi.org/10.3897/zoologia.34.e13228

Latorre-Valencia, L. 2020. Effect of artificial feeders on hummingbird blood glucose levels of a cloud forest in Colombia. Universidad Icesi.

Lee, C., L.A. Tell, T. Hilfer & R.L. Vannette. 2019. Microbial communities in hummingbird feeders are distinct from floral nectar and influenced by bird visitation. Proceedings of the Royal Society B: Biological Sciences 286(1898):1–7. https://doi.org/10.1098/rspb.2018.2295

Lepczyk, C.A., A.G. Mertig & J. Liu. 2003. Landowners and cat predation across rural-to-urban landscapes. Biological Conservation 115(2):191–201. https://doi.org/10.1016/S0006-3207(03)00107-1

Lepczyk, C.A., A.G. Mertig & J. Liu. 2004. Assessing Landowner Activities Related to Birds Across Rural-to-Urban Landscapes. Environmental Management 33(1):110–125. https://doi.org/10.1007/s00267-003-0036-z

Loreau, M., B.J. Cardinale, F. Isbell, T. Newbold, M.I. O'Connor & C. de Mazancourt. 2022. Do not downplay biodiversity loss. Nature 601(7894):E27–E28. https://doi.org/10.1038/s41586-021-04179-7

Losapio, G., B. Schmid, J. Bascompte, R. Michalet, P. Cerretti, C. Germann, J.P. Haenni, R. Neumeyer, F.J. Ortiz-Sánchez, A.C. Pont, P. Rousse, J. Schmid, D. Sommaggio & C. Schöb. 2021. An experimental approach to assessing the impact of ecosystem engineers on biodiversity and ecosystem functions. Ecology 102(2):1–12. https://doi.org/10.1002/ecy.3243

Maglianesi, M.A., K. Böhning-Gaese & M. Schleuning. 2015. Different foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant-pollinator interactions. Journal of Animal Ecology, 84(3):655–664. https://doi.org/10.1111/1365-2656.12319

Maguiña, R. & N. Muchhala. 2017. Do artificial nectar feeders affect bat–plant interactions in an Ecuadorian cloud forest? Biotropica 49(5):586–592. https://doi.org/10.1111/btp.12465

Márquez-Luna, U., M.M. Vázquez González, I. Castellanos & R. Ortiz-Pulido. 2016. Number of hummingbird visits determines flower mite abundance on hummingbird feeders. Experimental and Applied Acarology 69(4):403–411. https://doi.org/10.1007/s10493-016-0047-0

Martínez del río, C. 1990. Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. The Condor 92(4):1022–1033. https://doi.org/10.2307/1368738

McCaffrey, R.E. & S.M. Wethington. 2008. How the presence of feeders affects the use of local floral resources by hummingbirds: A case study from Southern Arizona. Condor 110(4):786–791. https://doi.org/10.1525/cond.2008.8621

Montgomerie, R. & C. Gass. 1981. Energy limitation of hummingbird populations in tropical and temperate communities. Oecologia 50(2):162–165. https://doi.org/10.1007/BF00348031

Morneau, F., R. Décarie, R. Pelletier, D. Lambert, J.L. DesGranges, & J.P. Savard. 1999. Changes in breeding bird richness and abundance in Montreal parks over a period of 15 years. Landscape and Urban Planning 44(2–3):111–121. https://doi.org/10.1016/S0169-2046(99)00002-X

Nuñez-Rosas, L.E. & M.C. Arizmendi. 2019. Differential Use of Nectar Feeders Among Migrant and Resident Hummingbirds. Tropical Conservation Science 12(1):1–5. https://doi.org/10.1177/1940082919878960

Nyffeler, M., M.R. Maxwell & J.V. Remsen. 2017. Bird Predation by Praying Mantises: A Global Perspective. Wilson Journal of Ornithology 129(2):331–344. https://doi.org/10.1676/16-100.1

Parsons, H., R.E. Major & K. French. 2006. Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. Austral Ecology 31(2):17–227. https://doi.org/10.1111/j.1442-9993.2006.01584.x

Prescott, J.F., D.B. Hunter & G.D. Campbell. 2000. Hygiene at winter bird feeders in a southwestern Ontario city. Canadian Veterinary Journal 41(9):695–698.

Pyke, G.H. 1981. Hummingbird foraging on artificial inflorescences. Behaviour Analysis Letters 1(1):11–15.

Pyke, G.H. 2016. Plant–pollinator co-evolution: It's time to reconnect with Optimal Foraging Theory and Evolutionarily Stable Strategies. Perspectives in Plant Ecology, Evolution and Systematics, 19(2016):70–76. https://doi.org/10.1016/j.ppees.2016.02.004

Ramírez-Burbano, M.B., F.W. Amorim, A.M. Torres-González, J. Sonne & P.K. Maruyama. 2022. Nectar provision attracts hummingbirds and connects interaction networks across habitats. Ibis 164(1):88–101. https://doi.org/10.1111/ibi.12988

Remsen, J.V., J.I. Areta, E. Bonaccorso, S. Claramunt, A. Jaramillo, D.F. Lane, F. Pacheco, M. Robbins, F.G. Stiles & K.J. Zimmer. 2022. A classification of the bird species of South America. American Ornithological Society. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm

Restrepo-Zuleta, M.F. 2017. Cambios en la composición de especies en una comunidad de colibríes (Trochilidae), asociada a un recurso alimenticio fijo en el tiempo en un bosque nublado de Chicoral. In Universidad ICESI.

Rico-Guevara, A., L. Echeverri-Mallarino & C. Clark. 2022. Oh, snap! A within-wing sonation in Black-tailed trainbearers. Experimental Biology 225(8). https://doi.org/10.1242/jeb.243219

Rico-Guevara, A., T.H. Fan & M.A. Rubega. 2015. Hummingbird tongues are elastic micropumps. Proceedings of the Royal Society B: Biological Sciences 282(1813):1–8. https://doi.org/10.1098/rspb.2015.1014

Rico-Guevara, A., K.J. Hurme, R. Elting & A.L. Russell. 2021. Bene"fit" Assessment in Pollination Coevolution: Mechanistic Perspectives on Hummingbird Bill-Flower Matching. Integrative and Comparative Biology 61(2):681–695. https://doi.org/10.1093/icb/icab111

Rico-Guevara, A., K.J. Hurme, M.A. Rubega & D. Cuban. 2023. Nectar feeding beyond the tongue: hummingbirds drink using phase-shifted bill opening, flexible tongue flaps and wringing at the tips. Journal of Experimental Biology 226. https://doi.org/10.1242/JEB.245074

Rico-Guevara, A. & M.A. Rubega. 2011. The hummingbird tongue is a fluid trap, not a capillary tube. Proceedings of the National Academy of Sciences of the United States of America 108(23):9356–9360. https://doi.org/10.1073/pnas.1016944108

Rico-Guevara, A., M.A. Rubega, K.J. Hurme & R. Dudley. 2019. Shifting paradigms in the mechanics of nectar extraction and hummingbird bill morphology. Integrative Organismal Biology 1(1):1–15. https://doi.org/10.1093/iob/oby006

Robb, G.N., R.A. McDonald, D.E. Chamberlain & S. Bearhop. 2008. Food for thought: Supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6 (9):476–484. https://doi.org/10.1890/060152

Rodriguez-Ramirez, I. 2020, August 24. ¿Cómo atraer de manera responsable a nuestros vecinos voladores y peludos? Biología Tropical. https://www.biologiatropical.org/blog/como-atraer-de-manera-responsable-a-nuestros-vecinos-voladores-y-peludos

Rojas-Sandoval, J., K. Budde, M. Fernández, E. Chacón, M. Quesada & J.A. Labo. 2008. Phenology and pollination biology of *Ceiba pentandra* (Bombaceae) in the wet forest of south-eastern Costa Rica. Stapfia 80:539–545. https://doi.org/10.1093/icb/icab124

Sargent, A.J., D.J.E. Groom & A. Rico-Guevara. 2021. Locomotion and Energetics of Divergent Foraging Strategies in Hummingbirds: A Review. Integrative and Comparative Biology 61(2):736–748. https://doi.org/10.1093/icb/icab124

Savard, J.P.L., P. Clergeau & G. Mennechez. 2000. Biodiversity concepts and urban ecosystems. Landscape and Urban Planning 48(3–4):131–142. https://doi.org/10.1016/S0169-2046(00)00037-2

Scheuerlein, A. & E. Gwinner. 2002. Is Food Availability a Circannual Zeitgeber in Tropical Birds? A Field Experiment on Stonechats in Tropical Africa. Journal of Biological Rhythms 17:171–180.

Schoech, S.J. & T.P. Hahn. 2007. Food supplementation and timing of reproduction: Does the responsiveness to supplementary information vary with latitude? Journal of Ornithology 148(Supl. 2):S625–S632. https://doi.org/10.1007/s10336-007-0177-6

Schondube, J.E. & C. Martínez Del Rio. 2003. Concentration-dependent sugar preferences in nectar-feeding birds: Mechanisms and consequences. Functional Ecology 17(4):445–453. https://doi.org/10.1046/j.1365-2435.2003.00749.x

Sekercioglu, C.H. 2002. Impacts of birdwatching on human and avian communities. Environmental Conservation 29 (3):282–289. https://doi.org/10.1017/S0376892902000206

Serrano-Serrano, M.L., J. Rolland, J.L. Clark, N. Salamin, & M. Perret. 2017. Hummingbird pollination and the diversification of angiosperms: An old and successful association in Gesneriaceae. Proceedings of the Royal Society B: Biological Sciences 284(1852):1–10. https://doi.org/10.1098/rspb.2016.2816

Sherman, R. 1913. Experiments in feeding hummingbird during seven summers. Journal of Ornithology xxv(86).

Sonne, J., P. Kyvsgaard, P.K. Maruyama, J. Vizentin-Bugoni, J. Ollerton, M. Sazima, C. Rahbek & B. Dalsgaard. 2016. Spatial effects of artificial feeders on hummingbird abundance, floral visitation and pollen deposition. Journal of Ornithology 157(2):573–581. https://doi.org/10.1007/s10336-015-1287-1

Stiles, F.G. 1978. Ecological and Evolutionary Implications of Bird Pollination. American Zoologist 18:715–727. https://academic.oup.com/icb/article/18/4/715/2004949

Stiles, F.G. 1981. Geographical aspects of bird-flower coevolution with particular reference to Central America. Annals Missouri Botanical Garden 68(2):323–351. https://doi.org/10.2307/2398801

Stromberg, M.R. & P.B. Johnsen. 1990. Hummingbird Sweetness Preferences: Taste or Viscosity? The Condor 92(3):606. https://doi.org/10.2307/1368680

Süld, K., H. Valdmann, L. Laurimaa, E. Soe, J. Davison & U. Saarma. 2014. An invasive vector of zoonotic disease sustained by anthropogenic resources: The raccoon dog in Northern Europe. PLoS ONE 9(5):1–9. https://doi.org/10.1371/journal.pone.0096358

Teixeira, J.G., M.A. Assunção & C. Melo. 2012. Efeito da introdução de bebedouros artificiais na partição de nicho entre Apodiformes (Aves: Trochilidae) e Passeriformes. Horizonte Científico 6(1):1–20. https://seer.ufu.br/index.php/horizontecientifico/article/view/14771

Tejeda-Valencia, L.D. 2020. Influencia de los bebederos artificiales de colibríes en la polinización de *Centropogon congestus* (Campanulaceae) y *Glossoloma schultzei* (Gesneriaceae). Pontificia Universidad Javeriana Cali.

Téllez-Colmenares, N. 2018. Agresión y forrajeo de néctar en colibríes (Aves: Trochilidae) en comederos artificiales cerca de Fusagasugá, Colombia [Universidad Nacional de Colombia]. https://repositorio.unal.edu.co/handle/unal/63686

Téllez-Colmenares, N. & A. Rico-Guevara. 2023. El efecto de la concentración del néctar sobre las estrategias de forrajeo entre colibríes (Aves: Trochilidae) en bebederos artificiales. Ornitología Colombiana 24:2–22. https://doi.org/10.59517/oc.e568

Tello-Ramos, M.C., C.L. Branch, D.Y. Kozlovsky, A.M. Pitera & V.V. Pravosudov. 2019. Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. Animal Behaviour 147:129–136. https://doi.org/10.1016/j.anbehav.2018.02.019

Torres-Vanegas, F., A.S. Hadley, U.G. Kormann, F.A. Jones, MG. Betts & H.H. Wagner. 2019. The Landscape Genetic Signature of Pollination by Trapliners: Evidence From the Tropical Herb, *Heliconia tortuosa*. Frontiers in Genetics 10(1206):1–12. https://doi.org/10.3389/fgene.2019.01206

Torres, I., L. Salinas, C. Lara & C. Castillo-Guevara. 2008. Antagonists and their effects in a hummingbird-plant interaction: Field experiments. Ecoscience 15(1):65–72. https://doi.org/10.2980/1195-6860(2008)15[65:AATEIA]2.0.CO;2

True, D. 1995. Feeding Hummingbirds. In UNM Press (Ed.), Hummingbirds of North America: attracting, feeding, and photographing (Ilustrada, pp. 51–89).

U.S. Fish and Wildlife Service, & U.S. Census Bureau. 2018. 2011 National survey of fishing, hunting, and wildlife-associated recreation—National Overview.

Velasquez, J., P. Salaman & C.H. Graham. 2013. Effects of climate change on species distribution, community structure, and conservation of birds in protected areas in Colombia. Regional Environmental Change 13:235–248 https://doi.org/10.1007/s10113-012-0329-y

Vimal, R. 2022. The impact of the Covid-19 lockdown on the human experience of nature. Science of the Total Environment 803:1–6. https://doi.org/10.1016/j.scitotenv.2021.149571

Wethington, S. & S.M. Russell. 2003. The seasonal distribution and abundance of hummingbirds in oak woodland and riparian communities in southeastern Arizona. The Condor 105(3):484–495. https://doi.org/10.1093/condor/105.3.484

White, M.P., I. Alcock, J. Grellier, B.W. Wheeler, T. Hartig, S.L. Warber, A. Bone, M.H. Depledge & L.E. Fleming. 2019. Spending at least 120 minutes a week in nature is associated with good health and wellbeing. Scientific Reports 9(1):1–11. https://doi.org/10.1038/s41598-019-44097-3

Wilson, J. 2001. The effects of supplemental feeding on wintering Black-capped Chickadees (*Poecile atricapilla*) in central Maine: Population and individual responses. Wilson Bulletin 113(1):65–72. https://doi.org/10.1676/0043-5643(2001)113[0065:teosfo]2.0.co;2

Wolf, L.L., R.F. Hainsworth & F.G. Stiles. 1972. Energetics of foraging: Rate and efficiency of nectar extraction by hummingbirds. Science 176(4041):1351–1352. https://doi.org/10.1126/science.176.4041.1351

Supplementary Table 1. Database of 26 references included in the literature review regarding hummingbird feeders in the plant-animal interaction. A) articles, B) graduate and undergraduate theses. (Download here).

Supplementary Table 2. First 40 websites of official pages, institutional pages, avitourism companies, universities, state websites, blogs specialized in avifauna or companies that distribute objects related to the feeding of summary birds where possible effects of feeders on the plant-hummingbird relationship (Google® search engine). (Download here).