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HOW MANY PLANT SPECIES DO HUMMINGBIRDS VISIT? ¿CUÁNTAS ESPECIES DE PLANTAS SON VISITADAS POR LOS COLIBRÍES?

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Resumen. - ¿Cuántas especies de plantas son visitadas por colibríes?- Los colibríes son aves nectrívoras que polinizan plantas en América. En esta relación mutualista los colibríes se alimentan de néctar y transportan los gametos de las plantas llevado a cabo su reproducción. Para poder tener un mejor conocimiento del número e identidad de las plantas visitadas por colibríes compilamos una base de datos que incluye datos de reportes publicados y no publicados (tesis, reportes no publicados, y datos personales y de colegas) a nivel comunidad o de pares de especies. Un total de 111 artículos, 43 tesis y 11 libros se revisaron. Encontramos 1339 especies de plantas pertenecientes a 108 familias y 294 especies de colibríes en la matriz de interacción. La matriz se analizó utilizando un análisis de agrupamiento jerárquico agrupando a las plantas por familia y a los colibríes en los clados filogenéticos. Se formaron grupos claros que reflejan relaciones geográficas y preferencias alimenticias.

Abstract. - How many plant species do hummingbirds visit? - Hummingbirds are nectar-feeding birds that pollinate plants in the Americas. This is a mutualistic relationship where hummingbirds feed on nectar while transporting pollen among flowers, thus aiding plant reproduction. This relationship has received a lot of attention and many studies have been published. In order to provide a more accurate estimate of the number and identity of plant species visited by hummingbirds, we compiled a data set of published surveys of plant-hummingbird interactions. A total of 111 papers, 43 academic theses, and 11 books were reviewed. A total of 1339 plant species belonging to 108 families and 294 hummingbird species were included in the interaction matrix. The matrix was analyzed using hierarchical clusters, grouping by plant families and phylogenetic groups in hummingbirds. Clear groups were formed indicating geographical relationships and preferences.

Key words: Hummingbirds, hummingbird plants, plant-hummingbird interactions

INTRODUCTION

Hummingbirds are specialized nectar-feeding birds that live only in the Americas. Here, they are the second most diverse family of birds (328 described species) with specialized morphology and physiology adapted to feed mainly on sugars obtained from flowers. They act as pollinators, transporting gametes among flowers (Stiles 1981, Schuchmann 1999). This large family is divided into two subfamilies:1) Phaethornitinae or Hermit hummingbirds that can be characterized by long, decurved bills, their behavior as understory trapliners (Stiles & Wolf 1979, Stiles 1981, 1985, Cotton 1998, Hilty & Brown 2001), and their higher dominance and diversity in humid lowland forests (lower than 1000 m asl) especially in the Amazon region (Stiles 1981); and 2) Trochilinae, a more diverse group, of smaller hummingbirds with short to long bills and a diversity of behaviors from traplining to highly territorial, that live in a variety of environments,

from dry warm lowlands to cool wet highlands, and habitats, from scrubby vegetation to dense forest (Schuchmann 1999). Hummingbirds have been divided into nine phylogenetic clades (McGuire *et al.* 2007): one, called Hermits, in Phaethornithinae, and eight in Trochilinae (Bees, Brilliants, Coquettes, Emeralds, Gems, Mangoes, Patagoni, Topaces).

Hummingbird flowers are generally described to be long, tubular and red or of a contrasting color (Faegri & van der Pijl 1979). Nectar produced by hummingbird flowers is a dilute solution frequently between 22 to 26% of mainly sucrose (Baker & Baker 1975, Stiles & Freeman 1993). Interactions between hummingbirds and their food plants have been described extensively. However, the importance of hummingbird pollination to flowering plants has not been addressed. It has been estimated that hummingbirds pollinate about 400 plant species (Schuchmann 1999).

In order to provide a more accurate estimate of the number and identity of plant species visited by hummingbirds, we compiled a data set of published and unpublished community level or species level surveys of plant-hummingbird interactions. Our goals were to determine 1) the number and identity of plants visited by hummingbirds, and 2) the existence of a pattern of relationship between plant families and phylogenetic groups of hummingbirds.

METHODS

Data were compiled by searching published indexed papers where hummingbird visitation to specific plant species was recorded. Studies of both communities and species were considered. Dissertations from universities in Mexico, USA and Colombia that were accessible via the Internet were also searched. Unpublished reports and Chilean Passerine Seasonal Body Mass data were also used. The resulting database is a matrix with plant species as rows and hummingbird species as columns. The matrix cells have a value of 1 if interaction(s) was reported and 0 if no reference of visitation was found.

Plants were classified in Families and hummingbirds phylogenetically (McGuire et al. 2007, 2009). Descriptive analyses were done and a hierarchical two-way cluster analysis were done to test for associations (JMP, SAS Institute Inc., Cary, NC, USA).

RESULTS

A total of 111 papers, 43 academic theses and 11 books were reviewed. A total of 1339 plant species belonging to 108 families and 294 hummingbird species were included in the interaction matrix. Thirteen plant families accounted for 57% of all matrix entries (Fabaceae, Bromeliaceae, Rubiaceae, Gesneriaceae, Lamiaceae, Asteraceae, Malvaceae, Heliconiaceae, Bignoniaceae, Campanulacea, Ericaceae, Solanaceae, Acanthaceae; Fig 1). From analyzing the matrix, it is clear that groups of hummingbirds are associated with groups of plants. Mainly South American species, Hermits and Mangoes, are the main visitors to Heliconiaceae, Gesneriaceae, Bromeliaceae and Rubiaceae. Brilliants and Coquettes were frequently recorded visiting more species of Ericaceae, Rubiaceae, and Fabaceae, and less with Gesneriaceae. Bees and Gems visited more species of Lamiaceae, Rubiaceae and Fabaceae. Emeralds visited many species of Bromeliaceae, Malvaceae, Rubiaceae and Fabaceae.

In a hierarchical cluster analysis of the 31 plant families that comprised 80% of the entries and the 294 hummingbird species grouped in the 9 clades, three groups of plants grouped by their hummingbird visitors can be found (Fig. 2). The first one included Acanthaceae, Bignoniaceae, Malvaceae and Lamiaceae associated mainly with Emeralds and Bees but also visited by some Hermits. The second and biggest included 21 plant families and was visited by a variety of hummingbirds in a non

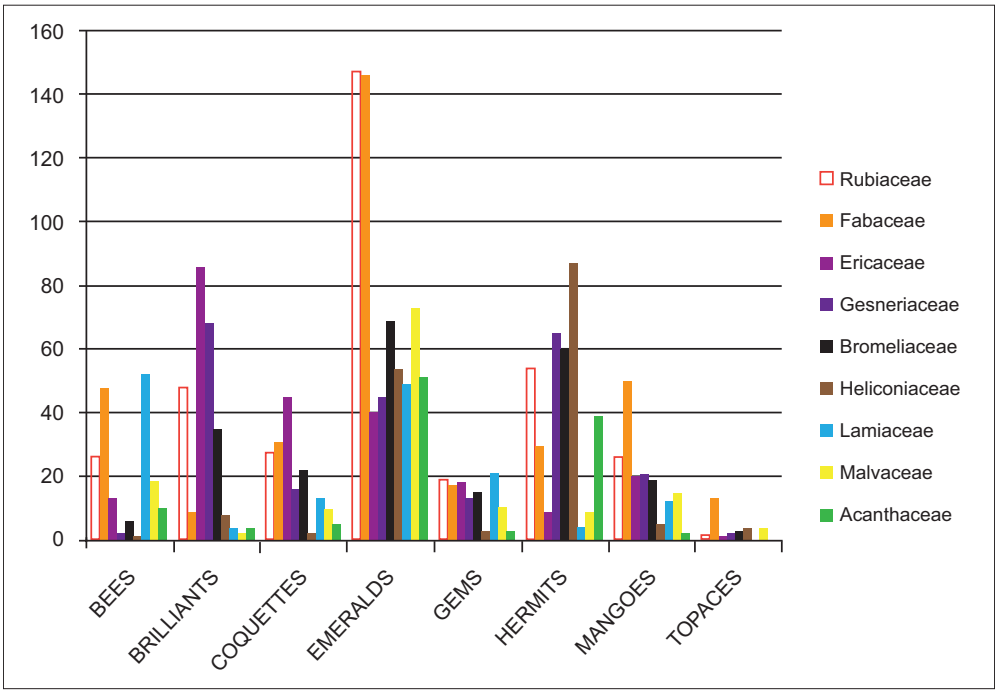

FIG 1. Number of plant species visited by the different Hummingbird clades.

intensive way. The last one included 6 plant families (Bromeliaceae, Gesneriaceae, Heliconiaceae, Ericaceae, Fabaceae and Rubiaceae) associated with Brilliants, Hermits and Emeralds and with Mangoes, Coquettes, and Bees.

Hummingbirds formed four groups: the first one comprised by Bees, Coquettes, Gems and Mangoes and associated with Ericaceae, Fabaceae, Rubiaceae and Lamiaceae; the second included Topaces and Patagoni (for which very little information exists); the third included Brilliants and Emeralds and associated with Rubiaceae, Heliconiaceae, Bromeliaceae, Ericaceae, Gesneriaceae, Fabaceae and Acanthaceae; and the fourth included only Emeralds, which associated with Rubiaceae, Heliconiaceae, Bromeliaceae, Ericaceae, Gesneriaceae, Fabaceae and also with Lamiaceae, Malvaceae, Bignoniaceae and Acanthaceae.

Emeralds, Bees, and Gems are the predominate hummingbirds in North America. These three groups were associated with Lamiaceae, Malvaceae, Bignoniaceae and Acanthaceae, plant families key for hummingbird conservation in North America. On the other hand, Hermits, Mangoes, Brilliants and Coquettes are dominant in South America and their association with Rubiaceae, Heliconiaceae, Bromeliaceae, Ericaceae, Gesneriaceae, Fabaceae and Acanthaceae is strong.

DISCUSSION

This study demonstrates that hummingbirds visit a much wider array of plants than previously reported, making them an important group of pollinators in the Americas. Other works have highlighted their importance (Grant & Grant 1968, Schuchman 1999) but did not address which plants depend on them for pollination. The associations of some hummingbird groups with specific plant groups have received much atten-

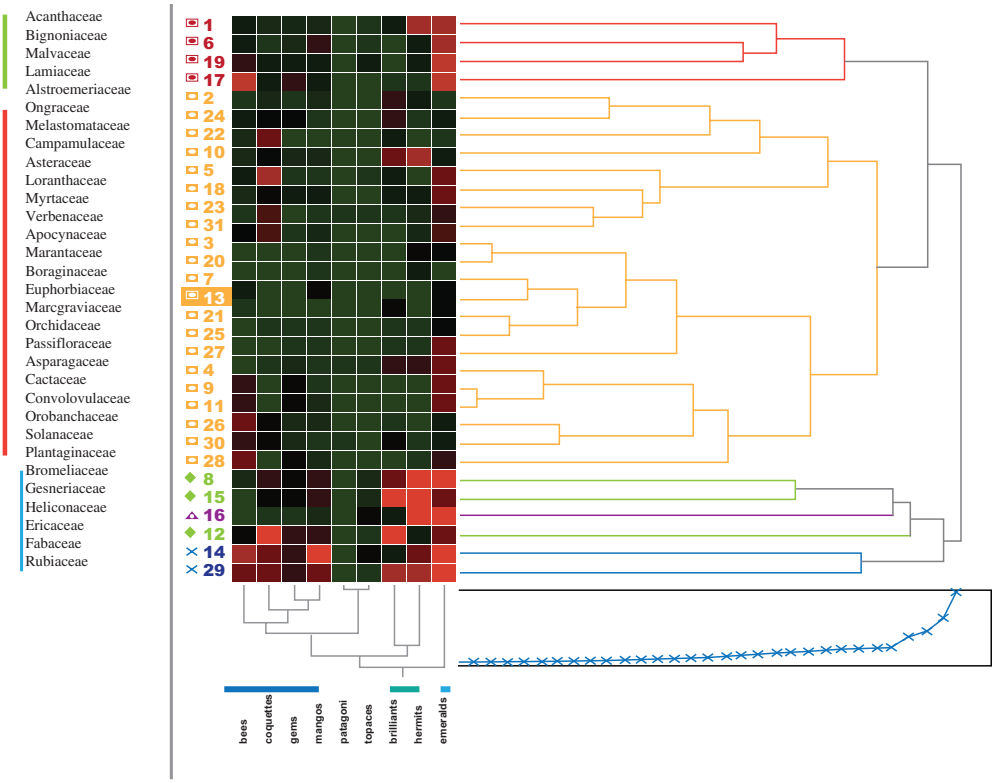

FIG 2. Hierarchical cluster analysis of plant families and hummingbird clades showing the interrelation of both groups.

tion. For example, Hermits have been associated with Heliconiaceae (Stiles 1975); these plants the preferred food of Hermits, and Hermits are the plants' main pollinators in the lowlands of Central and South America. This association is fully corroborated here, enhanced by the association with other families such as Gesneriaceae, Acanthaceae and Bromeliaceae (Stiles 1975, McDade 1984, Machado & Semir 2006). Mangoes visited many of the same plants as Hermits in Amazonian lowlands (Stiles 1975, McGuire *et al.* 2009). On the other side, Bees and Gems visited more species of Lamiaceae, Rubiaceae and Fabaceae, plants more diverse in North and Central America (Grant & Grant 1968, Grant 1994). Coquettes and Bees visited more Ericaceae, Fabaceae and Rubiaceae, while Emeralds were regular visitors of Bromeliaceae, Malvaceae, Rubiaceae and Fabaceae. These hummingbirds are smaller, with short, straight bills and are more diverse in Central and South America lowlands and highlands (Schuchmann 1999).

Hummingbird-plant interactions represent a key process in biodiversity conservation (Stiles 1978). Knowledge of these interactions is crucial to effectively address the conservation issues facing hummingbirds specifically and pollinators generally. Conservation of pollination mutualisms is important to preserve biodiversity and to secure food for humans (Kearns *et al.* 1998, Aizen *et al.* 2009, Ollerton *et al.* 2011).

Conservation of plants used by hummingbirds can ensure conservation of hummingbirds monitoring the phenological processes

of both mutualists is also crucial, as climate change could disrupt the links between them (Hegland *et al.* 2009).

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