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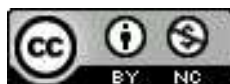
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# Macroevolution of the plant–hummingbird pollination system

Elisa Barreto<sup>1,\*</sup> , Manfred M. A. Boehm<sup>2</sup> , Ezgi Ogutcen<sup>3</sup> ,  
Stefan Abrahamczyk<sup>4,5</sup> , Michael Kessler<sup>6</sup> , Jordi Bascompte<sup>7</sup> , Agnes S. Dellinger<sup>8</sup> ,  
Carolina Bello<sup>9</sup> , D. Matthias Dehling<sup>1,10</sup> , François Duchenne<sup>1</sup> ,  
Miriam Kaehler<sup>11</sup> , Laura P. Lagomarsino<sup>12</sup> , Lúcia G. Lohmann<sup>13,14</sup> ,  
María A. Maglianesi<sup>15</sup> , Hélène Morlon<sup>16</sup> , Nathan Muchhala<sup>17</sup> ,  
Juan Francisco Ornelas<sup>18</sup> , Mathieu Perret<sup>19</sup> , Nelson R. Salinas<sup>20</sup> ,  
Stacey D. Smith<sup>21</sup> , Jana C. Vamosi<sup>22</sup> , Isabela G. Varassin<sup>1,11</sup>  and  
Catherine H. Graham<sup>1</sup> 

<sup>1</sup>Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, Birmensdorf 8903, Switzerland

<sup>2</sup>Biodiversity Research Centre, University of British Columbia, 2212 Main Mall, Vancouver, BC, Canada

<sup>3</sup>Department of Environment and Biodiversity, Paris Lodron University of Salzburg, Hellbrunner Straße 34, Salzburg 5020, Austria

<sup>4</sup>Nees Institute for Biodiversity of Plant, University of Bonn, Meckenheimer Allee 170, Bonn 53115, Germany

<sup>5</sup>State Museum of Natural History Stuttgart, Botany Department, Rosenstein 1, Stuttgart 70191, Germany

<sup>6</sup>Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, Zurich 8008, Switzerland

<sup>7</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurestrasse 190, Zurich 8057, Switzerland

<sup>8</sup>Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, Vienna 1030, Austria

<sup>9</sup>Department of Environmental Systems Science, Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 16, Zurich 8092, Switzerland

<sup>10</sup>Securing Antarctica's Environmental Future, School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton 3800, Victoria, Australia

<sup>11</sup>Departamento de Botânica, Universidade Federal do Paraná, Avenida Coronel Francisco H. dos Santos 100, Curitiba 81531-980, Brazil

<sup>12</sup>Department of Biological Sciences, Shirley C. Tucker Herbarium, Louisiana State University, Life Science Annex Building A257, Baton Rouge 70803, LA, USA

<sup>13</sup>Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Rua do Matão 277, Butantã, São Paulo 05508-090, Brazil

<sup>14</sup>Department of Integrative Biology, University and Jepson Herbaria, University of California, Berkeley, 1001 Valley Life Sciences Building, Berkeley 94720-2465, CA, USA

<sup>15</sup>Escuela de Ciencias Exactas y Naturales, Universidad Estatal a Distancia, San José 474-2050, Costa Rica

<sup>16</sup>Institut de Biologie de l'École Normale Supérieure (IBENS), École Normale Supérieure, CNRS, INSERM, Université PSL, UMR 8197, 46 rue d'Ulm, Paris 75005, France

<sup>17</sup>Department of Biology, University of Missouri – St. Louis, St. Louis 63121, MO, USA

<sup>18</sup>Departamento de Biología Evolutiva, Instituto de Ecología, A.C. (INECOL), Xalapa, Veracruz 91073, Mexico

<sup>19</sup>Department of Plant Sciences, Conservatoire et Jardin Botaniques de Genève, University of Geneva, Chem. de l'Impératrice 1, 1292 Pregny-Chambésy, Geneva, Switzerland

<sup>20</sup>Pfizer Plant Research Laboratory, New York Botanical Garden, 2900 Southern Blvd., Bronx, New York City 10458, NY, USA

<sup>21</sup>Department of Ecology and Evolutionary Biology, University of Colorado-Boulder, 1900 Pleasant St, Boulder 80302, CO, USA

<sup>22</sup>Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary T2N1N4, AB, Canada

## ABSTRACT

Plant–hummingbird interactions are considered a classic example of coevolution, a process in which mutually dependent species influence each other's evolution. Plants depend on hummingbirds for pollination, whereas hummingbirds rely on

\* Author for correspondence (Tel.: +41 77 947 31 97; E-mail: [elisabpereira@gmail.com](mailto:elisabpereira@gmail.com)).

nectar for food. As a step towards understanding coevolution, this review focuses on the macroevolutionary consequences of plant–hummingbird interactions, a relatively underexplored area in the current literature. We synthesize prior studies, illustrating the origins and dynamics of hummingbird pollination across different angiosperm clades previously pollinated by insects (mostly bees), bats, and passerine birds. In some cases, the crown age of hummingbirds pre-dates the plants they pollinate. In other cases, plant groups transitioned to hummingbird pollination early in the establishment of this bird group in the Americas, with the build-up of both diversities coinciding temporally, and hence suggesting co-diversification. Determining what triggers shifts to and away from hummingbird pollination remains a major open challenge. The impact of hummingbirds on plant diversification is complex, with many tropical plant lineages experiencing increased diversification after acquiring flowers that attract hummingbirds, and others experiencing no change or even a decrease in diversification rates. This mixed evidence suggests that other extrinsic or intrinsic factors, such as local climate and isolation, are important covariables driving the diversification of plants adapted to hummingbird pollination. To guide future studies, we discuss the mechanisms and contexts under which hummingbirds, as a clade and as individual species (e.g. traits, foraging behaviour, degree of specialization), could influence plant evolution. We conclude by commenting on how macroevolutionary signals of the mutualism could relate to coevolution, highlighting the unbalanced focus on the plant side of the interaction, and advocating for the use of species-level interaction data in macroevolutionary studies.

**Key words:** coevolution, foraging behaviour, mutualism, pollinator shifts, pollination syndrome, specialization, trait evolution, trait matching.

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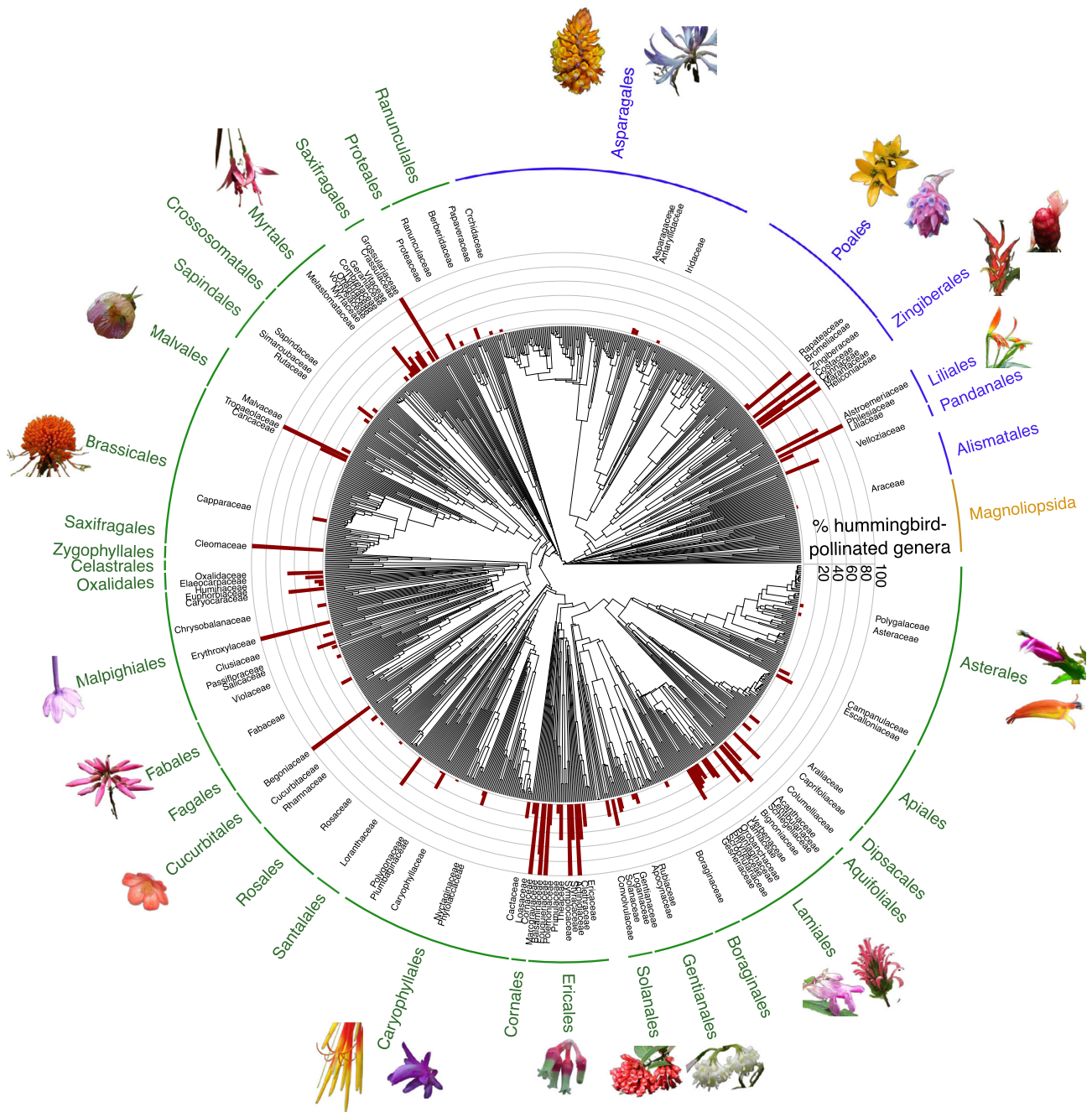
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## I. INTRODUCTION

The 366 extant hummingbird species interact with about 7,000 plant species of varying growth forms (e.g. herbs, epiphytes, shrubs, and, to a lesser extent, trees) spread across ~100 families (Fig. 1) (Fleming & Muchhala, 2008; Abrahamczyk & Kessler, 2015; Rodríguez-Flores *et al.*, 2019). Plants pollinated by hummingbirds tend to have scentless, often red, yellow, or purple flowers with long corolla tubes, protruding stigmas and stamens, no landing platform (Fig. 1) (Grant & Grant, 1968; Feinsinger & Colwell, 1978; Abrahamczyk & Kessler, 2015) and copious amounts of dilute, sucrose-rich nectar [23–25% (Pyke & Waser, 1981; Ornelas *et al.*, 2007)]. This convergence of multiple flower characteristics across various angiosperm clades indicates that hummingbirds imposed a strong selective pressure on flowers (Fenster *et al.*, 2004; Dellinger, 2020;

Rico-Guevara *et al.*, 2021). Hummingbirds are the most species-rich family of bird pollinators and are among the most specialized groups of nectarivorous vertebrates in the world (Fleming & Muchhala, 2008; Zanata *et al.*, 2017). These small birds with vibrant colours and great variation in bill size and curvature are highly dependent on nectar to fuel their extremely fast-paced hovering flight (Schuchmann, 1999; Rico-Guevara *et al.*, 2021). Although hummingbirds also feed on insects, most of their energy intake comes from nectar, which explains the evolution of morphological and behavioural adaptations that optimize energy expenditure and facilitate the location and acquisition of nectar (Hainsworth, 1981; Pigot *et al.*, 2020; Rico-Guevara *et al.*, 2021).

Despite the extensive ecological research on plant–hummingbird interactions (for a recent review, see Leimberger *et al.*, 2022), knowledge of the macroevolutionary consequences of this mutualism remains fragmented. Most macroevolutionary



**Fig. 1.** Family-level phylogeny of angiosperms derived from Smith & Brown (2018) with red bars indicating the percentage of genera native to the Americas with reported hummingbird pollination syndrome or hummingbird visitation within each family (Abrahamczyk & Kessler, 2015; Rodríguez-Flores *et al.*, 2019; Govaerts *et al.*, 2021). The outer arc displays orders, with colours indicating the following major angiosperm clades: yellow, Magnoliidales; blue, Monocotyledoneales; green, Eudicotyledoneales. Photographs illustrate flowers adapted to hummingbird pollination belonging to each order (photographs by Francisco Tobar and Tiago Machado-de-Souza). The phylogeny was obtained using the R package *V.PhyloMaker* (Jin & Qian, 2019) and the figure was produced using *ggTree* (Yu *et al.*, 2017).

explorations of the mutualism focus on the impact of hummingbirds on plants. By reconstructing ancestral states and estimating trait-dependent diversification rates, researchers have identified the direction and timing of the evolutionary shifts in pollination

syndromes and the impact of the mutualism on plant diversification (e.g. Serrano-Serrano *et al.*, 2017; Lagomarsino *et al.*, 2017; Kriebel *et al.*, 2019). By contrast, the evolution of hummingbirds has mostly been explored in relation to their traits, and

environmental and geographic factors (e.g. McGuire *et al.*, 2014; Rombaut *et al.*, 2022; Barreto *et al.*, 2023), with no study examining the role of mutualism on their evolution. In addition, extensive research on plant–hummingbird mutualism has emphasized an ecological perspective, considering aspects such as network structure and the roles of different species within networks (e.g. Tinoco *et al.*, 2017; Dalsgaard *et al.*, 2021). Although the evolution of these network structures and species roles have been explored in a few mutualisms (Gu, Goodale & Chen, 2015; Burin, Guimarães & Quental, 2021), plant–hummingbird networks are not among these.

Herein we review the evolutionary origins of hummingbird pollination, the existing evidence for the influence of hummingbirds on plant evolution, and the potential mechanisms underlying pollinator-driven diversification. We also highlight the challenge of linking such macroevolutionary patterns to the process of coevolution, given the broad range of alternative processes that result in similar patterns. Finally, we propose two future directions. We suggest a detailed evaluation of the role of hummingbirds in plant diversification, considering variation within hummingbird clades and functional groups (e.g. based on morphological features and feeding behaviours). In addition, we emphasize the need to focus on the role of plants in the diversification of hummingbirds. Expanding our understanding of these factors will bring us closer to determining the role of coadaptation in the evolution of this mutualistic system. Both future directions can be leveraged by integrating empirical data from network ecology with macroevolutionary tools.

## II. EVOLUTIONARY ORIGINS OF HUMMINGBIRD POLLINATION

The asymmetry in the number of interacting hummingbird and plant species ( $\sim 366$  and  $\sim 7,000$ , respectively) is likely the result of the evolutionary history and ecological characteristics of these clades. Angiosperms are considerably older, with an estimated origin 140–270 million years ago (Ma) (Sauquet, Ramírez-Barahona & Magallón, 2022). Hummingbirds on the other hand are comparatively younger, with a stem age of  $\sim 43$  Ma, a crown age of around 22 Ma (McGuire *et al.*, 2014) and hummingbird-like fossils found in Europe dating back to the lower Oligocene (30–35 Ma; Mayr, 2003, 2004). Despite the uncertainty of the age estimates of both angiosperms and hummingbirds, it is certain that angiosperm diversity was already high when hummingbirds originated (Cronk & Ojeda, 2008). There were thus many candidate lineages of plants that potentially could adapt to the comparatively smaller number of ancestral hummingbird species, partially explaining the asymmetry in richness among these groups. In addition, plants only flower during a limited time of the year, from several days to months depending on the species. Thus, to meet their energy requirements, hummingbirds interact with many plant species within a year (Stiles, 1985). Considering that

animal-pollinated plants rely on pollinators for moving gametes and that plant reproductive organs are directly involved in the attraction and morphological match with pollinators, even small changes in flower morphology or phenology can lead to pollinator shifts and reproductive isolation (Schemske & Bradshaw, 1999; Wessinger, 2024), trigger adaptive radiations (van der Niet, Peakall & Johnson, 2014), and impact plant diversification rates (Stebbins, 1970; Chomicki *et al.*, 2019; Hernández-Hernández & Wiens, 2020). By contrast, there is no direct link between the mutualism with plants and hummingbird reproductive isolation.

Numerous shifts in pollination mode have occurred throughout the evolutionary history of angiosperms (van der Niet & Johnson, 2012; Stephens *et al.*, 2023). Documenting the timing, frequency, and directionality of such shifts across major angiosperm clades has become a common approach as the availability of large phylogenies and trait databases has increased (reviewed by van der Niet *et al.*, 2014). However, this body of literature has not been synthesized to provide a global estimate of how many times pollination by hummingbirds originated, and when and from which ancestors. Here, we review the literature on the frequency, timing, and evolutionary consequences of the transitions from and to hummingbird pollination. We queried the *Web of Science* for papers in indexed journals using search terms of three classes: first, those related to hummingbirds (e.g. hummingbird, Trochilidae, avian pollinator); second, those related to plants (e.g. flowering plants, angiosperm); and lastly, those related to pollinator shifts or diversification rates (e.g. evolutionary transition, stochastic mapping, speciation rate). The complete list of searched terms is available in online Supporting Information, Appendix S1, while the collected data and details about the methods used to reconstruct ancestral states are summarized in Tables 1 and S1.

### (1) Age of the mutualism

The age of the mutualism between hummingbirds and plants is hard to determine precisely and varies across different families. The oldest plant clade to interact with hummingbirds in the Americas is likely *Heliconia*, a nearly obligatory hummingbird-pollinated Neotropical plant group that originated about 39 Ma (Iles *et al.*, 2017) (Table 1). However, hummingbird fossils found in the Old World are around 32 Ma (Mayr, 2003, 2004), whereas they have only been in the New World for about 22 Ma, based on estimates from the phylogeny of extant species (McGuire *et al.*, 2014). These differences in timing and lack of understanding of the biogeography of early hummingbirds prevent a more detailed understanding of how the close relationship with *Heliconia* came about. Despite such knowledge gaps, the burst in speciation events in *Heliconia* during the Oligocene ( $\sim 34$ –23 Ma) and early Miocene ( $\sim 23$ –16 Ma) (Iles *et al.*, 2017) coincides broadly with the hummingbird radiation in the Americas ( $\sim 22.4$  Ma; McGuire *et al.*, 2014), suggestive of codiversification. However, this time period also coincides with radiations in the hispine rolled-leaf beetles that feed on *Heliconia*,

Table 1. Estimated age of the earliest transition to hummingbird pollination for various angiosperm groups and the effect of hummingbirds on plant diversification rates. Ma = million years ago. Methods used for reconstructing ancestral states and estimating the number of shifts and variations in diversification rates are: BMM = Bayesian analysis of macroevolutionary mixtures, BI = Bayesian inference, BiSSE = binary state speciation and extinction model, ClaSSE = cladogenetic state change speciation and extinction model, DR statistic = species-level lineage diversification rate, FiSSE = fast intuitive state-dependent speciation-extinction analysis, HiSSE = hidden state speciation and extinction model, ML = maximum likelihood, and MP = maximum parsimony. Dashes indicate that no ancestral reconstruction or diversification analyses were carried out for the plant group.

Plant group	Family	Transition from	Earliest transition to hummingbird pollination (Ma)	Age of plant group (Ma)	Method for reconstructing ancestral state	Effect on plant diversification rates	Method for estimating diversification rate	Geographic distribution	Reference
<i>Ruellia</i>	Acanthaceae	Bec	5.8	9	ML and BI	Increase	BiSSE	Temperate and tropical	Tripp & McDade (2013); Tripp & Tsai (2017)
<i>Chauquiara</i>	Asteraceae	Insect	10.81	17.8	BI	-	-	Tropical	Abrahamczyk <i>et al.</i> (2017)
Bromeliaceae	Bromeliaceae	Insect	15.9	22.7	MP and BI	Increase	BiSSE and rate of net species diversification (D)	Tropical	Givnish <i>et al.</i> (2014)
<i>Vriesea</i> and <i>Stigmatodon</i>	Bromeliaceae	Bat	5.8 to 5.4	10.1	BI	-	-	Tropical	Neves <i>et al.</i> (2023)
Andean	Campanulaceae	-	-	5.02	-	Increase	BiSSE	Tropical	Lagamarsino <i>et al.</i> (2016)
Campanulaceae	Compositae	Bec	Not reported	1.99	BI	Decrease	FiSSE and DR statistic	Temperate	Siniscalchi <i>et al.</i> (2023)
North American	Costaceae	Bec	~2.2	3	BI	No effect	BiSSE	Tropical	Vargas <i>et al.</i> (2020); Kay & Grossenbacher (2022)
<i>Cirsium</i>	Costaceae	Bec	~2.2	3	BI	No effect	BiSSE	Tropical	Kriebel <i>et al.</i> (2023a)
<i>Costus</i>	Costaceae	Bec	~2.2	3	BI	No effect	BiSSE	Tropical	Vargas <i>et al.</i> (2020); Kay & Grossenbacher (2022)
Ericaceae	Ericaceae	Insect	14.5	85	ML	-	-	Temperate and tropical	Souza <i>et al.</i> (2021)
<i>Hymenaea</i>	Fabaceae	Bat	11.95	23.9	BI	-	-	Tropical	Roalson & Roberts (2016); Serrano-Serrano <i>et al.</i> (2017)
Gesnerioideae	Gesneriaceae	Insect	18.5	~48	ML and BI	Increase	BiSSE, ClaSSE and HiSSE	Tropical	Souza <i>et al.</i> (2021)
<i>Heliconia</i>	Heliconiaceae	Unknown	Unknown	39	ML	-	-	Tropical	Iles <i>et al.</i> (2017)
<i>Salvia</i>	Lamiaceae	Bec	~22	~31.5 (American lineages <i>ca.</i> 20–22 Ma)	ML	Increase in subgenus <i>Calosphaea</i>	BMM	Temperate and tropical	Kriebel <i>et al.</i> (2019)
<i>Passiflora</i> subg. <i>Tacsonia</i>	Passifloraceae	Unknown	8.38	8.38	MP and ML	-	-	Tropical	Abrahamczyk <i>et al.</i> (2014)
Antirrhineae	Plantaginaceae	Bec	~13.5	~26	MP and ML	No effect	BMM	Temperate and tropical	Ogutten <i>et al.</i> (2017)
<i>Penstemon</i>	Plantaginaceae	Bec	Not reported	Not reported	ML and BI	Decrease	BiSSE, FiSSE and HiSSE	Temperate	Wessinger <i>et al.</i> (2019)
<i>Aquilegia</i>	Ranunculaceae	Bec	3.13	6.38	MP and BI	-	-	Temperate	Bastida <i>et al.</i> (2010)
<i>Salpichroa</i>	Solanaceae	Moth	3.09	7.1	BI	-	-	Tropical	Ibañez <i>et al.</i> (2019)

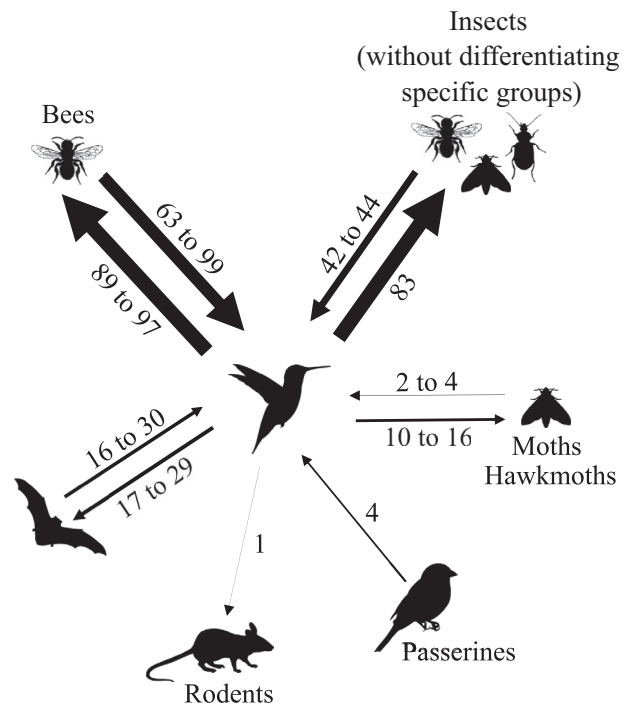
hypothesized as the result of an arms race between the two (McKenna & Farrell, 2006; Iles *et al.*, 2017). Thus, the extent to which the radiation of *Heliconia* is a result of the mutualistic interactions with hummingbirds or the antagonistic interactions with beetles, or both, remains unclear.

Later transitions to hummingbird pollination either occurred contemporaneously or when hummingbirds were presumably well established. For example, the estimated age of the first hummingbird-pollinated species in *Salvia* (Lamiaceae; Kriebel *et al.*, 2019) and Gesneriaceae (Roalson & Roberts, 2016; Serrano-Serrano *et al.*, 2017) (Table 1), coincides with a burst in the diversification of these plant groups and the hummingbird radiation in South America [ $\sim 20$  Ma (McGuire *et al.*, 2014; Serrano-Serrano *et al.*, 2017)], supporting a scenario of co-diversification. At the species level, similar crown ages among interacting partners have been reported for various plant clades, including the morphologically specialized interaction between long-tubed *Passiflora* and the sword-billed hummingbird *Ensifera ensifera* (Abrahamczyk, Souto-Vilarós & Renner, 2014; Abrahamczyk *et al.*, 2015; Abrahamczyk, Poretschkin & Renner, 2017; Abrahamczyk & Renner, 2015), suggesting that the diversity of both groups developed fairly simultaneously. Nonetheless, there are also cases in which hummingbirds are older than the plants they pollinate (e.g. 20 Ma older than *Ruellia*), suggesting that rather than codiversifying, plant diversification was facilitated by pre-existing hummingbird diversity (Tripp & McDade, 2013; Abrahamczyk *et al.*, 2017).

## (2) Ancestral pollination mode and transitions to hummingbird pollination

Our systematic review confirmed that hummingbird pollination evolved repeatedly in at least 22 plant families, often originating from bee-pollinated plants, with an estimated 63 to 99 transitions (Fig. 2; Table S1; Cronk & Ojeda, 2008). Less frequently, pollination by hummingbirds originated from ancestors pollinated by insects other than bees – as is the case for pollination by moths in *Ruellia*, Acanthaceae (Tripp & Manos, 2008) – or by other vertebrates, such as bats [e.g. Bromeliaceae (Givnish *et al.*, 2014); Centro-pogonids: Campanulaceae (Lagomarsino *et al.*, 2017); and Gesneriaceae (Serrano-Serrano *et al.*, 2017)], and passerine birds [e.g. *Erythrina*: Fabaceae (Bruneau, 1997)] (Fig. 2, Table S1).

The context in which transitions to hummingbird pollination occurred remains largely unknown, as exploration of this phenomenon has begun only recently (Vargas *et al.*, 2020; Dellinger *et al.*, 2021; Hamilton & Wessinger, 2022). The occupation of new habitats and changes in flower or pollinator abundances or effectiveness partially explain shifts from bee to hummingbird pollination (Dellinger *et al.*, 2021; Hamilton & Wessinger, 2022). Ecological studies have documented hummingbird visits to flowers lacking the hummingbird pollination syndrome, particularly in situations where these are abundant and ornithophilous flowers are scarce



**Fig. 2.** Estimated number of evolutionary shifts to and from hummingbird pollination in various angiosperm groups as retrieved from the literature (Table S1). Arrows indicate the direction of the shift in pollination mode. Thickness of the arrows represents the average estimated number of shifts, and the numeric values on the arrows reflect the minimum and maximum estimated number of shifts given the multiple studies for particular plant groups and the uncertainty in the reconstruction reported by these studies. Pollinator shifts estimated from studies that do not differentiate between groups of pollinating insects are illustrated under the broad categorization of ‘insects’. Silhouettes are public domain and were obtained from PhyloPic (<https://www.phylopic.org/>).

(Dalsgaard *et al.*, 2009; Abrahamczyk & Kessler, 2015; Waser, CaraDonna & Price, 2018). Such context-dependent foraging on non-ornithophilous plants by hummingbirds may represent the beginnings of directional selection acting on plants, eventually leading to a pollinator shift, trait evolution (e.g. convergence to a hummingbird pollination syndrome), and reproductive isolation (Grant, 1949; Thomson & Wilson, 2008). Compared to insect pollination, hummingbird pollination is presumably more effective in terms of outcrossing (Abrahamczyk *et al.*, 2022; Dellinger *et al.*, 2022), which could facilitate shifts from insect to hummingbird pollination.

Evolution is expected to promote trait matching between interacting partners to maximize their mutual benefit (Thompson, 1999; Garibaldi *et al.*, 2015; Manceau, Lambert & Morlon, 2016; Lopes *et al.*, 2022). Matching is frequently observed in species interactions from resource–service mutualisms, from pollination and seed dispersal to predator–prey interactions in food webs (Eklöf *et al.*, 2013).

There is evidence of morphological and phenological trait matching in pairs of interacting plants and hummingbirds across spatial, temporal, and phylogenetic scales often leading to specialized interactions (e.g. McKinney *et al.*, 2012; Weinstein & Graham, 2017; Sonne *et al.*, 2020; reviewed in Leimberger *et al.*, 2022). Trait matching increases flower visitation rates (Maglianesi *et al.*, 2014; Weinstein & Graham, 2017), reduces hummingbird handling times by increasing nectar extraction (Temeles *et al.*, 2009; Maglianesi *et al.*, 2014), and promotes increased pollen deposition and seed set (Bustos *et al.*, 2023). Two prominent examples of trait matching are those between the corolla length of some *Passiflora* (Passifloraceae) species pollinated by the long-billed *Ensifera ensifera* (Abrahamczyk *et al.*, 2014) and between the corolla curvature of *Centropogon* (Campanulaceae) pollinated by curved-billed sicklebill hummingbirds (Lagomarsino *et al.*, 2017). Nonetheless, some hummingbirds circumvent trait mismatch by piercing the base of the corolla or using holes made by other piercers to access the nectar of long-tubed flowers (Colwell, 1973; Lara & Ornelas, 2001; Duchenne *et al.*, 2023). By disrupting the mutualistic relationship and impacting fitness, nectar robbing likely influences evolutionary processes (Lara & Ornelas, 2001; Irwin *et al.*, 2010); however the mechanism by which this evolved is beyond the scope of this review.

Strong trait matching can emerge from trait convergence at one trophic level, even in the absence of coevolution (Janzen, 1980; Nuismer, Gomulkiewicz & Ridenhour, 2010), or as a result of other selective pressures unrelated to the mutualism (Stebbins, 1970; Strauss & Irwin, 2004; Hembry & Weber, 2020). One example of convergent evolution is the extreme curvature of floral tubes in *Heliconia* and *Centropogon*. Both plants interact with the curved-billed sicklebill (*Eutoxeres* sp., stem age 21.5 Ma), which likely coevolved with *Heliconia* in the lowlands (stem age 39 Ma) and also pollinates the recently diverged Andean *Centropogon* (stem age 3.6 Ma) (Abrahamczyk *et al.*, 2017; Lagomarsino *et al.*, 2017; Iles *et al.*, 2017). An example of a selective pressure unrelated to mutualism includes predation pressure selecting for longer feeding apparatus in the pollinator and indirectly triggering the evolution of long corollas (Wasserthal, 1997; Whittall & Hodges, 2007). In plant–hummingbird interactions, it remains to be tested whether plants evolved long tubular corollas because of reciprocal evolution (i.e. coevolution) (Abrahamczyk *et al.*, 2014) or from tracking long-billed hummingbirds whose bills evolved mostly in response to intraspecific competition, where the bills are used to fight (Rico-Guevara *et al.*, 2019, 2021). Additional examples in which trait matching can emerge from processes other than coevolution include response to herbivory (Jogesh *et al.*, 2017) and environmental trait filtering (Nuismer *et al.*, 2010).

Mutualistic systems also involve the evolution of mismatching traits (de Andreazzi, Astegiano & Guimarães, 2020) that act as barriers to avoid certain species interactions (so-called forbidden links; Jordano, Bascompte & Olesen, 2003). Thus, shifts to hummingbird pollination could also be triggered by

the selection of traits to restrict bees or other pollinators (Martén-Rodríguez, Almarales-Castro & Fenster, 2009); e.g. red flowers, tubular corollas, basal corolla constriction, reduced landing platforms, and the absence of floral guides in many hummingbird-pollinated flowers (Clark, Clavijo & Muchhala, 2015; Zung *et al.*, 2015; Bergamo *et al.*, 2019). Red flowers could have evolved to limit attractiveness to bees, since these insects perceive wavelengths only up to 550 nm [anti-bee hypothesis (Lunau *et al.*, 2011; Camargo *et al.*, 2019)]. By contrast, these flowers could have evolved to favour hummingbird pollination, as hummingbirds perceive colours from 300 to 660 nm and the median reflectance of Neotropical red flowers is above 585 nm [pro-bird hypothesis (Chittka & Waser, 1997; Shrestha *et al.*, 2013)].

### (3) Transitions away from hummingbird pollination

Reversals from hummingbird to bee pollination were initially thought to be rare (Wilson *et al.*, 2007; Tripp & Manos, 2008; Barrett, 2013), but our review of the literature shows that reversals can be relatively common in some plant groups (Fig. 2, Table S1). The expectation that reversals are rare stemmed from several assumptions: hummingbirds are more efficient pollinators than insects (Castellanos, Wilson & Thomson, 2003; Cardona, Lara & Ornelas, 2020; Mackin *et al.*, 2021); the genetic pathway for the reversal of traits selected to favour hummingbird pollination, or to deter visitation by bees, is difficult (Smith & Rausher, 2011; Barrett, 2013; Wessinger, 2024); and flowers with a hummingbird pollination syndrome would rarely attract insect visitors, limiting the evolutionary potential for such transitions. Empirical evidence, however, suggests that reversals to insect pollination vary across plant groups, ranging from none [e.g. Antirrhineae: Plantaginaceae (Ogutcen *et al.*, 2017); *Cos-tus*: Costaceae (Kay & Grossenbacher, 2022)] to many [e.g. Gesneriaceae (Serrano-Serrano *et al.*, 2017); Bromeliaceae (Givnish *et al.*, 2014); *Salvia* (Kriebel *et al.*, 2019)] (Fig. 2, Table S1). In Gesneriaceae, for example, reversal to insect pollination was more than twice as frequent ( $76.5 \pm 18$  times) as shifts from insect to hummingbird pollination ( $31.5 \pm 10$  times) (Serrano-Serrano *et al.*, 2017). Such reversals might be advantageous for plants whenever the cost of producing large flowers with copious nectar is not compensated by hummingbird efficiency, for example, in conditions of high resource availability and competition for pollinators, when hummingbirds forage on multiple plant species (Tinoco *et al.*, 2017), which could increase heterospecific pollen deposition. Even among hummingbird-pollinated plants, those that evolved highly specialized morphologies, as is the case for the long-tubed *Passiflora*, have sometimes reversed to more generalized morphologies (Abrahamczyk *et al.*, 2014).

Evolutionary shifts away from hummingbird pollination may also lead to generalization, with plants being pollinated by more than one functional group if pollinators are equally efficient or abundant (Manning & Goldblatt, 2005). Such mixed-pollination systems are common in angiosperms and are often associated with niche partitioning, such as temporal



partitioning among diurnal hummingbirds and nocturnal bats (Dellinger *et al.*, 2019a,b; Lagomarsino & Muchhala, 2019). Mixed pollination can reduce the effects of local extinction, fluctuation in the abundance of pollinators, or low diversity of pollinators (Wilson *et al.*, 2007). For instance, shifts from hummingbird to mixed pollination syndrome in plants invading islands with depauperate pollinator diversity likely increase plant pollination success (Armbruster & Baldwin, 1998; Martén-Rodríguez *et al.*, 2010). Across evolutionary time, mixed pollination can also be an intermediate state that precedes a complete shift between functional groups (i.e. intermediate stage of double function; Stebbins, 1970), such as the transition from hummingbird to bee pollination in *Salvia* (Lamiaceae) (Fragoso-Martínez *et al.*, 2018).

### III. HUMMINGBIRD POLLINATION AND PLANT DIVERSIFICATION

Several angiosperm clades whose species are pollinated by hummingbirds are more diverse than sister clades pollinated by insects (Beardsley, Yen & Olmstead, 2003; Berry *et al.*, 2004; Schmidt-Lebuhn, Kessler & Hensen, 2007), which raises the question as to whether hummingbirds positively influence rates of plant diversification (Schmidt-Lebuhn *et al.*, 2007). Bromeliaceae, Gesneriaceae, Campanulaceae, and Acanthaceae (*Ruellia*) clades with a hummingbird pollination syndrome have higher speciation rates than those with an insect pollination syndrome (Table 1) (Givnish *et al.*, 2014; Lagomarsino *et al.*, 2016; Serrano-Serrano *et al.*, 2017; Tripp & Tsai, 2017). However, in other plant clades, hummingbird pollination had either no effect [e.g. Antirrhineae: Plantaginaceae (Ogutcen *et al.*, 2017); *Costus* (Kay & Grossenbacher, 2022)], or even was related to decreased diversification rates [*Penstemon* (Wessinger, Rausher & Hileman, 2019); *Cirsium* (Siniscalchi, Ackerfield & Folk, 2023)] (Table 1).

Plant diversification rates correlate with several intrinsic and extrinsic biotic and abiotic factors (Vamosi & Vamosi, 2011; Hembry & Weber, 2020), making it difficult to tease apart the relative impact of hummingbirds on plant diversification (Kessler, Abrahamczyk & Krömer, 2020). The species-rich Bromeliaceae, for example, a group in which half of the 3,700 species are likely pollinated by hummingbirds (Kessler *et al.*, 2020), experienced twofold higher diversification rates in lineages that are hummingbird-pollinated compared to those pollinated by other animals (Schmidt-Lebuhn *et al.*, 2007; Givnish *et al.*, 2014). However, increased diversification rates in Bromeliaceae are also correlated with other factors, such as tank formation, epiphytism, and mountain habitats. Increased diversification rates in mountains, in particular, may result from hummingbirds being more efficient than other pollinators at high elevations (Cruden, 1972; see Sections IV.1 and IV.2). Similarly, bell-flowers (Campanulaceae) in the Andes that are pollinated by vertebrates, including hummingbirds, diversified six times

faster than those pollinated by insects (Lagomarsino *et al.*, 2016). However, non-pollination factors also relate to variation in the diversification rates of this group, such as the Andean uplift and decreasing temperature (Lagomarsino *et al.*, 2016). All these non-pollination factors could either directly affect diversification and/or be indirectly favouring vertebrate pollination and thus accelerating plant diversification rates. Interdisciplinary studies that combine biotic interactions, macroevolution and geodynamics are thus needed for a more holistic understanding of the relative importance of interactions on species diversity (Harmon *et al.*, 2019).

Increased net diversification related to hummingbird pollination could also result from frequent transitions between different pollinator groups, coupled with floral changes, divergent selection, and reproductive isolation (i.e. Grant–Stebbins pollinator-shift model) (Schiestl & Schlüter, 2009; Johnson, 2010; Chomicki *et al.*, 2019). Gesneriaceae is currently the only group for which studies have attempted to discern whether plant diversification is influenced by hummingbird pollination or by the shift in pollinator groups (Serrano-Serrano *et al.*, 2017). Hummingbird-pollinated clades exhibited a speciation rate twice as high as bee-pollinated ones, but transitions among pollinator groups were not associated with higher rates of cladogenesis (Serrano-Serrano *et al.*, 2017). Frequent transitions to hummingbird pollination could also take place without resulting in accelerated diversification rates. This is the case for *Penstemon* in western North America, for which hummingbird pollination originated at least 17 times, and mostly on terminal branches, but is associated with reduced diversification rates (Wessinger *et al.*, 2019). Other hummingbird-pollinated plant clades in North America also seem to have experienced frequent transitions from bee pollination followed by little or no increase in diversification (Abrahamczyk & Renner, 2015).

Data to explore the potential influence of hummingbirds on plant diversification are increasingly available, but many plant families in which hummingbird pollination is frequent have not yet been thoroughly studied, such as Acanthaceae (except for *Ruellia*; Tripp & Tsai, 2017), Ericaceae, Cactaceae, Rubiaceae, and Solanaceae. Further, there are no tests for differential effects of specific hummingbird clades (i.e. hermits on *Heliconia* and *Costus*, coquettes on canopy plants) on plant diversification (see Section VI). Filling these gaps will be an important step forward to understanding the role of evolution in the plant–hummingbird mutualism.

### IV. HUMMINGBIRDS AS POLLINATORS

The most effective pollinator principle posits that flower characteristics are shaped by the most frequent and effective pollinator (Stebbins, 1970). These pollinators increase plant fitness by increasing plant reproduction because of the higher frequency of conspecific pollen deposition, greater and better seed production, and reduced pollen loss and mechanical

damage to the flower (Montgomerie, Eadie & Harder, 1984; Vázquez & Aizen, 2004; Cronk & Ojeda, 2008). Here we review the characteristics of hummingbirds that may render them effective (potential for successful pollination) and/or efficient (cost–benefit ratio between resources expended and pollination or foraging output) pollinators (Ne'eman *et al.*, 2010), both as groups of morphologically similar species and as individual species. We then describe the specific contexts in which hummingbirds can be more or less effective and/or efficient than other pollinators and how this might impact plant diversity.

### (1) Effectiveness and efficiency

Certain ecological characteristics of hummingbirds make them particularly effective and/or efficient pollinators. Hummingbirds have no interest in pollen, unlike other pollinators, notably bees, who actively collect it as food for their brood (Schlindwein *et al.*, 2005; Muchhala & Thomson, 2010). Hummingbirds also groom less than bees, which reduces pollen loss and increases the chance that pollen will be gradually deposited in multiple flowers (i.e. greater pollen carryover) (Castellanos *et al.*, 2003; Holmquist, Mitchell & Karron, 2012). The multiple paternity promoted by such pollen transfer can have positive effects on plant diversification by decreasing rates of selfing and increasing seed set (Wessinger, 2021; Abrahamczyk *et al.*, 2022). Lastly, the large body size of hummingbirds, compared to insects, offers plants a larger area of contact for depositing pollen. Placing pollen on specific parts of the pollinator body helps to ensure greater conspecific pollen delivery that promotes plant species coexistence through niche partitioning (Brown & Kodric-Brown, 1979; Murcia & Feinsinger, 1996; Sazima, Buzato & Sazima, 1996). Such divergent use of the same pollinator can also trigger speciation by reproductive isolation (Armbruster & Muchhala, 2009).

Pollinator mobility has direct consequences for the geographic and genetic structure of plant populations, which could have contrasting effects on plant diversification (Wessinger, 2021). Pollinating birds are expected to move pollen over long distances given their great flight capacity (Warrick *et al.*, 2012; Ortega-Jimenez *et al.*, 2016; Krauss *et al.*, 2017). On the one hand, the long-distance pollen dispersal and gene flow promoted by these highly mobile pollinators results in outcrossed plant populations with weaker genetic structure than those pollinated by insects (Krauss *et al.*, 2017; Gamba & Muchhala, 2020, 2023; Dellinger *et al.*, 2022). Such genetic cohesion among populations is likely to reduce the chances of allopatric speciation events (Claramunt *et al.*, 2012; Harvey *et al.*, 2017). On the other hand, it is possible that long-distance pollen dispersal positively affects plant diversification by reducing the likelihood of self-pollination, thereby increasing genetic variance and evolutionary potential (Krauss *et al.*, 2017; Wessinger, 2021; Abrahamczyk *et al.*, 2022). Finally, while there is evidence that hummingbirds move larger distances than bees, recent work by Schmidt-Lebuhn *et al.* (2019) found bee-pollinated

species of *Justicia* to have pollen carried longer distances than hummingbird-pollinated species, calling into question the assumption that greater mobility in hummingbirds results in greater pollen movement and leaving room for further investigation.

Pollination by hummingbirds is also advantageous when considering the relatively wide range of environmental conditions that these birds tolerate. Given their thermoregulatory capacity and high visual acuity (Cruden, 1972; Altshuler & Dudley, 2002; Cronk & Ojeda, 2008), hummingbirds thrive in a broad range of environments, such as rainy, cold, and foggy conditions typical of high-elevation tropical mountains (Stiles, 1978). By contrast, the richness, abundance, and pollination efficiency of insects (mostly bees) decreases in cold environments with poor visibility (Cruden, 1972; Arroyo, Primack & Armesto, 1982; Armbruster & Berg, 1994; Dellinger *et al.*, 2021). Bats are likely also more constrained by rain and cold than hummingbirds because of their membranous wings and nocturnal habits, resulting in bat pollination being rare at high latitudes and elevations (Stiles, 1978).

### (2) Spatial variation

Environmental conditions and biogeographical context likely influence the tempo and mode of plant diversification in response to hummingbirds and result in spatial variation in plant diversity (Sletvold, 2019). As detailed above, the moist, cold and oxygen-limited environment of tropical mountains negatively impacts bee activity, but hummingbirds can still forage efficiently (Cruden, 1972; Dellinger *et al.*, 2021). As a result, hummingbird pollination becomes more common with increasing elevation in the Neotropics (Dellinger *et al.*, 2023), a pattern found for various individual plant groups [Loasaceae (Ackermann & Weigend, 2006); Bromeliaceae (Givnish *et al.*, 2014; Kessler *et al.*, 2020); Rubiaceae (Lehmann *et al.*, 2019); and Merianieae: Melastomataceae (Dellinger *et al.*, 2021, 2022)]. The sole exception thus far is *Costus*, whose elevational range does not extend as high as the aforementioned groups (Vargas *et al.*, 2020; Kay & Grossenbacher, 2022). Great efficiency together with high hummingbird richness in Neotropical mountains likely favours the selection of plant traits that attract and promote hummingbird fidelity (e.g. changes in nectar composition; Ackermann & Weigend, 2006), increasing the chances of pollinator shifts from bee to hummingbird pollination (Kessler *et al.*, 2020; Dellinger *et al.*, 2021, 2023; Maguiña-Conde, Zuñiga-Rivas & Kay, 2023). In bromeliads, for example, the evolution of hummingbird pollination correlates with the occupation of moist habitats above 1,000 m elevation, and both are correlated with accelerated evolutionary rates (Givnish *et al.*, 2014). This elevational pattern however is not the same in the temperate zone, where hummingbird pollination is more strongly associated with lower elevations and milder climatic conditions (Grant & Grant, 1968; Hamilton & Wessinger, 2022; Dellinger *et al.*, 2023).

The biogeographical history, the diversity of hummingbirds, and their migratory status could explain latitudinal

variation in how hummingbird pollination influences plant diversity. Hummingbirds likely migrated from Eurasia to North and then South America sometime between 40 and 22 Ma and then went extinct in both Eurasia and North America, so that all extant hummingbirds descend from lineages that colonized South America (McGuire *et al.*, 2014). Over the past 22 Ma, hummingbirds diversified extensively in South America, and around the last 15 to 12 Ma they recolonized Central and North America (McGuire *et al.*, 2014; Licona-Vera & Ornelas, 2017). This reticulate biogeographical history is reflected in the estimated age when plants began interacting with hummingbirds on the different continents (Table 1). The plant–hummingbird mutualism is typically older in South than in North America, dating at least to 22 Ma (Table 1) as opposed to around 9 to 5 Ma in most North American lineages (Grant & Grant, 1968; Abrahamczyk & Renner, 2015; Licona-Vera & Ornelas, 2017). The sole exception so far is the North American *Salvia* subgenus *Calosphaea*, for which the hummingbird syndrome could have evolved about 20 to 12 Ma, indicating adaptation to hummingbirds during the first wave of colonization (Kriebel *et al.*, 2023a,b; Sazatornil *et al.*, 2023). A positive effect of hummingbirds on plant diversification in the Neotropics could be partially explained by the longer history of these birds in South America, as opposed to a negative or negligible effect on the North American flora due to the relative recency of plant–hummingbird interactions (Yoder *et al.*, 2010). In addition, the greater taxonomic and functional diversity of hummingbirds in the Neotropics than in temperate North America (only 11 species in total belonging to two hummingbird clades), together with the fact that most species are not long-distance migrants, may prompt plant diversification and pollinator specialization in response to increased interspecific competition for pollinators (Grant & Grant, 1968; Muchhala, Johnsen & Smith, 2014; Wessinger *et al.*, 2019). In fact, nectarivory is prevalent in tropical and subtropical zones, where flowers are available year-round (Cronk & Ojeda, 2008; Kissling *et al.*, 2012).

### (3) Interspecific variation

Hummingbird morphological and behavioural diversity may yield selective pressures on plants potentially resulting in divergent selection in floral traits and specialization to different hummingbird species (reviewed in Leimberger *et al.*, 2022). Hummingbird morphological traits vary dramatically across species; their body mass varies from 1.9 to 20.2 g (mean  $\pm$  SD  $4.8 \pm 2.18$  g) and their bill length from 1.10 to 9.73 cm ( $2.19 \pm 0.80$  cm) (Tobias *et al.*, 2022). This trait variation can exert selection on floral traits that result in reproductive isolation (Kay, 2006; Muchhala *et al.*, 2014), new ecological opportunities (Chomicki *et al.*, 2019), and different diversification regimes across geographic gradients (see Section IV.2). An example of how hummingbird niche partitioning can lead to plant reproductive isolation is the Caribbean purple-throated hummingbird (*Eulampis jugularis*), whose sexual dimorphism in body size, bill shape, and foraging strategies result in male and females visiting different *Heliconia* species (Temeles &

Kress, 2003; Temeles *et al.*, 2019). From the pollinator perspective, morphological traits of hummingbirds correlate with their diversification rates, with higher rates among smaller short-billed species (Barreto *et al.*, 2023). These small and short-billed hummingbirds are often generalists and might more easily take advantage of primarily insect-pollinated flowers given their comparatively lower nectar requirements, which facilitates coexistence (Feinsinger & Colwell, 1978; Maglianesi *et al.*, 2014). Although bill morphology is known to mediate interactions with plants, whether hummingbird trait evolution and diversification correlate with plant diversification rates remains unexplored.

The foraging strategy adopted by hummingbirds influences pollen dispersal which can have cascading effects on plant diversity and evolution (Wessinger, 2021). Two foraging strategies, territoriality and trap-lining, lie at the ends of a behavioural spectrum. Territorial species (mostly non-hermit hummingbirds) exploit clumped, defensible resources, often foraging on several plant species within a limited area (Feinsinger & Colwell, 1978; Sargent, Groom & Rico-Guevara, 2021). On one hand, such behaviour restricts pollen movement, which could increase inbreeding and facilitate speciation events by increasing spatial differentiation among plant populations (McDade, 1985; Cronk & Ojeda, 2008; Abrahamczyk *et al.*, 2022). On the other hand, the aggressive behaviour of territorial birds could increase pollen dispersal by individuals that are chased away from a foraging patch (Stiles, 1975; Temeles & Kress, 2010; Krauss *et al.*, 2017). Trap-lining hummingbirds are ecologically more specialized than territorialists, and follow a circuit in which they successively visit flowering plants with long flower tubes and plentiful nectar, such as *Heliconia* (Stiles, 1975; Linhart *et al.*, 1987; Sargent *et al.*, 2021). As a result, they likely move pollen over longer distances and promote greater outcrossing rates and multiple paternity (Snow & Snow, 1972; Stiles, 1975; Torres-Vanegas *et al.*, 2019; Wessinger, 2021). Despite these hypothesized relationships between hummingbird behaviour and plant reproduction, there is limited evidence of how different hummingbird foraging strategies relate to plant fitness (Betts, Hadley & Kress, 2015; Torres-Vanegas *et al.*, 2019). From a macroevolutionary perspective, alternative foraging behaviours have not shown differential impacts on hummingbird diversification (Rombaut *et al.*, 2022), and as yet, there have been no tests if these pollinator behaviours have affected plant evolution. The fact that hummingbirds can be flexible in their foraging behaviour depending on the context poses a challenge to addressing questions at the species level (Sargent *et al.*, 2021).

## V. ARE THERE MACROEVOLUTIONARY SIGNALS OF COEVOLUTION AMONG PLANTS AND HUMMINGBIRDS?

Interacting species experience reciprocal selection and potentially influence each other's evolution in a process

called coevolution (Darwin, 1862; Ehrlich & Raven, 1964; Janzen, 1980; Thompson, 1994). Plant–hummingbird interactions are considered a classic example of coevolution because of the striking correspondence in corolla and bill morphology, and how specialized they are in their interactions (reviewed in Leimberger *et al.*, 2022), which is suggestive, but not definite proof, of coevolution. In the broadest sense, coevolution among angiosperms and hummingbirds is evident from the evolutionary convergence of flower traits that attract hummingbirds while discouraging visits from other functional groups of pollinators (Guimarães Jr, Jordano & Thompson, 2011; Abrahamczyk & Kessler, 2015), and from hummingbirds' physiological and morphological adaptations to feed from flowers (Rico-Guevara *et al.*, 2021). While this broad-level evidence supports a scenario of coevolution, empirical evidence for it remains scarce due to the difficulty of quantifying hummingbird fitness and limited assessments of how plant reproductive success varies in response to different hummingbirds (reviewed in Rico-Guevara *et al.*, 2021; Leimberger *et al.*, 2022).

Evidence for coevolution in mutualisms comes mostly from 1:1 obligate mutualisms, in which interacting organisms depend on each other for reproduction (e.g. figs and wasps, yucca and yucca moths) (Hembry, Yoder & Goodman, 2014; Anderson, 2015). Free-living mutualisms on the other hand often involve several species that interact with each other at different frequencies and with different efficiencies, as is the case for plants and hummingbirds (reviewed by Leimberger *et al.*, 2022). If coevolution is indeed happening in such systems, it is most likely a case of multispecies coevolution, in which coevolution involves multiple species tangled in a network of interactions (Thompson, 1982, 2005). Empirical studies of multispecies coevolution are challenging because each interacting species can impose different selective pressures on different traits, in addition to indirect effects from non-interacting species (Bergamo *et al.*, 2017; Guimarães *et al.*, 2017). Thus, plant–hummingbird interactions present both a challenge and an opportunity to study coevolution.

Tests of hypotheses for multispecies coevolution should involve multiple lines of evidence including micro- and macroevolutionary patterns and processes. Coevolution operates at microevolutionary scales through reciprocal selection among interacting populations (Thompson, 2005; Carmona, Fitzpatrick & Johnson, 2015). Local-scale studies that measure fitness on both sides of the plant–hummingbird interaction would provide direct evidence of coevolution (reviewed in Leimberger *et al.*, 2022). Such studies would be particularly illuminating if they measured trait and fitness variation across spatial or environmental gradients (Thompson, 2005; Pauw, Stofberg & Waterman, 2009; Ocampo-Sandoval *et al.*, 2021). However, given that microevolutionary processes often leave detectable macroecological and macroevolutionary signals (Kiestler, Lande & Schemske, 1984; Yoder & Nuismer, 2010; Guimarães Jr *et al.*, 2011; Zhang, Hui & Pauw, 2013; Maliet, Loeuille & Morlon, 2020), additional lines of evidence could come from studying macroevolutionary patterns (Hembry *et al.*, 2014).

Trait convergence within the same trophic level (e.g. pollination syndromes) and trait matching among interacting partners, both of which are common in plant–hummingbird interactions, align with theoretical predictions arising from simulations of multispecies coevolution (Guimarães Jr *et al.*, 2011). However, trait matching is not exclusively the result of coevolution and can emerge from processes such as one-sided evolution, trait-tracking, and similar responses to environmental conditions (detailed in Section II.2). In addition, mutualistic interactions could be under a coevolutionary arms race, a dynamic often overlooked in simulation models that typically attribute greater fitness with increasing trait matching (Yoder & Nuismer, 2010; Guimarães Jr *et al.*, 2011; de Andreazzi *et al.*, 2020; Maliet *et al.*, 2020). In this coevolutionary arms race, pollinator fitness increases with feeding apparatus longer than the corolla, while the opposite is true for the plant, resulting in trait escalation (Pauw *et al.*, 2009; Week & Nuismer, 2021). To gain additional evidence on whether mutualistic coevolution could be at play, one could determine if the traits of interacting partners evolved in a correlated manner by testing for congruence in the timing, pace, and direction of changes in traits related to the mutualism (e.g. bill and corolla length and curvature) (Lomáscolo *et al.*, 2019). This approach has yet to be applied to the plant–hummingbird mutualism. An additional way to explore macroevolutionary signals of coevolution is based on patterns of diversification. In most plant groups studied so far, accelerated rates of diversification were detected among hummingbird-pollinated lineages. Conversely, a few other plant groups exhibit declining rates or no effect of the adaptations to hummingbird pollination (Table 1). Increased net diversification of one or both interacting groups is one possible outcome of coevolutionary diversification in which coevolution acts as a source of divergent selection (Thompson, 2005; Althoff, Segraves & Johnson, 2014; Hembry *et al.*, 2014). However, simulations suggest that evolutionary stasis, not diversification, is the most probable outcome because of stabilizing selection (Yoder & Nuismer, 2010; Chomicki *et al.*, 2019; Maliet *et al.*, 2020).

Although these micro- and macroevolutionary tests could yield patterns consistent with coevolution, a major challenge is ruling out alternative processes. Further, additional intrinsic and extrinsic factors are known to influence diversification rates and these should be accounted for simultaneously with the role of the mutualism (Givnish *et al.*, 2014; Lagomarsino *et al.*, 2016; see Section III). To date, these alternative factors have not been sufficiently explored. This limitation stems mostly from a shortage of phylogenetic comparative methods that integrate data on species interaction and coevolution with macroevolutionary dynamics (Weber *et al.*, 2017; Harmon *et al.*, 2019; Maliet *et al.*, 2020); this is an important area for future development given the difficulty of linking interactions among individuals at the microscale with phylogenetic patterns at the macroscale.

## VI. FUTURE DIRECTIONS

We illustrate two examples of how interaction data at finer taxonomic scales could offer a more nuanced assessment of macroevolutionary patterns in plant–hummingbird systems. First, most of the evidence we reviewed here treats hummingbirds collectively, particularly in the context of pollinator shifts and pollinator-mediated evolution of plants (but see Abrahamczyk *et al.*, 2014; Lagomarsino *et al.*, 2017). Employing similar approaches but with species or group-level information on hummingbirds, in addition to comparing them to other functional groups (e.g. bees, bats) could prove insightful. This could be done, for example, by categorizing hummingbirds in various ways, including morphological groups (e.g. long- or short-billed, straight or decurved-billed hummingbirds), phylogenetic clades (e.g. coquettes, hermits, etc.), feeding/foraging behaviour (e.g. territorialists, trapliners, and generalists; species that rely on clinging to a branch while foraging *versus* non-clingers), and their role or position in the interaction network (e.g. interaction modules) (Feinsinger & Colwell, 1978; Stiles, 1985; Colwell *et al.*, 2023). Morphologically similar and/or phylogenetically related plant species tend to interact with a similar set of hummingbird species and *vice versa* (Martín González *et al.*, 2015; Rodríguez-Flores *et al.*, 2019; Dalsgaard *et al.*, 2021), resulting in interaction modules where specific groups of species specialize and share similar interaction partners (Bascompte & Jordano, 2007; Olesen *et al.*, 2007). These groups of interacting species offer a viable unit of analysis for evolutionary studies in systems where the evolutionary pressure acts among groups of interacting species (Hutchinson, Cagua & Stouffer, 2017; Blasco-Costa *et al.*, 2021). By focusing on hummingbird-specific relationships or characteristics, in addition to comparisons with other pollinator groups, a more granular understanding of the evolution and coevolution of plant–hummingbird interactions could be achieved.

Previous work has documented how shifts to hummingbird pollination affect diversification rates in plants. However, our understanding of how plants mediate hummingbird trait evolution and diversification rates remains scarce (Pauw, 2019; Ocampo-Sandoval *et al.*, 2021) and represents a second open research area (Rico-Guevara *et al.*, 2021). Only more recently has the macroevolution of pollinators been investigated in the context of the plants they interact with (Dorchin *et al.*, 2021; Peris & Condamine, 2024). Macroevolutionary signals of the interaction with plants on the hummingbirds are especially rare because nectarivory originated only once in hummingbirds, unlike angiosperms where hummingbird pollination evolved multiple times. Multiple origins of a character state make it possible to test for its effect on the evolution of the group, as is the case for seed dispersal by primates (Gómez & Verdú, 2012) and pollination by Phyllostomidae bats (Rojas *et al.*, 2012). We suggest that one could conduct a finer-grained study within hummingbirds by, for example, comparing the evolutionary dynamics of different plant groups on hummingbird evolution. Reported plant–hummingbird

interactions show a phylogenetic pattern in which specific hummingbird clades interact mostly with specific plant clades (Rodríguez-Flores *et al.*, 2019). For example, while all hummingbird clades interact with Asteraceae and Bromeliaceae, Cactaceae have no reported interaction with the hermits, brilliants and topazes (Rodríguez-Flores *et al.*, 2019). Lastly, network properties, the degree of ecological specialization and specific pollinator traits could also be used for reconstructing the timing and diversification rates of the interacting partners (Harmon *et al.*, 2019; Burin *et al.*, 2021). The integration of species interaction data into macroevolutionary hypotheses is now possible due to the increasing availability of interaction records across diverse geographic regions and times (e.g. Weinstein & Graham, 2017; Dalsgaard *et al.*, 2021; López-Segoviano *et al.*, 2021; Maglianesi *et al.*, 2024), well-resolved phylogenetic trees (McGuire *et al.*, 2014; Smith & Brown, 2018), and comprehensive species trait data (Dalsgaard *et al.*, 2021; Tobias *et al.*, 2022).

## VII. CONCLUSIONS

- (1) Hummingbird pollination evolved independently multiple times across different angiosperm clades (Fig. 1), mostly from bee-pollinated ancestors, but also from species pollinated by moths/hawkmoths and other insects, as well as passerine birds and bats (Fig. 2). Reversals from hummingbird pollination are also common. The context under which pollinator shifts happened is still largely unexplored.
- (2) The timing when a plant clade shifted to hummingbird pollination and the consequences on diversification vary considerably among angiosperms. In some groups both plant and hummingbird diversity developed contemporaneously, whereas in others the plants are younger than the hummingbirds they interact with.
- (3) The emergence of flowers with the hummingbird pollination syndrome coincides with accelerated diversification rates in some angiosperm clades (Bromeliaceae, Gesneriaceae, Campanulaceae, Acanthaceae: *Ruellia*), but not in others (Plantaginaceae: Antirrhineae and *Penstemon*, Costaceae: *Costus*).
- (4) Transitions to hummingbird pollination are more common at higher elevations and tropical latitudes due to a combination of historical and physiological factors. A current challenge is to evaluate the relative influence of different factors, such as geographic processes, mutualistic interactions, behaviour of pollinators, and plant intrinsic factors, on plant diversification.
- (5) There are many mechanisms through which hummingbirds can influence plant diversification. These include tolerance to a broad range of environmental conditions, great mobility, and interspecific morphological variation among hummingbirds, e.g. bill morphology. While all these factors could influence floral evolution, aspects of interspecific variation in hummingbirds are rarely considered in macroevolutionary studies.

(6) We stress the need for studies from the hummingbird perspective (i.e. plant-mediated selection on hummingbirds), and more fine-grain comparative studies among different hummingbird groups (e.g. phylogenetic, or functional groups), which is possible with the rich set of network data available for this system.

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## X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Terms used in a search of *Web of Science* to investigate the frequency, timing, and evolutionary consequences of transitions from and to hummingbird pollination.  
**Table S1.** Estimated number of evolutionary shifts from and to hummingbird pollination across angiosperms.

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