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The evolution, ecology, and conservation of hummingbirds and their interactions with flowering plants

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ABSTRACT

The ecological co-dependency between plants and hummingbirds is a classic example of a mutualistic interaction: hummingbirds rely on floral nectar to fuel their rapid metabolisms, and more than 7000 plant species rely on hummingbirds for pollination. However, threats to hummingbirds are mounting, with 10% of 366 species considered globally threatened and 60% in decline. Despite the important ecological implications of these population declines, no recent review has examined plant–hummingbird interactions in the wider context of their evolution, ecology, and conservation. To provide this overview, we (*i*) assess the extent to which plants and hummingbirds have coevolved over millions of years, (*ii*) examine the mechanisms underlying plant–hummingbird interaction frequencies and hummingbird specialization, (*iii*) explore the factors driving the decline of hummingbird populations, and (*iv*) map out directions for future research and conservation. We find that, despite close associations between plants and hummingbirds, acquiring evidence for coevolution (*versus* one-sided adaptation) is difficult because data on fitness outcomes for both partners are required. Thus, linking plant–hummingbird interactions to plant reproduction is not only a major avenue for future coevolutionary work, but also for studies of interaction networks, which rarely incorporate pollinator effectiveness. Nevertheless, over the past decade, a growing body of literature on plant–hummingbird networks suggests that hummingbirds form relationships with plants primarily based on overlapping phenologies and trait-matching between bill length and flower length. On the other hand, species-level specialization appears to depend primarily on local community context, such as hummingbird abundance and nectar availability. Finally, although hummingbirds are commonly viewed as resilient opportunists that thrive in brushy habitats, we find that range size and forest dependency are key predictors of hummingbird extinction risk. A critical direction for future research is to examine how potential stressors – such as habitat loss and fragmentation, climate change, and introduction of non-native plants – may interact to affect hummingbirds and the plants they pollinate.

Key words: coevolution, interaction networks, mutualism, pollination ecology, pollen dispersal, specialization, species interactions, Trochilidae

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I. INTRODUCTION

For centuries, hummingbirds have fascinated naturalists with their brilliantly coloured plumage, rapid and acrobatic movements, miniature size, and striking bill shapes (Schuchmann, 1999; Turner & Bhattacharyya, 2016; Sobrevilla *et al.*, 2018). Hummingbirds diverged from swifts (Apodidae) between 30 and 70 million years ago (Ma) (Mayr, 2004; Klimov, Mironov & OConnor, 2017), and their subsequent evolutionary radiation has resulted in ~360 extant species across ~100 genera and nine major clades: Topazes, Hermits, Mangoes, Brilliants, Coquettes, the genus *Patagona*, Mountain Gems, Bees, and Emeralds (McGuire *et al.*, 2014; IUCN, 2020a). Although hummingbird fossils have been discovered in Europe (Mayr, 2004), extant hummingbirds are found only in the Americas and nearby islands, ranging from south-eastern Alaska in North America to Tierra del Fuego, the southernmost point of South America (Fig. 1, see Appendix S1). Within this latitudinal range, a diverse array of behavioural strategies and morphological adaptations has enabled hummingbirds to thrive and radiate into diverse habitat types and climatic regimes, from humid tropical rainforests and seasonal wildflower meadows to arid savannas and cold Andean mountain ridges.

Within this geographical distribution, approximately 7000 plant species exhibit a suite of floral characteristics, such as brightly coloured flowers and large amounts of nectar, that attract and reward hummingbirds for their pollination services (Abrahamczyk & Kessler, 2015). These adaptations associated with bird pollination ('ornithophily') are particularly common in the tropics, where several primarily hummingbird-pollinated genera – such as *Heliconia* (Heliconiaceae), *Columnea* (Gesneriaceae), and *Pitcairnia* (Bromeliaceae) – each comprise at least 200 species (Givnish *et al.*, 2014; Abrahamczyk & Kessler, 2015). The number of plant taxa benefitting from hummingbird pollination probably surpasses these tallies of ornithophilous plants, however, because hummingbirds are opportunistic foragers that also visit flowers shared with other pollinator groups (Arizmendi & Ornelas, 1990; Araujo & Sazima, 2003; Dalsgaard *et al.*, 2009; Maruyama *et al.*, 2013; Waser, CaraDonna & Price, 2018; Rodríguez-Flores *et al.*, 2019).

Due to their impressive taxonomic and functional diversity and roles as pollinators, hummingbirds are a particularly attractive taxon for evolutionary and ecological study. For example, hummingbirds are conducive to studying questions related to functional trait assembly (Graham *et al.*, 2012), how environmental factors and community context shape dietary specialization (Feinsinger & Swarm, 1982; Maglianesi *et al.*, 2015a; Dalsgaard *et al.*, 2018), and the ecological implications of losing certain species to environmental change (Hadley *et al.*, 2018; Tinoco, Santillán & Graham, 2018). Moreover, with the fastest metabolism of any vertebrate (Suarez, 1998), hummingbirds rely so extensively on floral

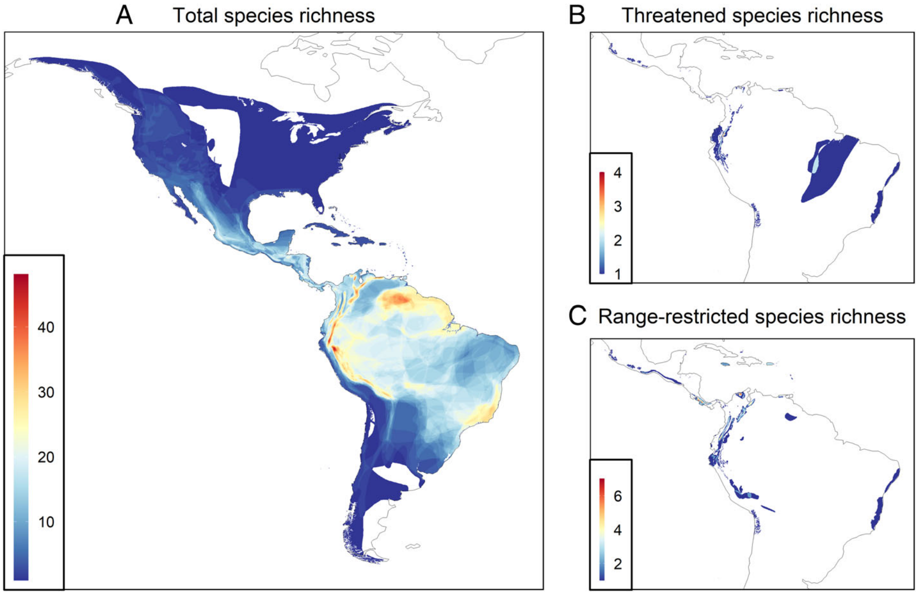


Fig. 1. Maps of (A) total, (B) threatened, and (C) range-restricted hummingbird species richness according to IUCN *Red List* (IUCN, 2020b) and BirdLife International species range maps (BirdLife International and Handbook of the Birds of the World, 2019). Species classified as Vulnerable, Endangered, or Critically Endangered are considered threatened, and those with estimated extent of occurrence (breeding and resident) below 50000 km^2 are considered range restricted. Richness was computed at a resolution of approximately 1 km^2 and resampled to 5 km^2 for visualization; see Appendix S1 for additional details. The numbers of species associated with each map are: 366 (total species), 40 (threatened species), and 93 (range-restricted species).

nectar that their close relationships with plants are ideal for understanding the economics of territoriality (Ewald & Carpenter, 1978; Hixon, Carpenter & Paton, 1983) and reciprocal evolutionary pressures (Temeles & Kress, 2003). Due to the relative ease of in-field identification and larger sizes compared to insect pollinators, hummingbirds are also natural candidates for studies of mutualistic plant–pollinator networks (Dalsgaard *et al.*, 2011) and pollinator movements (Hadley & Betts, 2009), both of which are expected to be influenced by global anthropogenic change. Finally, hummingbirds' remarkable physiology, bejewelled appearance, and reliable presence at backyard feeders make them attractive candidates for citizen science projects (Givot *et al.*, 2015; Courter, 2017; Greig, Wood & Bonter, 2017).

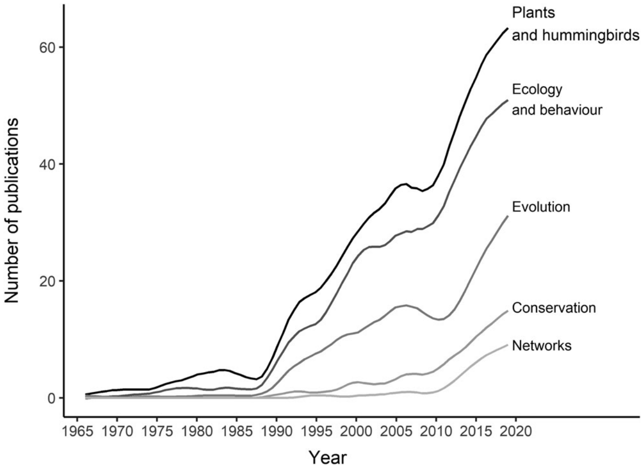


Fig. 2. Research on plant–hummingbird interactions has increased over time. Lines show the overall number of publications related to hummingbirds and plants (uppermost line), as well as the subcategories of research discussed in this review (1966–2019). Searches were conducted on the title, abstract, and author-provided key words using the *Web of Science* database. Note that the same publication may be present in several subcategories. Details of search terms and overlap between subcategories are provided in Appendix S1, Table S1 and Fig. S1.

Previous reviews combining ecological and evolutionary perspectives on hummingbird pollination have mainly surveyed hummingbird morphological and behavioural diversity in foraging contexts (Feinsinger & Colwell, 1978; Stiles, 1995; Abrahamczyk & Kessler, 2015) and, more recently, linked these topics to the biomechanics of flight and nectar extraction (Altshuler & Dudley, 2002; Rico-Guevara *et al.*, 2021; Sargent, Groom & Rico-Guevara, 2021). Numerous reviews have also addressed the evolution of bird-mediated pollination more generally (Stiles, 1978a, 1981; Cronk & Ojeda, 2008; Pauw, 2019) or summarized the physiology and behaviour of nectarivorous birds as a whole (Carpenter, 1987; Collins & Paton, 1989; Paton & Collins, 1989; Nicolson & Fleming, 2003, 2014). The last all-inclusive reviews of the hummingbird literature, however, were published more than 20 years ago (Johnsgard, 1997; Schuchmann, 1999). Since that time, the total number of publications related to plant–hummingbird interactions has more than doubled, and new research

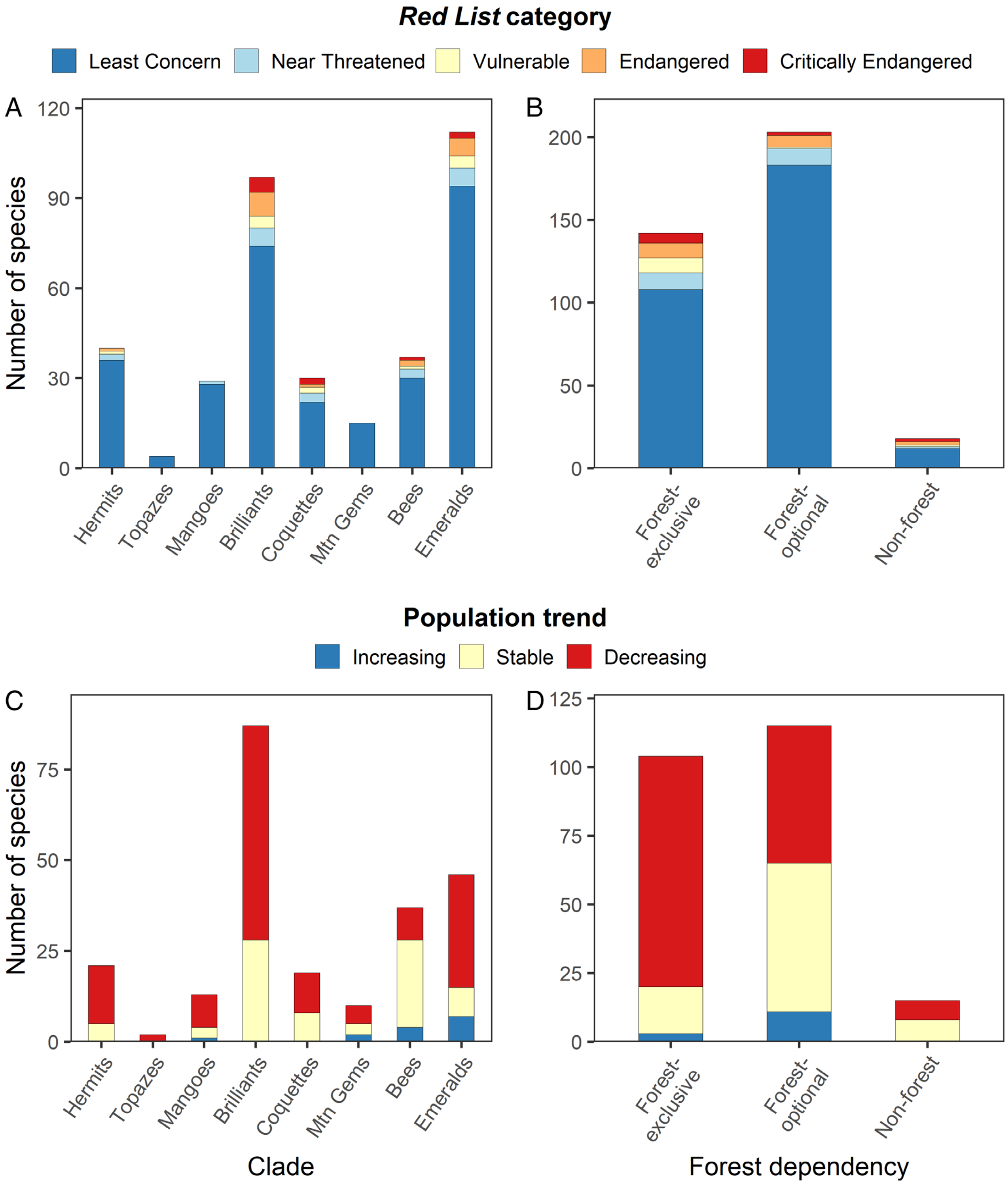


Fig. 3. Number of hummingbird species per IUCN *Red List* category (A and B) and population trend (C and D), partitioned by hummingbird clade (A and C) and level of forest dependency (B and D). Out of 366 extant hummingbird species, the total number of species included per panel are: 364 (A), 363 (B), 235 (C), and 234 (D). The monotypic clade *Patagona* is not included in these plots. Additional details are provided in Appendix S1, including data in tabular form (Tables S2 and S3). Mtn Gems, Mountain Gems.

paradigms have emerged, such as the theory of interaction networks (Fig. 2, Table S1, Fig. S1). Moreover, although only 10% of hummingbird species are considered threatened by the International Union for Conservation of Nature (IUCN), populations are declining in 60% of species with data available for estimating population trends (Fig. 3; Tables S2 and S3; IUCN, 2020a). These trends are alarming, yet hummingbird declines have not been examined in relation to species traits, which precludes generalizations about potential causes. Moreover, no reviews have synthesized current research to predict how habitat loss and climate change may affect hummingbird populations and thus plant–hummingbird interactions.

In this review, we synthesize research related to the evolution, ecology, and conservation of plant–hummingbird interactions (Fig. 4) while incorporating recent findings made possible due to theoretical developments and technological advances, including new statistical tools to quantify network structure, the development of the geographic mosaic theory of coevolution, and the availability of miniaturized radio transmitters for monitoring movements (Bascompte *et al.*, 2003; Thompson, 2005; Hadley & Betts, 2009). Across four major sections, we (*i*) evaluate the evidence for coevolutionary plant–hummingbird relationships and outline approaches for studying coevolution in species-rich communities (Section III), (*ii*) synthesize current knowledge about the mechanisms structuring plant–hummingbird interaction networks and explore differences in pollinator effectiveness among hummingbird species (Section IV), (*iii*) predict how hummingbirds and their interactions with plants might be affected by climate change, habitat loss, and habitat fragmentation (Section V), and (*iv*) identify future directions for research and conservation of plant–hummingbird interactions (Section VI). To set the stage for these hummingbird-focused sections, we begin by briefly reviewing the evolution of bird-mediated pollination (Section II).

II. THE EVOLUTION OF BIRD POLLINATION

Thousands of plant species, spanning at least 500 genera, are adapted for pollination by birds that consume floral nectar (Renner & Ricklefs, 1995; Abrahamczyk & Kessler, 2015). The most speciose taxonomic groups of avian nectarivores are hummingbirds and two passerine families that occur in Africa, Asia, and/or Oceania: sunbirds (Nectariniidae: 132 species, all three regions) and honeyeaters (Meliphagidae: 180 species, Oceania only) (Collins & Paton, 1989; Cronk & Ojeda, 2008; Zanata *et al.*, 2017; Pauw, 2019). Across these geographical regions, bird pollination has evolved multiple times, often from an ancestral state of bee pollination (e.g. Kay *et al.*, 2005; Whittall & Hodges, 2007; Wilson *et al.*, 2007; Specht *et al.*, 2012; Valente *et al.*, 2012). Many floral traits associated with certain pollinator groups ('pollination syndrome' *sensu* Fenster *et al.*, 2004) relate to nectar reward. Compared to bee-pollinated plants, ornithophilous flowers produce larger nectar volumes [approximately 30 μl/day, on average, in hummingbird and sunbird flowers (Stiles & Freeman, 1993; Ornelas *et al.*, 2007; Johnson & Nicolson, 2008)], albeit with relatively dilute sugar concentrations [approximately 20–25% sucrose-equivalent mass/total mass, on average (Baker, 1975; Pyke & Waser, 1981; Stiles & Freeman, 1993; Johnson & Nicolson, 2008)]. Nectar chemistry, namely sugar composition and amino acid concentration, has also been linked to certain pollinator groups, including nectarivorous birds (Baker & Baker, 1973, 1982, 1983). While the nectar chemistry of plants associated with honeyeaters has not been studied extensively (Fleming *et al.*, 2008; Napier *et al.*, 2013), hummingbird and sunbird flowers tend to have high percentages of sucrose and lesser amounts of its constituent hexose sugars, fructose and glucose [approximately 60–70% sucrose, on average (Stiles & Freeman, 1993; Baker, Baker & Hodges, 1998; Johnson & Nicolson, 2008)]. Although amino acids have received relatively little research attention, existing evidence suggests that ornithophilous nectars are low in amino acids (Baker & Baker, 1973), especially in hummingbird-pollinated plants (Cruden & Toledo, 1977; Baker & Baker, 1982; Tiedge & Lohaus, 2017; but see: Nicolson, 2007a). Finally, the nectar of ornithophilous plants is frequently odourless, available during the day, advertised with red-orange displays, and concealed within the tubular, fused corolla ('corolla tube') of flowers that lack a landing platform for insects (Faegri & Van der Pijl, 1979; Stiles, 1981; Cronk & Ojeda, 2008).

Evolutionary explanations for these plant characteristics have traditionally been ornithocentric, focusing on how plants adapt to the activity patterns, energetic and nutritional requirements, and preferences of avian pollinators (Baker & Baker, 1982; Martínez del Rio, Baker & Baker, 1992; Schondube & Martínez del Rio, 2003). For example, larger body sizes are associated with higher metabolic demands and therefore larger nectar volumes (Brown, Calder & Kodric-Brown, 1978; Stiles, 1978a; Cruden, Hermann-Parker & Peterson, 1983; Nicolson, 2007b). Similarly, low amino acid concentrations within the nectar of bird-associated flowers have been linked to the alternative protein sources available to birds (Baker & Baker, 1982, 1983). Hummingbirds, for example, obtain protein from insects, rather than nectar (Stiles, 1995; Abrahamczyk & Kessler, 2015). Additionally, the predominance of high-sucrose nectar corresponds to early studies demonstrating that hummingbirds prefer sucrose (Stiles, 1976; Martínez del Rio, 1990; but see Fleming *et al.*, 2004).

Although these adaptive interpretations are firmly engrained within the hummingbird literature, some authors have questioned whether ornithocentric hypotheses can fully explain these nectar properties (Nicolson & Fleming, 2003; Schondube & Martínez del Rio, 2003; Fleming *et al.*, 2004). For example, why do ornithophilous plants secrete sucrose-dominated nectar when hummingbirds can utilize the monosaccharides glucose and/or fructose just as efficiently – if not more easily – than sucrose (Martínez del Rio, 1990; McWhorter & Martínez del Rio, 2000; Welch *et al.*, 2006; Chen & Welch, 2014)? Multiple explanations exist (reviewed by Nicolson & Fleming, 2003), but hummingbird sucrose preference should also be confirmed using experiments with standardized methodology; in early studies, the sucrose solutions offered to hummingbirds were ~5% more caloric than the hexose alternative (Nicolson & Fleming, 2003; Fleming *et al.*, 2004; Brown, Downs & Johnson, 2008). Recent work using equicaloric sugar solutions suggests that hummingbird sucrose preference may be less ubiquitous than previously thought, varying with sugar concentration, ambient temperature, and hummingbird species (Schondube & Martínez del

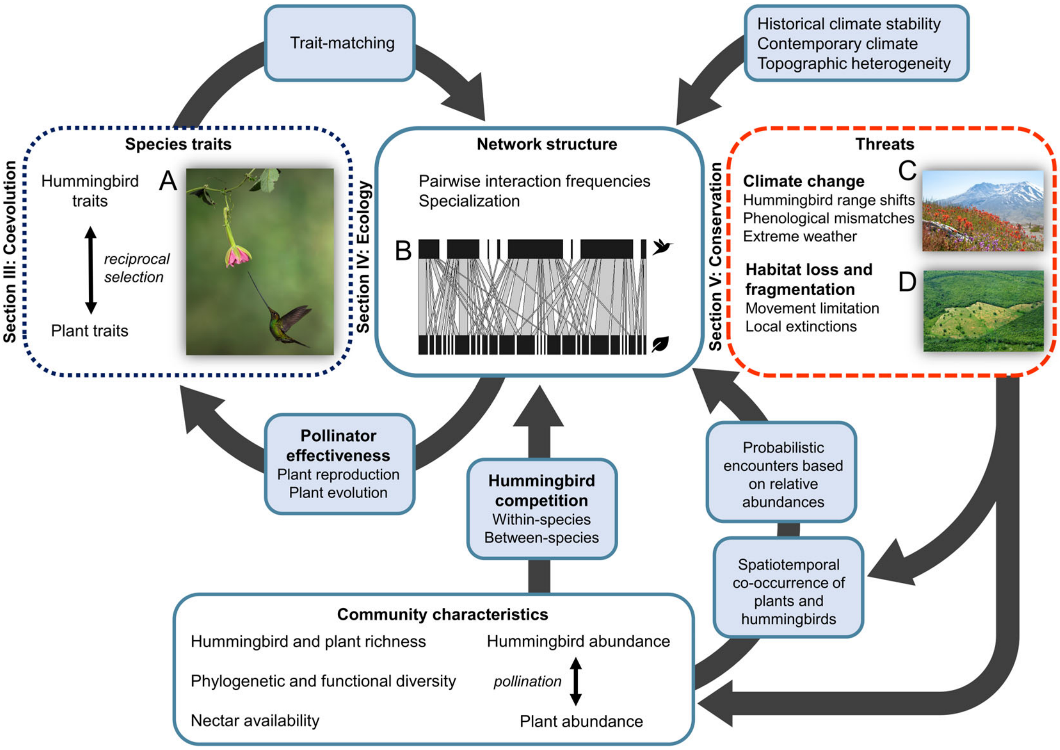


Fig. 4. Conceptual diagram showing the connections between the three main topics addressed in this review of hummingbird evolution, ecology, and conservation. Topics outlined in dark blue (dotted line) are covered in the coevolution section (Section III), topics outlined in blue (solid lines) are covered in the ecology section (Section IV), and topics outlined in red (dashed lines) are covered in the conservation section (Section V). Shaded boxes positioned over arrows represent mechanisms connecting different topics. Note that this figure is not intended to provide an exhaustive compilation of topics related to plant–hummingbird interactions, but rather to provide a roadmap of the topics presented in this review and highlight the connections among them. Plant–hummingbird relationships provide striking examples of trait-matching between bill shape and flower corolla shape (A; Section III), and these examples are highly suggestive of coevolution. Nevertheless, empirically demonstrating reciprocal selection remains an ongoing challenge (Section III.1), especially within species-rich communities where plants are visited by multiple hummingbird species and hummingbirds visit many species of plants (B). Within plant–hummingbird visitation networks, pairwise interaction frequencies (light grey bands in B) are primarily dictated by spatiotemporal co-occurrence and trait-matching between hummingbird bill length and flower corolla length, with probabilistic processes based on partner abundance playing a relatively minor role (Section IV.1*a*). Emerging from pairwise interaction frequencies are patterns such as specialization, which arises from the foraging decisions of individual hummingbirds and scales up to the level of species and networks. Existing research suggests that hummingbird specialization is largely determined by *l*ocal context – such as nectar availability, hummingbird abundance, and competition – more so than functional traits such as bill length (Section IV.1*b*). At macroecological scales, specialization of plant–hummingbird interaction networks increases with species richness, topographic heterogeneity, historical climate stability, and large amounts of precipitation (Section IV.2). Although hummingbirds are often considered resilient opportunists and only 10% of hummingbirds are considered threatened (Vulnerable, Endangered, or Critically Endangered) by the IUCN, 60% of hummingbirds are thought to have declining populations (Section V). The primary threats to hummingbirds are climate change and habitat loss, which may reduce hummingbird survival directly, or indirectly *via* nectar availability (Section V.2). For example, climate change may lead to phenological mismatches between migratory hummingbird arrival and seasonal flowering peaks (C). Loss and fragmentation of native vegetation cover (D) has also been shown to reduce the abundance of large and morphologically specialized hummingbird species. Reductions in hummingbird abundance are expected to cause pollen limitation and subsequent declines in plant abundance (Section V.3). Additional details: (A) Sword-billed hummingbird (*Ensifera ensifera*) and *Passiflora mixta* flower. Photograph by Corey Hayes. (B) Plant–hummingbird visitation network from the Munchique Natural National Park in western Colombia, reproduced from Ramírez-Burbano *et al.* (2017). (C) Seasonally blooming wildflowers (primarily *Castilleja*) near Mount Saint Helens, Washington, USA. Photograph by Nav Tombros *via* CC BY-NC-SA 2.0. (D) Deforestation in the Amazon rainforest near Manaus, Brazil. Photograph by Neil Palmer/CIAT *via* CC BY-SA 2.0.

Rio, 2003; Fleming *et al.*, 2004; Medina-Tapia *et al.*, 2012). Another puzzling phenomenon involves ornithophilous flowers' dilute nectar, which is approximately 0.3–0.5 the concentration that hummingbirds prefer (Stiles, 1976; Pyke & Waser, 1981; Tamm & Gass, 1986; Roberts, 1996), sometimes leading to ornithophilous flowers and insect-adapted flowers having similar caloric values (Arizmendi & Ornelas, 1990; Waser *et al.*, 2018). This 'evolutionary paradox' has invited numerous explanatory hypotheses, and no one hypothesis has emerged as a leading explanation (reviewed by Nicolson, 2007b). That said, an accumulation of evidence over the past decade has revealed that hummingbird tongues do not rely on capillary action for nectar uptake (Rico-Guevara & Rubega, 2011; Rico-Guevara, Fan & Rubega, 2015; Rico-Guevara *et al*., 2019), weakening the argument that the viscosity of highly concentrated nectars limits hummingbird feeding efficiency (Baker, 1975).

For a comprehensive understanding of nectar properties and pollinator traits, it will be necessary to adopt a holistic approach that considers the evolutionary pressures and constraints experienced by both interaction partners. To understand the selection pressures imposed on plants by avian pollinators, future work could continue to investigate birds' sugar preferences, taste perception, and/or physiological constraints related to nectar uptake (Medina-Tapia *et al*., 2012; Nicolson & Fleming, 2014; Rico-Guevara *et al*., 2019). At the same time, there are many reasons why plants might *not* adapt to pollinators. First, plants do not necessarily evolve to suit pollinator preferences, but rather to manipulate pollinators into providing sufficient gene-transfer services (Zimmerman, 1988). Secondly, nectar properties may reflect plant physiology, phylogenetic constraints, and/or environmental factors such as water availability (Baker & Baker, 1982; Pacini & Nepi, 2007; Parachnowitsch, Manson & Sletvold, 2019) more so than pollinator-mediated selection. For instance, studies of individual plant lineages demonstrate that although nectar properties are sometimes associated with evolutionary transitions to hummingbird pollination (e.g. sugar concentration: Kaczorowski, Gardener & Holtsford, 2005; Krömer *et al*., 2008), numerous exceptions exist – especially for nectar chemistry (e.g. Perret *et al*., 2001; Galetto & Bernardello, 2004; Kaczorowski *et al*., 2005; reviewed by Nicolson & Thornburg, 2007).

Additional research is also needed to evaluate macroevolutionary explanations for transitions to ornithophily. The most common explanations invoke birds' (*i*) high mobility, which may provide long-distance pollen dispersal and thus higher gene flow (Stiles, 1978a; Cronk & Ojeda, 2008; Krauss *et al*., 2017; Pauw, 2019), and (*ii*) reliable flower visitation in areas with flight conditions too cold or wet for insects (Stiles, 1978a; Cronk & Ojeda, 2008), such as high-elevation cloud forests or deep, shady canyons (Cruden, 1972; Stebbins, 1989; Dalsgaard *et al*., 2009). Another hypothesized advantage is reduced pollen loss; unlike bees, which gather pollen to feed their offspring, birds adapted for nectar-feeding do not visit flowers to consume pollen (Martínez del Rio, 1994; Fleming *et al*., 2012) and do not groom pollen grains into pollen-carrying structures while foraging (Nicolson, 2007b). Thus, birds may transfer more pollen to subsequently visited plants (Thomson & Wilson, 2008; Krauss *et al*., 2017), as supported by experiments comparing pollen carryover in hummingbirds *versus* bumblebees (Waser, 1988; Castellanos, Wilson & Thomson, 2003). Other adaptive advantages relate to the relative longevity of birds in relation to insects, their spatial memory, and their ability to revisit patchily distributed plants year after year, and/or throughout a long flowering season (Stiles, 1978a; Stebbins, 1989; Gowda, Temeles & Kress, 2012). Additionally, birds have high visual acuity (Cronk & Ojeda, 2008), which may allow them to detect flowers hidden in thick vegetation. A promising approach for evaluating these potential mechanisms is to quantify pollen carryover, pollen flow, and fitness in plant species visited by pollinators from different functional groups (see also Section IV.3).

III. HUMMINGBIRDS AND PLANTS: A COEVOLUTIONARY HISTORY?

Understanding how reciprocal evolutionary change occurs in species-rich communities characterized by asymmetric, non-exclusive ('generalized') interactions is a conceptual challenge, because conflicting selection pressures may arise when plants are visited by a suite of different pollinator types (Janzen, 1980; Schemske, 1983; Jordano, 1987; Waser *et al*., 1996). Moreover, it is not straightforward to measure selection on pollinators, so empirically demonstrating coevolution (*versus* one-sided adaptation) is challenging. In this section, we (*i*) discuss potential mechanisms for coevolution in species-rich communities, and (*ii*) recommend several methodological approaches, both direct and indirect, to advance our understanding of plant–hummingbird coevolution.

(1) Mechanisms of coevolution in species-rich communities

The conundrum of conflicting selection pressures quickly becomes apparent in hummingbird communities, which can be highly diverse and encompass a range of functional traits (Graham *et al*., 2012; Maruyama *et al*., 2018). For example, in the equatorial Andes, nearly 80 species occur within 1 × 1° latitude–longitude grids (~12300 km^2) (Rahbek & Graves, 2000), over 40 species can occur at a resolution of 5 km^2 (Fig. 1), and more than 25 species can occur at the scale of 1 ha (0.01 km^2) (Dziedzioch, Stevens & Gottsberger, 2003). Hummingbird communities can also be highly diverse outside the Andes; at a resolution of 5 km^2, the Atlantic Forest and Guiana Shield also emerge as richness hotspots (Fig. 1), and 15–20 species are the norm at study sites in Costa Rica and the Amazonian lowlands (Cotton, 1998a; Borgella, Snow & Gavin, 2001). Additionally, in Neotropical rainforests, ornithophilous plant diversity can exceed 100 species per 0.001 km^2 (Gentry, 1982), highlighting the likelihood of one-to-many (rather than one-to-one) relationships between hummingbirds and their nectar resources.

Despite the rarity of one-to-one plant–hummingbird relationships in nature, highly suggestive examples of coevolution nonetheless exist between hummingbirds and plants. Many of these examples involve morphological matching between hummingbird bills and floral corolla tubes. For example, the extremely decurved bill of the white-tipped sicklebill (*Eutoxeres aquila*) closely mirrors the sharply curved flowers of some *Heliconia* and *Centropogon* species (Fig. 5; Stein, 1992), although recent research suggests that the resemblance with *Centropogon* may have emerged without reciprocal selection (Abrahamczyk, Poretschkin & Renner, 2017; see also Section III.2*c*). Similarly impressive sword-billed hummingbirds (*Ensifera ensifera*) have 10-cm bills that permit access to long-tubed *Passiflora* and *Brugmansia* flowers (Fig. 5; Snow & Snow, 1980; Lindberg & Olesen, 2001; Abrahamczyk, Souto-Vilarós & Renner, 2014). Finally, in the islands of the Lesser Antilles, male and female purple-throated caribs (*Eulampis jugularis*) have sexually dimorphic body sizes and bill morphologies, concentrate their flower visitation on different *Heliconia* species, and employ different foraging strategies. Males are larger with shorter, straighter bills and defend highly rewarding inflorescences of short, straight *Heliconia caribea* flowers, while smaller females have longer, more curved bills and primarily visit less-rewarding inflorescences of long, curved *Heliconia bihai* flowers (Fig. 5; Temeles *et al.*, 2000; Temeles & Kress, 2003). In areas where one of the two *Heliconia* species is absent, the other *Heliconia* species has evolved a variant that serves as an 'ecological replacement'; that is, flower morphology and nectar reward match the bill morphology and body size of the hummingbird missing its preferred *Heliconia* partner (Temeles *et al.*, 2000; Temeles & Kress, 2003). Although purple-throated caribs inhabit islands with simplified hummingbird communities and relatively few ornithophilous plants, white-tipped sicklebills and sword-billed hummingbirds occur within species-rich communities of Central America and the Andes. How might such striking pairwise complementarity emerge from a noisy background of alternative partners?

There are two main ways through which pairwise, reciprocal selection could occur in the context of multispecies interactions. First, if groups of functionally similar hummingbird species exert convergent evolutionary pressures, the assumption of specialized pairwise relationships could be substantially relaxed (Fenster *et al.*, 2004). For instance, Neotropical hummingbird communities can be divided into functional groups exhibiting similar morphological features, foraging behaviours, and habitat preferences (Snow & Snow, 1972; Feinsinger & Colwell, 1978; Stiles, 1985; Hadley *et al.*, 2018). In plant–hummingbird interaction networks, such functional groups can also be identified as 'modules', which arise when linkages are concentrated within morphologically similar 'trait-matched' groups of plants and hummingbirds (e.g. Maruyama *et al.*, 2014; see also Section IV.1*b*). Modules have been suggested to behave as 'coevolutionary units' in which reciprocal evolution occurs between groups of morphologically similar partners (Olesen *et al.*, 2007).

Coevolution in species-rich networks could also occur if only some pollinators contribute to plant reproduction and therefore plant evolution (Fenster *et al.*, 2004; Santiago-Hernández *et al.*, 2019; see also Section IV.3*a*). Contributions to plant reproduction have rarely been quantified for different hummingbird species, but existing evidence suggests that hummingbirds may differ in their effectiveness as pollinators. For example, Betts, Hadley & Kress (2015) discovered that hummingbirds with long, curved bills are nearly six times better at pollinating *Heliconia tortuosa* than short-billed species. To determine the generality of pollinator effectiveness as a mechanism for coevolution, additional research quantifying pollinator contributions to plant reproduction will be essential (see also Section IV.3*a*). Notably, to understand coevolution in plants visited by multiple pollinator groups, comprehensive assessments of pollinator effectiveness will require researchers to measure the contributions of both hummingbird and non-hummingbird visitors (e.g. Medel, Botto-Mahan & Kalin-Arroyo, 2003; Fumero-Cabán & Meléndez-Ackerman, 2007; Lehmann *et al.*, 2019).

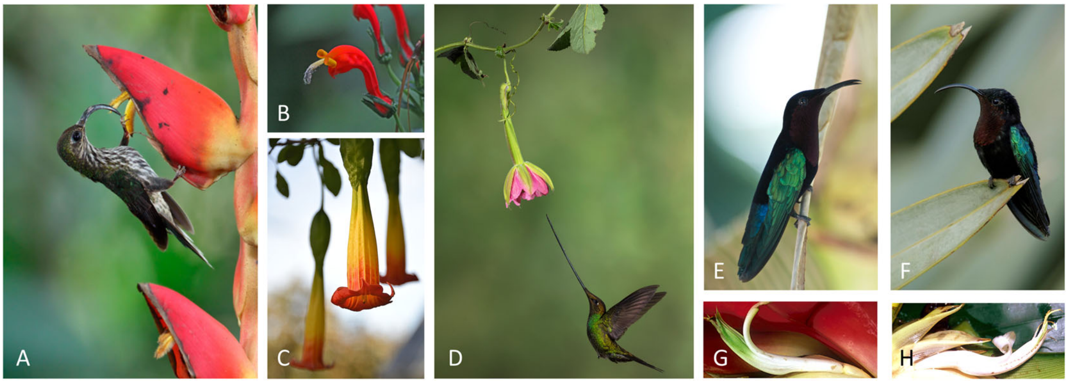


Fig. 5. Extreme examples of trait-matching between hummingbird bill and flower corollas. (A) White-tipped sicklebill (*Eutoxeres aquila*) and *Heliconia pogonantha* flower. Photograph by Juan Carlos Vindas. (B) Flower of *Centropogon granulosus*. Corolla curvature aligns closely with the bill shape of white-tipped sicklebill in A. Photograph by Jerry Oldenettel *via* CC BY-NC-SA 2.0. (C) *Brugmansia sanguinea* flower, approximately 15 cm in length (Soteras *et al.*, 2018) and visited by sword-billed hummingbirds (*Ensifera ensifera*; D). Photograph by Rod Waddington via CC BY-SA 2.0. (D) Sword-billed hummingbird and *Passiflora mixta* flower. Photograph by Corey Hayes. (E) Male purple-throated carib (*Eulampis jugularis*). Photograph by John Mittermeier. (F) Female purple-throated carib (*Eulampis jugularis*). Photograph by Glenn Bartley. (G) Flower of *Heliconia caribea*. Note correspondence between the less curved corolla tube and the shorter, straight bill of the male purple-throated carib in E. Photograph by Ethan Temeles. (H) Flower of *Heliconia bihai*. Note the correspondence between the more curved corolla tube and the longer, more curved bill of the female purple-throated carib in F. Photograph by Ethan Temeles.

(2) Studying the coevolution of plant–hummingbird interactions

Directly quantifying coevolution (i.e. reciprocal selection) requires measuring selection on both partners. In this subsection, we summarize ways to measure selection on plants and hummingbirds, then suggest how estimates of selection can be used to test Thompson's (1999, 2005) geographic mosaic theory of coevolution (GMTC; Section III.2*b*). Finally, recognizing that direct measures of selection are difficult to obtain, we review a growing body of literature that compares the estimated evolutionary ages of plant and hummingbird lineages; this approach indirectly tests for cospeciation, which could imply coevolution (Section III.2*c*).

(*a*) *Measuring selection on plants and hummingbirds*

Measuring selection on plants is relatively straightforward because individual fitness (i.e. contributions to the subsequent generation) can be approximated using standard metrics of reproductive success: seeds sired for male fitness and seed set for female fitness (Campbell, 1989), assuming that seed set correlates with seed germination probability and seedling survival (Young, 1982). Measures of reproductive success can then be linked to floral traits such as corolla length (e.g. Nattero, Sérsic & Cocucci, 2010; Temeles *et al.*, 2013; Temeles & Bishop, 2019), assuming that floral traits are heritable (Campbell, 1996). Quantifying fitness for hummingbirds is substantially more challenging. Very few estimates of hummingbird survival and reproduction exist (see also Section V.2*a*), and potential fitness proxies (e.g. body condition: González-Gómez & Estades, 2009) have not been formally validated. In fact, body mass might *not* confer fitness benefits in hummingbirds due to aerodynamic constraints on flight performance and unique physiological adaptations, such as use of torpor to withstand short-term energy shortages (Barnett *et al.*, 2015; Graham *et al.*, 2016). To date, the strongest inference for selection on pollinators comes from experimental studies of feeding efficiency. These types of experiments measure time spent extracting nectar (Temeles & Roberts, 1993; Temeles, 1996; Temeles *et al.*, 2009), volume of nectar consumed (Pauw, Stofberg & Waterman, 2009), and/or energy intake rate (Rico-Guevara *et al.*, 2021) at flowers of different lengths, widths, and curvatures. Additional studies of feeding performance will be essential for furthering our understanding of coevolution between plants and hummingbirds (Section III.2*b*) – and for understanding potential fitness trade-offs between feeding efficiency and other selective pressures on hummingbird bill morphology [e.g. fighting ability (Rico-Guevara & Araya-Salas, 2015; Rico-Guevara *et al.*, 2019)].

(*b*) *Geographic mosaics of coevolution: examining how selection varies through space and time*

The GMTC recognizes that, because selection pressures vary across space and time, the most biologically relevant approach to studying coevolution is to examine multiple populations across a geographic landscape (Thompson, 1999, 2005). The GMTC hypothesizes that populations experiencing reciprocal selection ('coevolutionary hotspots') are interspersed with 'coevolutionary coldspots' where populations experience one-sided selection or species do not co-occur. Moreover, even within coevolutionary hotspots, the outcome of selection may vary across space, producing a 'selection mosaic'; for example, an interaction may be mutualistic in one part of the geographic range but antagonistic in another (Thompson & Cunningham, 2002). Finally, the GMTC recognizes that these evolutionary processes exist against a background of continual trait remixing (e.g. gene flow, mutation), so selection pressures constantly change over time.

Thus, quantifying selection is paramount to studying coevolution within the framework of the GMTC. Specifically, researchers must collect data, for each interacting species, on (*i*) traits relevant to the interaction, such as bill length and flower length, and (*ii*) fitness consequences of the interaction (Gomulkiewicz *et al.*, 2007). As noted in Section III.2*a*, quantifying bird fitness is a particularly arduous task, most feasible using proxies such as feeding efficiency (e.g. Benkman, 1999).

Due to the challenges associated with identifying coevolutionary hotspots and coldspots, many researchers have adopted an incremental approach to testing the GMTC, starting by identifying patterns congruent with – although not necessarily indicative of – the underlying evolutionary processes. For example, patterns consistent with the GMTC include: few coevolved traits at the species level (across all populations), trait-matching in some populations but mismatching in others, and trait variation across a species' geographic range (Gomulkiewicz *et al.*, 2007). Hummingbird research in this area is still nascent, but several studies have linked geographic variation in corolla shape to the identity of hummingbird visitors (Temeles & Kress, 2003; Nattero & Cocucci, 2007; Gowda & Kress, 2013), suggesting the potential for coevolutionary hotspots and coldspots. Moreover, geographic variation in hummingbird bill length has been documented within multiple species and lineages [e.g. *Phaethornis* (Hinkelmann, 1996); *Metallura* (Heindl & Schuchmann, 1998); *Adelomyia* (Chaves *et al.*, 2007)]. Intriguingly, geographic variation in bill length is correlated with climate and associated habitat type in *Metallura tyrianthina* (Benham & Witt, 2016) and *Adelomyia melanogenys* (Chaves *et al.*, 2007; Chaves & Smith, 2011) but has not yet been linked to the presence of certain plant species. Examining geographic turnover in plant assemblage and the associated changes in floral traits would be an exciting next step.

(*c*) *Detecting contemporaneous co-speciation*

Several recent studies have explored plant–hummingbird coevolution indirectly by using molecular data to estimate when hummingbird and plant lineages evolved (Tripp & McDade, 2013; Abrahamczyk *et al.*, 2015, 2017; Abrahamczyk & Renner, 2015). In some instances, plant lineages have similar evolutionary ages as their hummingbird pollinators, suggesting cospeciation and possibly coevolution

(Page, 2003). For instance, the oldest hummingbird clades (Hermits and Topazes) likely began evolving in the Neotropics between 18 and 25 Ma (Bleiweiss, 1998; McGuire *et al*., 2014; Abrahamczyk & Renner, 2015), and diversification rates in Heliconiaceae and Gesneriaceae increased around this time (Specht *et al*., 2012; Roalson & Roberts, 2016; Serrano-Serrano *et al*., 2017). Approximately 10 million years later (~15 Ma), ornithophily arose in certain Andean bromeliad lineages (Bromeliaceae), coinciding with the origin of the Coquette and Brilliant clades (Givnish *et al*., 2014; McGuire *et al*., 2014). Similarly, the lineage of *Passiflora* (Passifloraceae) with extremely long corolla tubes began evolving about 11 Ma, which roughly coincides with the origin of the ancestral sword-billed hummingbird (Abrahamczyk *et al*., 2014). A notable exception to these parallel timings is the relationship between sicklebill hummingbirds and *Centropogon*; despite the uncanny resemblance between sharply curved flowers and bill shapes, the *Centropogon* lineage evolved approximately 15 Ma after *Eutoxeres*, which is thought to have originally depended on *Heliconia* species with curved corollas (Abrahamczyk *et al*., 2017). This finding highlights how traits of extant species may reflect adaptation to new mutualistic interactions arising long after speciation (e.g. Tripp & McDade, 2013; Abrahamczyk *et al*., 2017), and this ever-present possibility of asymmetric adaptation limits the conclusions that can be drawn from observations of coincident evolutionary ages and matching traits. For example, the evolution of floral traits might be affected by hidden drivers unrelated to hummingbird pollinators, such as resistance to desiccation, protection from insect herbivores, or deterrence of nectar thieves (Gannon *et al*., 2018; Gélvez-Zúñiga *et al*., 2018; Rusman *et al*., 2019). Moreover, the cospeciation approach to studying coevolution cannot differentiate between a plant coevolving with its current interaction partners *versus* coevolving with other (potentially extinct) hummingbird species with similar morphologies. Thus, while this approach is useful for identifying past evolutionary asymmetries and generating hypotheses about present-day coevolutionary relationships, we recommend that researchers investigating coevolutionary mechanisms build on cospeciation studies by measuring selection directly.

IV. ECOLOGICAL RELATIONSHIPS BETWEEN HUMMINGBIRDS AND PLANTS

To fuel its fast-paced lifestyle, a single hummingbird can visit hundreds, and in some cases thousands, of flowers each day (Hainsworth & Wolf, 1972; Gass, Angehr & Centa, 1976; Waser *et al*., 2018) and must meet its caloric requirements within a community of competing nectarivores. Out of all the possible plant species a hummingbird could feed from, how do they choose which ones to visit? Are there any general patterns that emerge across hummingbird communities? Over recent decades, pollination ecologists have increasingly recognized that studying isolated subsets of interacting species is insufficient for understanding processes operating at the scale of communities;thus, network theory has become a popular approach for analysing plant–pollinator interactions at the community level (Jordano, 1987; Waser *et al*., 1996; Bascompte & Jordano, 2007). Although researchers have investigated how communities of plants and hummingbirds are organized since the 1970s (e.g. Snow & Snow, 1972; Colwell, 1973; Stiles, 1975; Feinsinger, 1976; Wolf, Stiles & Hainsworth, 1976), formal network theory has only recently been applied to plant–hummingbird systems (e.g. Dalsgaard *et al*., 2008, 2011; Rodríguez-Flores, Stiles & Arizmendi, 2012; Maglianesi *et al*., 2014; Vizentin-Bugoni, Maruyama & Sazima, 2014).

In this section, we synthesize a growing body of literature about the structure of plant–hummingbird interaction networks and place it in the context of earlier hummingbird literature. Specifically, we evaluate (*i*) why hummingbirds visit certain plant species more frequently than others, (*ii*) what factors determine the level of specialization in a plant–hummingbird relationship, and (*iii*) why different communities vary in their overall level of specialization at continental scales and across environmental gradients. We also point out that, although networks are usually constructed from interactions among species, individuals within hummingbird species may differ in their foraging choices. Finally, taking the plant perspective, we discuss the functional equivalence of different hummingbird species as pollinators. First, we emphasize the need to measure effectiveness when quantifying plant–hummingbird interaction networks and then explore the common assumption that territorial defence reduces pollen dispersal distance. Understanding differential contributions to plant reproduction is particularly important if certain hummingbird species (or species groups) become locally extinct due to habitat loss and/or climate change (Hadley *et al*., 2018; Tinoco *et al*., 2018; Maruyama *et al*., 2019; see also Section V.2).

(1) Network structure within communities

(*a*) *Pairwise interaction frequencies*

Network structure emerges from pairwise interactions between plants and animals; some partners interact frequently, while others interact rarely or not at all (Vázquez, Chacoff & Cagnolo, 2009b). What factors determine whether two species interact? Answering this question and developing a predictive framework for interaction frequencies has become a major research area (Vázquez *et al*., 2009a; Eklöf *et al*., 2013; Poisot, Stouffer & Gravel, 2015; Olito & Fox, 2015), from which two primary mechanisms have emerged: (*i*) neutral, probabilistic processes guided largely by partner abundance, and (*ii*) species traits and preferences (e.g. Vázquez *et al*., 2009b). In other words, an individual hummingbird could frequent a co-occurring plant species simply because it encounters it regularly, or because the hummingbird has morphological or behavioural adaptions to facilitate feeding at that species. To distinguish between these competing mechanisms, interaction patterns expected under the null hypothesis of abundance can be compared to patterns that arise after including information about various species traits (e.g. Vizentin-Bugoni *et al.*, 2014; Maruyama *et al.*, 2014; Sonne *et al.*, 2020).

Many early studies of plant–hummingbird interactions noted that hummingbirds visit different plant species at different rates and emphasized the role of hummingbird foraging strategy in structuring these interactions (e.g. Linhart, 1973; Colwell, 1973; Stiles, 1975; Feinsinger, 1976). Building upon these observations, Feinsinger & Colwell (1978) developed a classification of hummingbird 'community roles' that linked hummingbird foraging strategy to the spatial distribution (and thus defensibility) of floral resources, as well as the nectar reward offered per flower. This classification included (*i*) 'high-reward trapliners' that repeatedly visit a sequence of spatially dispersed, nectar-rich flowers, (*ii*) 'low-reward trapliners' that piece together an assortment of scattered, less valuable floral resources, (*iii*) 'territory holders' that defend a localized clump of moderately to highly rewarding flowers, (4) 'territory parasites' that steal nectar from other birds' territories, and (5) 'generalists' that switch between stealing nectar and low-reward traplining. Although Hermits (subfamily Phaethornithinae) generally appear loyal to a single foraging strategy (i.e. have rarely been observed defending feeding territories: Stiles, 1975, 1985), species within the Trochilinae subfamily are not 'shackled to their roles' (Feinsinger & Colwell, 1978, p. 784). Rather, these hummingbirds adjust their strategy depending on community context and the spatiotemporal availability of nectar (reviewed by Sargent *et al.*, 2021). For example, when floral resources are not valuable or clumped enough to make territory defence energetically worthwhile – such as in the afternoon, when nectar secretion rate slows – territorial hummingbirds may abandon their perches (Stiles & Wolf, 1970; Cotton, 1998b; Temeles *et al.*, 2005; Justino, Maruyama & Oliveira, 2012). Similarly, birds that are typically territorial can behave as low-reward trapliners in communities where that foraging role is vacant (e.g. copper-rumped hummingbird, *Amazilia tobaci*: Feinsinger & Colwell, 1978). Perhaps due to this within-species variability across space and time, foraging strategies have not yet been incorporated into network-level studies of pairwise interaction frequencies; instead, the primary traits evaluated have been bill length (for hummingbirds) and corolla length (for plants). These traits, along with spatiotemporal co-occurrence of interaction partners, have been found to largely explain why hummingbirds visit certain plants more frequently than others (e.g. Dalsgaard *et al.*, 2021). Why might these mechanisms have such strong influences on the structure of plant–hummingbird networks?

First, for a hummingbird to interact with a plant, clearly both species must overlap in space and time. Spatial co-occurrence is particularly important to consider when studying networks at fine scales in heterogenous landscapes, because hummingbird habitat preferences may preclude or considerably reduce interaction rates with certain plant species. For example, Maruyama *et al.* (2014) found that, within the heterogenous landscape of Brazil's Cerrado ecoregion, hummingbird preference for forest *versus* savanna dictated habitat occupancy and therefore pairwise interaction frequencies. Combining networks across Brazil using a meta-network approach, Araujo *et al.* (2018) similarly found that within-network subgroups ('modules') largely corresponded to regional vegetation type. We suspect that these filtering effects, although rarely considered in studies of pairwise interaction frequencies, are widespread; hummingbirds exhibit preferences for different microhabitats (Cotton, 1998c; Borgella *et al.*, 2001; Tinoco *et al.*, 2018), and vertical resource partitioning between understorey and canopy strata has been well documented in forest-associated hummingbirds (Snow & Snow, 1972; Lack, 1973; Feinsinger, 1976; Stiles, 1985; Cotton, 1998c).

For an interaction to occur, hummingbird presence must also coincide with plant flowering; if temporal mismatches occur, then interactions are not realized (McKinney *et al.*, 2012). Given that hummingbird food plants typically exhibit seasonal flowering peaks (Stiles, 1978b; McKinney *et al.*, 2012; Maglianesi *et al.*, 2020), nearly 20% of hummingbird species make latitudinal or altitudinal migratory movements (BirdLife International, 2020; Wolf, 1970; Stiles, 1980; Arizmendi & Ornelas, 1990; Araujo & Sazima, 2003), and hummingbirds' foraging choices vary across seasons (Wolf *et al.*, 1976; Stiles, 1985), phenology is expected to exert strong influence on observed interaction frequencies. Accordingly, phenological overlap has repeatedly emerged as an important driver of interaction frequencies in plant–hummingbird networks (e.g. Vizentin-Bugoni *et al.*, 2014; Maruyama *et al.*, 2014; Gonzalez & Loiselle, 2016; Vitória, Vizentin-Bugoni & Duarte, 2018; Sonne *et al.*, 2020; Chávez-González *et al.*, 2020).

Beyond the crucial prerequisite of spatiotemporal co-occurrence, interactions can be realized primarily due to neutral, probabilistic processes guided largely by partner abundance or because of species traits (Vázquez *et al.*, 2009a; Vizentin-Bugoni *et al.*, 2014; García, 2016; Sonne *et al.*, 2020). In agreement with early studies noting an overall correspondence between flower corolla shape and hummingbird bill shape (e.g. Snow & Snow, 1972; Wolf *et al.*, 1976; Kodric-Brown *et al.*, 1984), studies of individual networks suggest that interaction frequencies emerge due to morphological matching more so than abundance (Vizentin-Bugoni *et al.*, 2014; Maruyama *et al.*, 2014; Weinstein & Graham, 2017; Vitória *et al.*, 2018; Chávez-González *et al.*, 2020). Recent analysis of more than 20 networks spanning a latitudinal gradient between Mexico and Brazil further underscores the importance of trait-matching, particularly in communities close to the Equator (Sonne *et al.*, 2020). Moreover, using a recent compilation of 93 plant–hummingbird networks, Dalsgaard *et al.* (2021) demonstrated that hummingbird bill length is highly correlated with mean corolla length of visited flowers, suggesting that trait-matching is a strong recurrent phenomenon in plant–hummingbird networks across the Americas (Fig. 6).

Why is trait-matching so common in these interaction networks? For one, short-billed hummingbirds cannot access flowers with long corolla tubes unless they pierce the flower

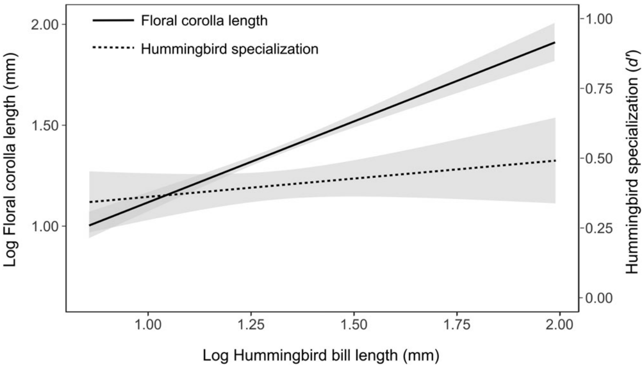


Fig. 6. Trait-matching and trait-mediated resource specialization (niche partitioning) in 93 plant–hummingbird interaction networks scattered across the Americas (figure modified from Dalsgaard *et al.*, 2021). The association between hummingbird bill length and mean floral corolla length of visited plant species (bold line, left *y*-axis) is strong and highly statistically significant ($R^2_{\text{marginal}} = 0.45$; $P < 0.01$), while the association between hummingbird bill length and mean species-level specialization (dotted line, right *y*-axis) is weak and statistically non-significant ($R^2_{\text{marginal}} = 0.01$; $P > 0.05$). Both lines are predicted values from linear mixed-effect models with hummingbird clade as a random effect. Hummingbird bill lengths were obtained from museum specimens and averaged across sexes ($N = 180$ species), and most floral corolla length estimates were gathered in the field ($N = 962$ species). Additional analysis that quantified specialization as niche breadth produced similar results. Details are available in Dalsgaard *et al.* (2021).

base or discover an unvisited flower overflowing with nectar (Wolf & Stiles, 1989; Feinsinger, 1983). Long-billed species, on the other hand, can extract nectar efficiently from flowers of all lengths, including short 'mismatched' flowers (Montgomerie, 1984; Temeles & Roberts, 1993), though they may make more insertion errors than short-billed hummingbirds when foraging on flowers with narrow openings (Temeles, 1996). For long-billed hummingbirds, trait-matching probably emerges because of several non-exclusive mechanisms. First, short-corolla flowers tend to produce less nectar than long-corolla flowers (Ornelas *et al.*, 2007; Tavares, Freitas & Gaglianone, 2016), making it more energetically profitable for large, long-billed species to feed on longer, more rewarding flowers (Snow & Snow, 1972; Dalsgaard *et al.*, 2009; but see Maruyama *et al.*, 2014). Moreover, due to life history trade-offs, plants with more nectar per flower may produce fewer flowers per inflorescence (e.g. Harder & Cruzan, 1990; Sargent *et al.*, 2007; but see Worley & Barrett, 2000; Caruso, Maherali & Benscoter, 2012). Because plants with smaller floral displays are less likely to constitute profitable territories, they may be avoided by hummingbird species prone to territoriality, which generally have short or medium-length bills (Feinsinger & Colwell, 1978). Finally, long-billed hummingbirds may prefer long-corolla flowers because of reduced competition with short-billed hummingbirds (Rodríguez-Gironés & Santamaría, 2006, 2007; Temeles *et al.*, 2019). For example, when Maglianesi, Böhning-Gaese & Schleuning (2015b) experimentally negated the need for competition by providing unlimited nectar accessible through different length tubes, long-billed hummingbirds preferred to drink from the *shortest* tubes. Altogether, this evidence suggests that morphological matching is the norm in hummingbird communities, although we might expect relaxed trait-matching in long-billed hummingbirds when costs to visiting mismatched flowers are low, such as when floral resources are abundant or not defended by morphologically well-matched competitors (but see Weinstein & Graham, 2017).

Beyond spatiotemporal overlap, morphological trait-matching, and abundance, few other mechanisms have been incorporated in studies exploring the drivers of pairwise interaction frequencies within plant–hummingbird networks. For instance, we found only one study that incorporated information about nectar reward and hummingbird body size to test whether larger hummingbirds interacted more frequently with highly rewarding plant species (Maruyama *et al.*, 2014). Contrary to expectations, these traits were poor predictors of plant–hummingbird interaction frequency, suggesting that trait-matching between body size and nectar reward may operate secondarily to trait-matching between bill and corolla length, at least in the tropical savannah of Brazil (Maruyama *et al.*, 2014). Because interference and exploitative competition may reinforce trait-matching within hummingbird communities (Maglianesi *et al.*, 2015b; Temeles *et al.*, 2019; Rico-Guevara *et al.*, 2021), future studies of interaction frequencies could include traits related to nectar defensibility, hummingbird foraging strategy, dominance rank, and/or competitive ability (Stiles & Wolf, 1970; Wolf *et al.*, 1976; Feinsinger & Colwell, 1978; Cotton, 1998b; Altshuler, 2006; Becker *et al.*, 2021). Experimental manipulations that temporarily remove dominant hummingbird species could also help elucidate the extent to which competition maintains the structure of plant–hummingbird interaction networks (for a non-hummingbird example, see Brosi & Briggs, 2013). Lastly, fine-scale examinations of interaction frequencies could include factors influencing nectar availability and/or hummingbird foraging preferences, such as nectar robbing (Irwin, 2000), nectar mites (Colwell, 1995; Lara & Ornelas, 2001; da Cruz, Righetti de Abreu & Van Sluys, 2007), nectar microbes (Vannette, Gauthier & Fukami, 2013), and flower sexual stage (Lara & Ornelas, 2001; Blanco, Galetto & Machado, 2013).

(*b*) *Specialization*

Ecological specialization can be conceptualized and measured in various ways, but it most commonly refers to a species having a relatively narrow niche breadth (Colwell & Futuyma, 1971; Futuyma & Moreno, 1988; Devictor *et al.*, 2010; Poisot *et al.*, 2011). That is, an ecologically specialized pollinator visits relatively few of the available floral resources compared to a generalist pollinator (Armbruster, 2017). Niche breadth was commonly measured in early studies of hummingbird community ecology (e.g. Feinsinger, 1976; Wolf *et al.*, 1976; Feinsinger & Swarm, 1982; Cotton, 1998c), but in recent studies taking a network perspective, 'resource specialization' is often quantified using two metrics indicating the degree of niche partitioning (e.g. Martín González *et al.*, 2015; Maruyama *et al.*, 2018; Sonne *et al.*, 2020). One such metric, complementary specialization (Blüthgen, Menzel & Blüthgen, 2006), occurs when a species shares its interaction partner(s) with few other species, indicating high niche exclusiveness (Blüthgen, 2010; Blüthgen & Klein, 2011). Conceptually, this metric is most comparable to measures of niche overlap used by early studies investigating how floral resources are divided among hummingbird species (e.g. Feinsinger, 1976; Feinsinger & Swarm, 1982). Another metric of niche partitioning, modularity, is highly correlated with complementary specialization and describes the extent to which subsets of species ('modules') interact frequently with each other but rarely with species outside the module (Olesen *et al.*, 2007; Dormann & Strauss, 2014). Modules are conceptually similar to functional groups (Fenster *et al.*, 2004; see also Section III.1) and analogous to 'subcommunities' described in earlier hummingbird literature (e.g. Kodric-Brown *et al.*, 1984; Stiles, 1985; Cotton, 1998c). We acknowledge that niche partitioning and niche breadth are distinct concepts and, in theory, may not always align (Sargeant, 2007). In this section, however, we discuss both niche-based properties under the umbrella of 'specialization', because they are likely correlated in nature (i.e. to avoid overlap, niches should be relatively narrow; Blüthgen & Klein, 2011).

Specialization is thought to promote speciation, facilitate species coexistence, and enhance ecosystem function but may also destabilize mutualistic networks if critical interaction partners go extinct (Blüthgen & Klein, 2011; Schleuning, Fründ & García, 2015; Phillips *et al.*, 2020). Thus, understanding the drivers of specialization within mutualistic interaction networks has attracted substantial attention, and numerous mechanisms, such as species traits, abundance, interspecific competition, and nectar availability, have been identified (Stang, Klinkhamer & Meijden, 2006; Brosi & Briggs, 2013; Fründ *et al.*, 2013; Junker *et al.*, 2013; Dehling *et al.*, 2016). To date, hummingbird researchers working towards a mechanistic understanding of specialization have largely focused on hummingbird traits (e.g. Cotton, 1998a; Maglianesi *et al.*, 2014; Dalsgaard *et al.*, 2018; Rodríguez-Flores *et al.*, 2019) and, to a lesser extent, nectar availability (e.g. Feinsinger, 1976; Feinsinger & Swarm, 1982; Tinoco *et al.*, 2017).

Many of these studies have investigated whether morphologically specialized hummingbirds (i.e. hummingbirds with long and/or curved bills) are also ecologically specialized foragers, but assembling consistent patterns has proved challenging. On the one hand, evidence suggests that long-billed hummingbirds have extremely wide niche breadths. For instance, Feinsinger *et al.* (1986) captured green hermits (*Phaethornis guy*) carrying pollen from >15 different plant species, and Cotton (1998a) similarly found that long-billed hummingbirds in the Colombian lowlands had wider diet breadths than short-billed species. Access to more floral resources has also been suggested to drive the evolution of bill length sexual dimorphism, because longer and/or more curved bills in subordinate females may provide an insurance policy during periods of nectar scarcity (Bleiweiss, 1999; Temeles, Miller & Rifkin, 2010). Conversely, a study of plant–hummingbird networks spanning a Costa Rican elevational gradient revealed *higher* levels of resource specialization in hummingbirds with long, curved bills (Maglianesi *et al.*, 2014), a finding congruent with recent findings at the level of hummingbird clades. For instance, Rodríguez-Flores *et al.* (2019) discovered that although most hummingbirds clades were 'super-generalists' following Olesen *et al.*'s (2007) classification, the relatively short-billed Emerald and Bee clades were exceptionally generalized, with each clade linked to approximately 80 plant families. Dalsgaard *et al.* (2021) arrived at a similar conclusion using a database of 93 quantitative plant–hummingbird interaction networks; species within the Emerald and Bee clades were the least specialized, while species within the Hermits and Mountain Gems (the clades with the longest bills) were the most specialized.

At the same time, comparative work has shown that specialization is *not* tightly linked to static species traits such as bill length, instead fluctuating with nectar availability, hummingbird abundance, and potentially the degree of interspecific competition (Tinoco *et al.*, 2017; Dalsgaard *et al.*, 2018; Simmons *et al.*, 2019; Morrison & Mendenhall, 2020). For example, in 19 networks comprising 103 hummingbird species, Simmons *et al.* (2019) found that resource specialization could largely be explained by species abundance; common species were more generalized, probably due to more chance encounters with potential plant partners. Moreover, in the largest comparative study to date, Dalsgaard *et al.* (2021) found that, across 181 hummingbird species, average resource specialization was only weakly mediated by bill length (Fig. 6). Although these are relatively new findings based on network theory and large databases of plant–hummingbird networks, the idea that specialization may depend on local conditions, notably nectar availability and competition, is not new. For instance, Feinsinger & Swarm (1982) found that copper-rumped hummingbirds on the island of Trinidad narrowed their niche breadth during a period of nectar scarcity, whereas niche expansion occurred during the same time period on nearby Tobago, which has fewer competing species of avian nectarivores. Findings from Tinoco *et al.* (2017) provide additional support for the influence of nectar availability on specialization; nectar declines led to niche contractions in long-billed species, which presumably intensified their foraging efforts on a narrow subset of long-corolla flowers inaccessible to short-billed competitors. Altogether, these findings suggest that although bill length may under certain conditions predict specialization, local conditions (e.g. nectar availability, abundance, and competition) are generally more important.

We suggest several avenues for future work on specialization within plant–hummingbird networks. One direction involves exploring the extent to which other species traits known to influence hummingbird feeding behaviour – such as bill curvature, body mass, competitive ability, or brain size – predict specialization (Temeles & Kress, 2003; Lefebvre, Reader & Sol, 2004; Altshuler, 2006; Maglianesi *et al.*, 2014). In addition, comparative studies could statistically model the interaction between morphological measurements and local conditions (such as nectar availability, habitat type, and community composition) to test the degree to which morphologically driven specialization is mediated by ecological context (e.g. Tinoco *et al.*, 2017). Finally, researchers could explore the extent to which specialization varies within species, as discussed in the next section.

(*c*) *A note about intraspecific variation*

Although plant–hummingbird interaction networks are typically constructed by aggregating observations to the level of species, overall network patterns emerge from the foraging choices of individual animals (Brosi, 2016). Because of this underlying process, a species that appears generalized could in fact comprise individual specialists, leading to differing predictions about network stability (Tur *et al.*, 2014; Brosi, 2016). Moreover, sex differences in foraging behaviour may lead to differences in plant reproduction (Smith, Bronstein & Papaj, 2019). Despite these potential implications of intraspecific variation and evidence that individual foraging choices can vary widely in hummingbirds (Maglianesi *et al.*, 2015a), few studies have addressed intraspecific variation in a network context. In this section, we suggest some reasons why niche differences might exist within hummingbird species and encourage future analyses of plant–hummingbird interactions to consider this possibility. Although hummingbird foraging strategy can vary with age (e.g. juvenile *versus* adult) and/or competitive environment (Carpenter *et al.*, 1993; Rodríguez-Flores & Arizmendi, 2016), here we focus on differences between hummingbird sexes.

Sex differences in floral resource use may be particularly common in hummingbirds, because parental care is conducted by females only (Schuchmann, 1999), an unusual pattern among birds (<10% of species: Cockburn, 2006). This division of labour may cause males and females to be spatially segregated for much of the annual cycle, leading to each sex encountering different floral resources. For example, male and female rufous hummingbirds *Selasphorus rufus* not only use different migration routes (Rousseau, Alexander & Betts, 2020), but are also believed to segregate altitudinally after reaching their wintering grounds in Mexico (Schondube *et al.*, 2004; Moran *et al.*, 2013; Rodríguez-Flores & Arizmendi, 2016). Interestingly, imbalanced sex ratios have been documented for many hummingbird species (e.g. Wolf, 1969; Borgella *et al.*, 2001; Howell & Gardali, 2003; Bassett & Cubie, 2009; Cubie, 2014), raising the possibility of widespread sexual segregation in hummingbirds, but further research is needed to eliminate alternative hypotheses (e.g. differential mortality or detection bias).

Moreover, sexual dimorphism in hummingbird bill shape and/or plumage coloration is common throughout the hummingbird phylogeny (Paton & Collins, 1989; Bleiweiss, 1999; Temeles *et al.*, 2010). Given that trait-matching between bill morphology and corolla morphology structures interactions at the species level (Section IV.1*a*, Fig. 6), it is not surprising that sex differences in bill shape have been linked to differences in floral resource use (e.g. Snow & Snow, 1980; Temeles *et al.*, 2000). Within the Trochilinae subfamily, sex differences in plumage coloration have also been linked to intraspecific differences in territoriality (Bleiweiss, 1985, 1999), presumably because interference competition in hummingbirds involves eye-catching displays of iridescent feathers (Stiles & Wolf, 1970; Ewald & Carpenter, 1978). For example, when males have brighter, more iridescent feathers than females (e.g. fork-tailed woodnymph, *Thalurania furcata*), they tend to establish feeding territories, while females of these species feed on spatially dispersed flowers except when defending nests (Wolf & Hainsworth, 1971; Bleiweiss, 1999). Conversely, when both sexes display flashy feathers (e.g. fiery throated hummingbird, *Panterpe insignis*; Wolf, 1969) or are equally lacklustre (e.g. steely vented hummingbird, *Amazilia saucerottei*; Stiles & Wolf, 1970), both males and females establish feeding territories. These differences in territoriality may translate into the use of different plant species (e.g. Temeles *et al.*, 2000), because territoriality is only profitable when plants offer highly valuable, defendable nectar (Stiles, 1975). A first step toward exploring this possibility would be to examine whether resource preferences and specialization vary between sexes with pronounced sexual dimorphism in bill shape (e.g. *Glaucis hirsutus*, *Phaethornis guy*, *P. longirostris*, *P. superciliosus*, *Campylopterus* spp., *Lafresnaya*; Temeles *et al.*, 2010). Resource preferences could be ascertained by observing certain plant species and recording the sex of each visitor (Taylor & White, 2007; Temeles *et al.*, 2010), while individual-level specialization could be quantified through intensive hummingbird mark–recapture studies that compare pollen types carried within *versus* among individuals (Maglianesi *et al.*, 2015a).

(2) **Network structure across communities**

Over the past decade, researchers have leveraged a compilation of plant–hummingbird visitation networks to explore the biotic and abiotic drivers of network-level resource specialization (*sensu* Blüthgen *et al.*, 2006; see also Section IV.1*b*). As found for plant–pollinator networks more generally (Dalsgaard *et al.*, 2013; but see Schleuning *et al.*, 2012), specialization of hummingbird networks increases closer to the equator (Dalsgaard *et al.*, 2011). Because lower latitudes have greater avian and plant biodiversity (Willig, Kaufman & Stevens, 2003), species richness has naturally emerged as a strong correlate of specialization. This pattern may arise if species-rich communities experience intense interspecific competition that triggers resource partitioning, especially among close relatives (Dalsgaard *et al.*, 2011, 2018; Martín González *et al.*, 2015). Alternatively, species-rich networks may simply have higher niche availability, particularly in communities with high plant diversity (Martín González *et al.*, 2015; but see Schleuning *et al.*, 2012).

In addition to species richness, specialized relationships between hummingbirds and their food plants have been linked to topographic heterogeneity, historically stable climates, large amounts of precipitation, and warm temperatures (Dalsgaard *et al.*, 2011, 2018; Martín González *et al.*, 2015; Sonne *et al.*, 2016; Maruyama *et al.*, 2018). The importance of both topographic heterogeneity and historical climate stability – which can be greater in mountainous areas due to microclimatic refugia and opportunities to move up or downslope (Sandel *et al.*, 2011; Suggitt *et al.*, 2018) – suggests that tropical mountains may have facilitated partner persistence during periods of climate upheaval, promoting exclusive relationships over evolutionary timescales (Dalsgaard *et al.*, 2011; Martín González *et al.*, 2015; Sonne *et al.*, 2016). Contemporary climate, especially precipitation, is also important; resource specialization is higher in areas with large amounts of rainfall (Dalsgaard *et al.*, 2011, 2018; Sonne *et al.*, 2016; Maruyama *et al.*, 2018). Two hypotheses have been proposed to explain this relationship. First, precipitation may have facilitated specialization between plants and hummingbirds (Dalsgaard *et al.*, 2009, 2011), because insect pollinators tend to be less active in rainy conditions (Cruden, 1972) and/or because water availability allows plants to produce large nectar volumes that attract hummingbirds (Aizen & Ezcurra, 1998). Second, because precipitation is strongly associated with Neotropical plant diversity (Gentry, 1982), precipitation may facilitate niche partitioning through its effects on plant richness and hummingbird functional trait diversity (Maruyama *et al.*, 2018). To understand further the mechanisms driving these macroecological patterns of specialization and to reduce confounds associated with the latitudinal biodiversity gradient [e.g. climate *versus* time since disturbance (Gaston, 2000; Willig *et al.*, 2003)], intermediate-scale studies that directly measure and account for confounding variables will be valuable (e.g. Craven *et al.*, 2019).

However, these explanations for latitudinal trends in specialization tend to focus on why tropical networks are *more* specialized, rather than why networks of temperate North America are *less* specialized. As mentioned previously, one potential reason for low specialization in North America is the relatively low species richness in temperate regions, particularly in seasonal mountain environments. For instance, the two temperate networks included in macroecological analyses of network specialization include two hummingbird species and no more than four plant species (Dalsgaard *et al.*, 2021). Additionally, plants in temperate regions frequently exhibit a mixed pollination system – relying on both migratory hummingbirds and insects (e.g. Chase & Raven, 1975; Miller, 1978; Waser, 1978; Lange & Scott, 1999) – rather than the classical ornithophilous pollination syndrome that is more common in the tropics (Abrahamczyk & Kessler, 2015). If the relatively few plant species present in temperate networks also exhibit more generalized floral morphologies, opportunities for niche partitioning may be scarce in these communities. Moreover, the hummingbird species that co-occur in North American communities can be close relatives with similar bill morphologies, such as the broad-tailed hummingbird (*Selasphorus platycercus*) and rufous hummingbird (*S. rufus*) (Calder, 2004). This similarity in functional traits may also preclude high levels of niche partitioning (Maruyama *et al.*, 2018). Macroecological analyses that include a more complete sample of plant–hummingbird networks from temperate regions may help disentangle these explanations.

(3) The plant perspective: are all hummingbirds equally effective pollinators?

(*a*) *Incorporating pollinator effectiveness into plant–hummingbird interaction networks*

From a plant's perspective, the importance of a given pollinator species depends on (*i*) how frequently the pollinator visits the plant, and (*ii*) pollinator performance during the visit, i.e. the pollinator's effectiveness at delivering pollen grains of sufficient quantity and quality (Ne'eman *et al.*, 2010; King, Ballantyne & Willmer, 2013; Ballantyne, Baldock & Willmer, 2015). Pollen *quantity* can be measured by counting conspecific pollen grains delivered to a stigma during a single visit ('single-visit deposition': King *et al.*, 2013; Ballantyne *et al.*, 2015), while pollen *quality* depends on numerous plant-specific variables (e.g. genetic compatibility, relatedness, presence of multiple sires) and is best ascertained through seed set (Ne'eman *et al.*, 2010; Santiago-Hernández *et al.*, 2019) or genetic measures (Torres-Vanegas *et al.*, 2021). Additionally, in plant species with pollinator filtering mechanisms (i.e. 'pollinator recognition'; Betts *et al.*, 2015), pollinator effectiveness may vary independently from pollen quantity or quality (Table 1).

To construct plant–hummingbird interaction networks, links between species are usually ascertained by (*i*) observing that hummingbirds contact the reproductive parts of various plant species ('visitation networks'), or (*ii*) identifying pollen grains collected from captured hummingbirds ('pollen transport networks') (Table 1). Within the hummingbird literature, pollen transport networks (e.g. Rodríguez-Flores *et al.*, 2012; Maglianesi *et al.*, 2015a) are generally less common than feeding observations collected by human observers or video cameras (e.g. Snow & Snow, 1980; Weinstein & Graham, 2017). Pollen networks have several potential advantages over visitation networks. First, they may detect more interactions (Ramírez-Burbano *et al.*, 2017; Zanata *et al.*, 2017), possibly because they sample a larger geographic area over which birds are moving. Moreover, pollen networks confirm that a given hummingbird species is transporting pollen, rather than only consuming nectar (Table 1). On the other hand, pollen-based approaches typically produce

Table 1. Quantification of plant–hummingbird interaction networks and limits to interpretation. Plant–hummingbird interactions are most frequently ascertained by directly observing hummingbirds visiting plants of various species, and less frequently by identifying pollen grains collected from captured hummingbirds. Neither of these methods fully characterizes potential contributions to plant reproduction, however, because different hummingbird species may vary in their effectiveness as pollinators. To better represent the plant perspective, studies that link single hummingbird visits to pollen deposition, fruit set, and/or seed set are warranted

		Limitations for interpretation	
Approach	Network type	Plant perspective	Bird perspective
Direct observations of birds visiting plants[a] (visitation networks)	Qualitative (unweighted)[b]	No data on interaction frequency; e.g. assumes one visit is equivalent to 100 visits.	No data on interaction frequency; e.g. assumes one visit is equivalent to 100 visits.
	Quantitative (weighted)[b]	Assumes interaction frequency translates to pollinator effectiveness.	Assumes interaction frequency translates to caloric importance, but not all plants are equal in nectar reward.
Pollen grains collected from captured birds (pollen transport networks)	Quantitative (weighted)[c]	Assumes pollen on a bird is deposited onto a conspecific stigma.	Assumes the bird visited that plant species, rather than secondarily picking up pollen from interspecific pollen transfer. Low taxonomic resolution of pollen identification may also preclude species-level identification of nectar resources used.
Single-visit deposition (amount of pollen deposited on stigma from a single hummingbird visit)	Quantitative (weighted)	Assumes no additional filters between pollen deposition and fruit/seed set (e.g. self-compatibility barriers, pollinator recognition).	Not applicable

[a] Visitation networks may include all plant species, regardless of apparent pollination syndrome (Dalsgaard *et al.*, 2011; Ramírez-Burbano *et al.*, 2017), or species thought to be visited by hummingbirds (e.g. ornithophilous species; Maglianesi *et al.*, 2014).
[b] Either including all visitors or omitting visitors that did not contact reproductive structures (e.g. nectar thieves).
[c] Networks constructed from pollen grains are generally analysed as quantitative networks, with interaction frequencies created by scoring presence/absence of a certain pollen species (or morphotype) in samples collected from individual hummingbirds (e.g. Maglianesi *et al.*, 2015a; Ramírez-Burbano *et al.*, 2017).

networks of lower taxonomic resolution because pollen grains can rarely be identified to species without genetic techniques. Further, pollen transport networks assume that pollen on a bird is deposited onto a conspecific stigma (Table 1). To reflect the plant perspective most accurately, we thus encourage researchers to begin generating networks from single-visit deposition data and eventually work towards creating networks that incorporate relative contributions of different hummingbird species to fruit and seed set (e.g. King *et al.*, 2013; Santiago-Hernández *et al.*, 2019; Table 1).

Understanding how different pollinators influence plant reproduction is not only important for understanding coevolution (Section III.1), but also for enhancing plant conservation, because strong dependencies on certain pollinators may trigger population declines if those pollinators are lost due to habitat loss or climate change (Section V). However, most published 'pollination networks' are in fact visitation networks, which tend to underestimate specialization relative to networks constructed using data on pollen deposition, fruit production, and/or seed production (Ballantyne *et al.*, 2015; Santiago-Hernández *et al.*, 2019). This underestimation could lead to overly optimistic predictions about how networks respond to species loss (Betts *et al.*, 2015), because theoretical work suggests that specialization may compromise the stability of mutualistic networks (Okuyama & Holland, 2008; Bastolla *et al.*, 2009; Thébault & Fontaine, 2010; Rohr, Saavedra & Bascompte, 2014).

Although several studies have compared the pollination performance of hummingbirds to that of insects (e.g. Castellanos *et al.*, 2003; Magalhães *et al.*, 2018; Lehmann *et al.*, 2019), less is known about how pollinator effectiveness differs among (or within) hummingbird species and how any differences may affect network stability. Clearly, hummingbirds that obtain nectar by puncturing the flower base and bypassing the plant's reproductive structures ('robbing') are unlikely to be good pollinators (Fumero-Cabán & Meléndez-Ackerman, 2007), and these observations are typically excluded from network analyses (Maruyama *et al.*, 2015). Of the hummingbirds that visit a given plant species without robbing, some evidence suggests that species (or sexes) with well-matched bills can be better pollinators. For example, aviary experiments comparing the effectiveness of six hummingbird species revealed that pollination of long, curved *Heliconia tortuosa* flowers was more likely following visitation by hummingbirds with longer and more curved bills, compared to shorter and straighter bills (Betts *et al.*, 2015). Similarly, long-billed hummingbirds were better at delivering pollen to long-corolla flowers of *H. bihai* (Temeles *et al*., 2019). On the other hand, bill–corolla mismatches may not necessarily preclude pollination, since long-billed hummingbirds can effectively deposit pollen on the stigmas of short-corolla flowers (Ornelas *et al*., 2004; Temeles *et al*., 2019). Short-billed hummingbirds might also be able to pollinate long-corolla flowers, at least when the corolla tube opening is wide enough to allow partial head insertion (Missagia & Alves, 2018). Additional studies will be necessary before drawing firm conclusions about the role of trait-matching and hummingbird pollination performance. Moreover, to understand reproductive isolation and/or ecological dependence within plant–pollinator interaction networks, information about pollinator performance must be combined with visitation rates from real-world networks. For instance, although *Heliconia caribea* received similar amounts of pollen from both sexes of purple-throated caribs, females rarely visited *H. caribea* during field observations, probably due to competitive exclusion (Temeles *et al*., 2019).

(*b*) *Effects of hummingbird foraging behaviour on pollen dispersal*

High pollinator mobility is believed to increase pollen dispersal, thereby decreasing rates of self-pollination and enhancing genetic diversity (Ghazoul, 2005; Krauss *et al*., 2017; Wessinger, 2021). In support of this hypothesis, a recent meta-analysis found higher rates of multiple paternity (genetic diversity within seeds) in bird-pollinated plants, compared to plants pollinated by insects only (Krauss *et al*., 2017). Within hummingbird-pollinated plants, however, few studies have tested how variation in hummingbird mobility influences plant genetic diversity. Early studies using fluorescent dye as a pollen analogue found that plants not defended by territorial hummingbirds had their pollen (dye) dispersed greater distances than defended plants (Linhart, 1973; Linhart & Feinsinger, 1980), and recent work demonstrates that highly mobile, traplining hummingbirds indeed disperse pollen widely, resulting in delivery of genetically diverse pollen grains from unrelated plants (Torres-Vanegas *et al*., 2019, 2021). Similarly, Maruyama, Justino & Oliveira (2016a) found that flowers within hummingbird territories received more compatible pollen grains when visited by territory intruders, rather than the territory holder. Thus, it has been suggested that visitation by hummingbird species prone to territoriality might decrease gene flow, increase plant inbreeding, and potentially compromise plant fitness (e.g. Betts *et al*., 2015).

To assess the generality of this hypothesis, further consideration and future study are warranted. Hummingbird territoriality varies with nectar availability and individual attributes (Section IV.1*c*), long-distance movements can occur between foraging bouts (Feinsinger, 1976; Campbell, 1991), and territory intruders may facilitate pollen exchange for plants within territories (Wolowski *et al*., 2013; Maruyama *et al*., 2016a). For these reasons, territorial behaviour may not necessarily hamper plant reproduction, particularly if plants that are normally defended are self-compatible and/or tolerant of inbreeding (Wolowski *et al*., 2013). However, empirical evidence supporting either scenario remains limited.

To evaluate the relationship between pollen dispersal and hummingbird foraging behaviour (i.e. territorial defence of a plant), we searched the literature for pollen dispersal experiments conducted in natural settings using plant species primarily visited by hummingbirds (Appendix S1, Table S4). We found a total of nine studies in which researchers applied fluorescent dye to the flowers of a central source plant and later inspected surrounding flowers for dye transfer events (Table 2). Five of these studies had comparable methods and were included in an exploratory analysis comparing pollen dispersal from defended *versus* undefended source plants. For this analysis, we digitized the original figures, fitted exponential decay curves to the digitized data points, and calculated summary statistics describing the dispersal distance and the fitted decay function (Fig. 7, Table S5; see Appendix S1 for full methods).

Overall, we found pollen was dispersed over shorter distances when defended by territorial hummingbirds, but there was substantial overlap in the dispersal curves between defence categories (Fig. 7). We caution that these conclusions stem from a small number of studies, many of which had relatively low replication (Table S4) and relatively short search distances (median: 50 m), which may have precluded detection of long-distance dispersal events. Ultimately, additional work is needed to determine how different hummingbird species (and sexes) influence pollen dispersal and plant reproduction. We recommend that researchers conduct dye dispersal experiments while simultaneously documenting all floral visitors to the source plant (e.g. by using video cameras), replicate the experiments across many days and/or source plants, and increase search radii as much as possible. Researchers could alternatively focus on pollen receipt by genotyping all plants within a certain radius, collecting pollen received by a focal plant during a single hummingbird visit, and using paternity analysis to pinpoint the exact location of the donor plant (e.g. Castilla *et al*., 2017). We also encourage a more nuanced, context-specific view of pollen dispersal and plant reproduction that considers resource context and species traits. For example, high nectar availability can concentrate pollinator movements (Castilla *et al*., 2017) but also increase intruder pressure (Ewald & Carpenter, 1978; Trombulak, 1990; Justino *et al*., 2012). Moreover, the extent to which territoriality hinders plant reproduction likely depends on the traits of each plant species, such as the number of outcross pollen grains needed for pollination and whether the plant is self-compatible (Wolowski *et al*., 2013; Maruyama *et al*., 2016a). Thus, future work could not only investigate the link between hummingbird foraging strategy and pollen flow, but also examine how resource context and plant traits mediate this relationship.

V. HUMMINGBIRD CONSERVATION

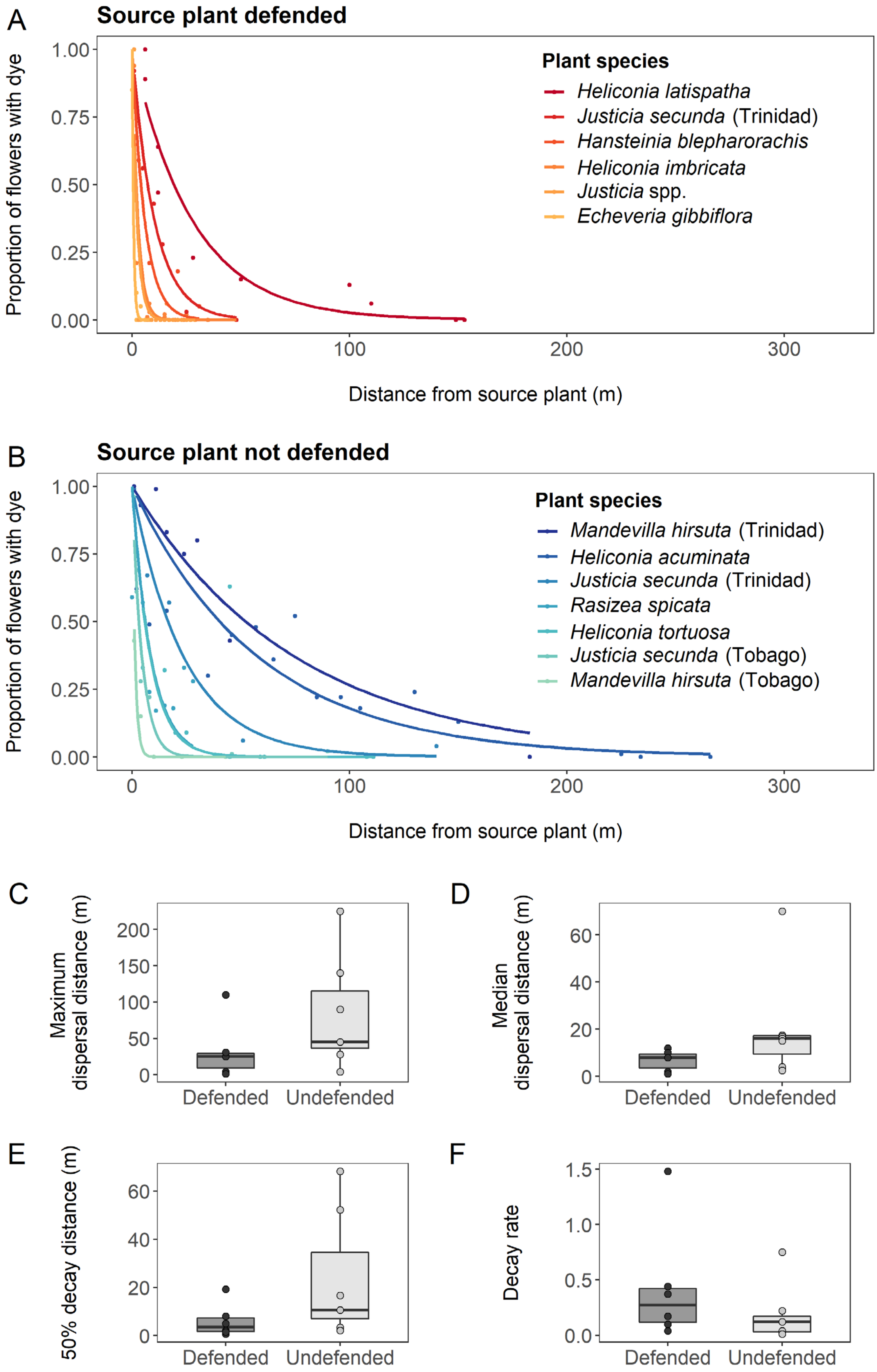
It is well established that pollinators are declining worldwide (Regan *et al*., 2015), and hummingbird populations are

Table 2. Summary of pollen dispersal experiments with hummingbirds. In these experiments, fluorescent dye (a pollen analogue) was applied to flowers of a central source plant prior to hummingbird visitation, and surrounding flowers were subsequently examined for dye transfer events. Exponential decay curves were fitted to data points digitized from original figures, which presented information about the proportion of flowers with dye (*y*-axis) and distance from the source plant (*x*-axis). Maximum and median dispersal distances were calculated from these data, while maximum search distance was inferred from the figures (i.e. the largest distance on the *x*-axis). The lower section of the table lists studies of dye dispersal not directly comparable to the studies included in our analysis, either because dispersal was quantified using a different response variable or the source flower was removed after a single visit.

Study	Plant species	Study site	Dye source defended	Max distance at which dye found (m)	Median distance at which dye found (m)	Max search distance (m)
Linhart (1973)	*Heliconia acuminata*	Tilarán, Costa Rica	No	225	70	266
	Heliconia imbricata	La Selva, Costa Rica	Yes (*Thalurania furcata*)	25	8	48
	Heliconia latispatha	Tilarán, Costa Rica	Yes (*Amazilia saucerottei*)	110	12	153
	Heliconia tortuosa	La Selva, Costa Rica	No	45	17.5	111
Linhart & Feinsinger (1980)	*Justicia secunda*	Tobago	No	90	4	90
	Justicia secunda	Arima Valley, Trinidad[a]	Yes (*Amazilia tobaci*)	25	10	48
	Justicia secunda	Arima Valley, Trinidad[b]	No	140	17	140
	Mandevilla hirsuta	Tobago	No	4	2.5	43
	Mandevilla hirsuta	Arima Valley, Trinidad[a]	No	45	16	183
Linhart *et al.* (1987)	*Hansteinia blepharorachis*	Monteverde, Costa Rica	Yes (*Lampornis calolaema*)	31	8	31
	Rasizea spicata	Monteverde, Costa Rica	No	28	15	28
Parra *et al.* (1993)	*Echeveria gibbiflora*	Mexico City, Mexico	Yes (*Cynanthus latirostris*)	4	2	8
Schmidt-Lebuhn *et al.* (2019)	*Justicia* spp.[c]	Yungas region, Bolivia	Yes (unknown species)	1[d]	1	30
Webb & Bawa (1983)	*Malvaviscus arboreus*	Hacienda La Pacifica, Costa Rica				
Murawski & Gilbert (1986)	*Psiguria warscewiczii*	Osa Peninsula, Costa Rica				
Campbell & Waser (1989)	*Ipomopsis aggregata*	Rocky Mountains, Colorado USA				
Campbell (1991)	*Ipomopsis aggregata*	Rocky Mountains, Colorado USA				

[a] Site with high flower density.
[b] Site with low flower density.
[c] Six *Justicia* species: *J. aequilabris*, *J. boliviensis*, *J. consanguinea*, *J. monopleurantha*, *J. oranensis*, and *J. tocantina* (all species were combined in original study).
[d] Dye was dispersed up to 7 m for some of the *Justicia* species, but central value digitized from boxplots (median) was zero at all distances >1 m.

consistent with this trend; for the 236 species with data available to estimate population trends, 60% are in decline (Fig. 3; Tables S2 and S3; IUCN, 2020a). Due to such declines and restricted range sizes for many species, 10% of hummingbird species are listed as Vulnerable, Endangered, or Critically Endangered (Fig. 3; Tables S2 and S3; IUCN, 2020a). Most of these threatened hummingbirds are tropical species with small geographical ranges (Fig. 1), although population declines have also been noted in Nearctic migrants, such as the rufous hummingbird (Sauer *et al.*, 2014; English *et al.*, 2021). Given the importance of hummingbirds as pollinators and the potential for specialization in pollination



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networks (Section IV), these population declines may eventually lead to secondary extinctions of the plants that depend on them (Lindberg & Olesen, 2001; Hadley *et al.*, 2014). In the following subsections, we first identify hummingbird traits associated with IUCN extinction risk, then synthesize research on the main threats to hummingbird populations: habitat loss and climate change.

(1) Hummingbird traits and extinction risk

To identify specific hummingbird traits associated with high conservation concern, we modelled hummingbird extinction risk as a function of various morphological and natural-history traits using phylogenetic logistic regression (Appendix S1, Table S6). Extinction risk was quantified using species-level conservation assessment data from the IUCN *Red List* (IUCN, 2020a); hummingbirds listed as Vulnerable, Endangered, or Critically Endangered (i.e. threatened) or having a decreasing population trend were considered at risk of extinction. Trait data were compiled from various existing data sets and included geographic range size (Tobias & Pigot, 2019), elevational range (Quintero & Jetz, 2018), morphology (body mass: Wilman *et al.*, 2014; bill length: Pigot *et al.*, 2020), overall human footprint within geographic range (Betts *et al.*, 2017), and natural history (forest dependency and migratory behaviour: BirdLife International, 2020). We also designated whether the species belonged to the Hermit clade (subfamily Phaethornithinae), because several species within this group exhibit reduced abundances and/or restricted movements in fragmented habitats [*Eutoxeres aquila* (Borgella *et al.*, 2001); *Phaethornis guy* (Hadley & Betts, 2009; Hadley *et al.*, 2018); *P. pretrei* (Maruyama *et al.*, 2019)]. Full methods are available in Appendix S1, together with bill length data compiled from 2172 individuals representing 336 hummingbird species (Table S7).

We found that the most important predictors of hummingbird extinction risk are range size and reliance on forests (Fig. 8, Table S9). For example, for a halving of range size, we estimate that the odds of a species being threatened increase by 5.33 times (95% CI: 3.09–10.69), and the odds of having a decreasing population trend increase by 1.67 times (95% CI: 1.19–2.48), accounting for all other predictor variables (Table S9). This finding corroborates widespread evidence supporting the strong relationship between range size and extinction risk (Tobias & Pigot, 2019), which in part reflects a methodological circularity because range size is one of the criteria by which conservation status is assigned (IUCN, 2012). We also found that, accounting for all other predictor variables, extinction risk was higher for forest specialists, with the odds of being threatened increasing by 3.03 times (95% CI: 1.02–9.8) and the odds of having a decreasing population trend increasing by 4.23 times (95% CI: 2.16–9.2 times) relative to hummingbirds without high forest dependency (Fig. 8, Table S9).

For all other predictors, we observed weaker effects, with confidence intervals of standardized coefficient estimates frequently approaching or overlapping zero. However, some notable trends emerged in the analysis of population declines. Specifically, the odds of having a decreasing population tended to be higher in species that had smaller elevational ranges or were non-migratory (Fig. 8, Table S9). For every one standard deviation increase in elevational range, the odds of having a decreasing population trend decreased by about 30% (0.69 times, 95% CI: 0.46–0.96), and the odds of a decreasing population trend in migratory species were about half that of non-migratory species (0.46 times, 95% CI: 0.20–1.0). The latter result is unexpected but may arise if sedentary species generally have lower dispersal abilities through non-habitat, which could hamper their ability to adapt to habitat loss and fragmentation at local scales (Şekercioğlu, 2007).

While we caution that the exact magnitudes of estimated effects depend on other predictor variables in the model, these results highlight the importance of range size and high forest dependency as key predictors of extinction risk. Thus, forest conservation efforts are a key strategy in buffering against further hummingbird declines. We also encourage additional research investigating how climate change may not only affect hummingbird range sizes, but also cause range shifts into unsuitable habitat (e.g. by linking projected range shifts to remotely sensed land cover data; Velásquez-Tibata, Salaman & Graham, 2012). These projections could be used in IUCN assessments and to prioritize monitoring efforts for species especially vulnerable to the combined effects of deforestation and climate change.

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Fig. 7. Summary of experiments using fluorescent dye, a pollen analogue, to measure pollen dispersal by hummingbirds (i.e. Linhart, 1973; Linhart & Feinsinger, 1980; Linhart *et al.*, 1987; Parra *et al.*, 1993; Schmidt-Lebuhn *et al.*, 2019; see also Table 2). In these experiments, dye was applied to flowers of a central source plant prior to hummingbird visitation, and surrounding plants were subsequently examined for dye transfer events. (A, B) Exponential decay curves fitted to data points digitized from original figures. In A, source plants were defended by territorial hummingbirds, while source plants in B were not defended. (C) Maximum distance that pollen was dispersed in experiments with defended *versus* undefended source plants. (D) Median distance that pollen was dispersed. (E) Distance at which the proportion of plants receiving pollen reached 50% of the initial value, calculated based on the fitted exponential decay equations. (F) Decay rate parameter of the fitted exponential decay equations. The decay rate parameter indicates whether pollen dispersal decays toward zero rapidly (larger values) or gradually (smaller values). In all boxplots, the median is indicated by the darker black line, while lower and upper lines represent the first and third quartiles, respectively. Whiskers extend from the first and third quartiles to the lowest and highest values within 1.5 times the interquartile range. Boxplots are overlaid by individual data points. See Appendix S1 for full methods.

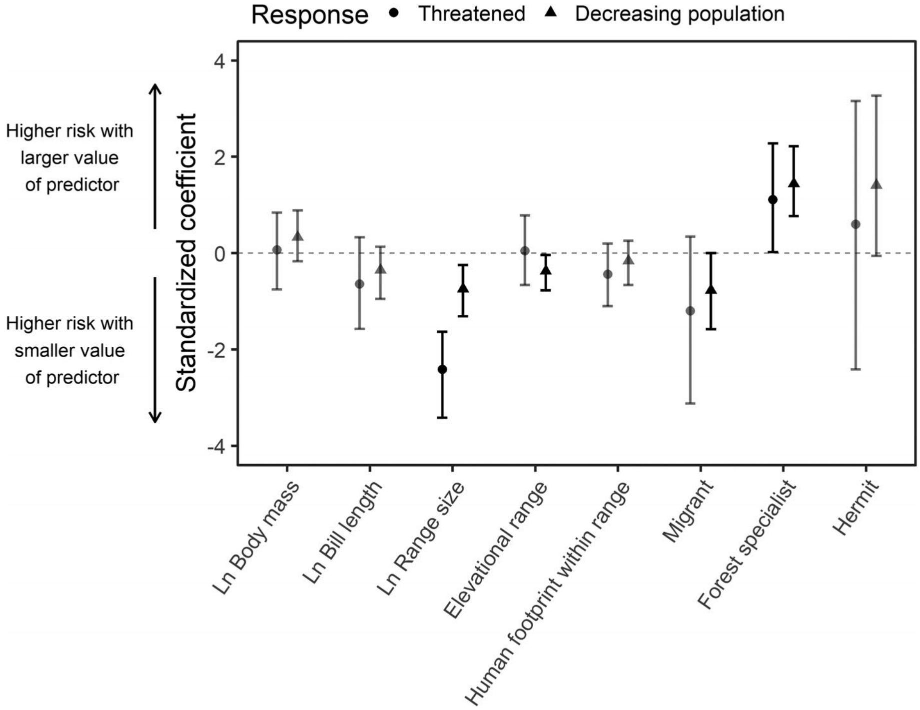

Fig. 8. Effects of morphological traits and natural history characteristics on hummingbird extinction risk as determined by the IUCN (International Union for Conservation of Nature). Hummingbird species considered at risk of extinction are Vulnerable, Endangered, or Critically Endangered (i.e. threatened) and/or exhibit a decreasing population trend. The categorical predictors 'Migrant', 'Forest specialist', and 'Hermit' are coded as '1' if the species migrates latitudinally or altitudinally, depends heavily on forests, or is in the subfamily Phaethornithinae (Hermits). The analysis of *Red List* category (i.e. threatened or not) included 307 species, and the analysis of population trend (i.e. decreasing or not) included 195 species. Standardized coefficient estimates and 95% bootstrap confidence intervals are calculated from a phylogenetic logistic regression and are thus conditional on estimates of phylogenetic relatedness (Table S9). For a given predictor variable, positive coefficient estimates indicate that higher extinction risk is associated with *larger* predictor values; negative coefficient estimates indicate that higher extinction risk is associated with *smaller* predictor values. For instance, extinction risk increases for species that have small range sizes or are forest specialists. Black error bars indicate 95% confidence intervals that do not overlap zero and are thus considered statistically significant. See Appendix S1 for full methods.

(2) Threats to hummingbirds

(*a*) *Habitat loss*

As is the case for plants (Brummitt *et al.*, 2015) and birds in general (Owens & Bennett, 2000), habitat loss or conversion is the greatest threat to hummingbirds; all 40 species listed as Vulnerable, Endangered, or Critically Endangered show habitat modification (i.e. agriculture or natural resource use) as a cause of threat (IUCN, 2020a). Since most (>95%) hummingbird species are at least partially forest dependent (Fig. 3; Table S3; BirdLife International, 2020) and forest dependency is associated with elevated extinction risk (Section V.1), forest loss is a primary determinant of hummingbird decline.

Surprisingly, early work on hummingbird responses to rainforest clearing showed hummingbird abundances were not strongly influenced by experimental isolation of forest fragments, initially or following regeneration of the surrounding matrix (Stouffer & Bierregaard, 1995; Stouffer *et al.*, 2006). These findings are consistent with other studies showing that some hummingbird species may be resilient to stand-replacing disturbance [e.g. fires (Smucker, Hutto & Steele, 2005; Kotliar, Kennedy & Ferree, 2007; Mestre, Cochrane & Barlow, 2013)] and tend to be associated with shrubby habitats (Blake & Loiselle, 2001; Barlow *et al.*, 2007; Tinoco *et al.*, 2009). However, it is important to note that these studies measured presence or abundance, not fitness, which is a critical metric when quantifying habitat quality (Van Horne, 1983). Shrubby, disturbed habitats may provide abundant nectar resources for hummingbirds but also act as population sinks or ecological traps (Schlaepfer, Runge & Sherman, 2002). For example, edge habitats have been linked to higher rates of avian nest predation (Paton, 1994; Weldon & Haddad, 2005), and nest predation is a major cause of hummingbird nest failure (Baltosser, 1986; Fierro-Calderón & Martin, 2007; Smith, Finch & Hawksworth, 2009). Unfortunately, studies on hummingbird reproduction and survival across human-modified habitats are exceedingly rare (we located two papers: Gleffe *et al.*, 2006 and Smith *et al.*, 2009). We thus recommend studies that examine fitness measures across gradients in expected habitat quality, especially given newly available radio-tagging techniques for tracking hummingbirds to their nests (Hadley & Betts, 2009; Zenzal, Diehl & Moore, 2014; Céspedes *et al.*, 2019).

Additionally, many studies showing hummingbird resilience to disturbance were carried out in locations or landscapes where permanent deforestation did not occur (i.e. forest was not converted to agriculture). Borgella *et al.* (2001) were the first to examine how such 'hard' habitat loss and fragmentation influenced hummingbirds, finding that hummingbird species richness increased asymptotically with forest patch size. Moreover, certain species such as the white-tipped sicklebill occurred only in the three largest patches (Borgella *et al.*, 2001). Subsequent studies have also shown that loss of native vegetation causes functional shifts in hummingbird communities by reducing the abundance of large and morphologically specialized traplining hummingbirds, such as sicklebills and hermits (Lindberg & Olesen, 2001; Matias, Maruyama & Consolaro, 2016; Hadley *et al.*, 2018; Tinoco *et al.*, 2018; Maruyama *et al.*, 2019; Morrison & Mendenhall, 2020). Because traplining hummingbirds are thought to travel long distances each day, such community shifts may stem from movement limitation in fragmented landscapes; for example, green hermits rely on forested corridors to traverse a landscape of cattle pasture and remnant forest patches (Hadley & Betts, 2009; Volpe *et al.*, 2014, 2016; Kormann *et al.*, 2016).

Thus, although shrubby secondary growth may support opportunistic, generalist hummingbirds, other species – especially those with larger body sizes, specialized morphologies, and/or fragmentation-sensitive movements – are unlikely to thrive in heavily disturbed habitats. Importantly, these specialist hummingbirds are also more likely to have highly coevolved relationships with native plants. For example, reliance on movement-limited traplining hummingbirds has likely contributed to reproductive declines in *Heliconia* within isolated forest fragments (Hadley *et al.*, 2014). Reconnecting landscapes with narrow corridors (Kormann *et al.*, 2016) or scrub habitat (Renjifo, 2001; Jackson, 2017) may facilitate hummingbird movement and preserve, or even restore, coevolved plant–hummingbird relationships.

(*b*) *Climate change*

Within the global range of hummingbirds, multiple dimensions of climate are expected to change over the coming decades. Mean global temperature has already increased by approximately 1°C relative to preindustrial levels, and northern latitudes are warming more quickly than this global average (Allen *et al.*, 2018). In addition to rising average temperatures, temperature extremes of 2–4°C above normal are forecast for central North America and the Brazilian Amazon by the year 2100 (Hoegh-Guldberg *et al.*, 2018). Temperature-associated changes in precipitation patterns, drought, and tropical cyclones are more difficult to predict with high certainty, but existing evidence points toward an overall reduction in mean precipitation across central North America, Central America, and much of South America (Hoegh-Guldberg *et al.*, 2018) and soil moisture deficits across the western United States and northern Mexico (Wehner *et al.*, 2017). Finally, the North Atlantic region – which includes the Caribbean islands that support 16 endemic hummingbird species (Abrahamczyk *et al.*, 2015; Feo *et al.*, 2015) – has experienced an increase in tropical cyclone activity since the 1970s, although experts are still uncertain whether a warmer world will lead to increased frequency of severe (Category 4–5) hurricanes in this area (Walsh *et al.*, 2016; Kossin *et al.*, 2017).

Despite some uncertainty about how rising temperatures will influence other aspects of climate, recent climate change is already exerting a clear influence on bird populations and biodiversity overall (Thomas *et al.*, 2004; Parmesan, 2006; Both *et al.*, 2006; Maclean & Wilson, 2011; Gutiérrez Illán *et al.*, 2014). We thus identify several potential mechanisms through which climate change could influence hummingbird populations directly (e.g. by exceeding thermoregulatory capabilities) or indirectly (e.g. by altering nectar resources), although research in this area is still nascent and most work to date projects future changes, rather than examining historical patterns or elucidating mechanisms for potential climate effects.

(i) Range shifts. Climate change is likely to cause geographic range shifts to higher latitudes and elevations (Parmesan, 2006), but elevational range shifts have been the focus of most hummingbird research on this topic. For instance, Buermann *et al.* (2011) used climate-envelope models (i.e. species distribution models with climate data as predictors; Thomas *et al.*, 2004) to predict the future distributions of five species of Andean hummingbird. All species were expected to shift their ranges 300–700 m upslope by the year 2080 (Buermann *et al.*, 2011). Similarly, Graham *et al.* (2017) predicted how Ecuadorian hummingbird communities might reshuffle under climate change, finding that novel species assemblages are particularly likely at the extreme ends of climatic gradients, such as high elevations; by year 2070, communities above 1000 m are expected to share fewer than 20% of their species with current assemblages (Graham *et al.*, 2017). We caution, however, that hummingbird range shifts may also be affected by factors other than temperature and precipitation, such as biotic interactions and land use.

Biotic interactions such as competition and mutualism may constrain range shifts, although these interactions are rarely incorporated into predictive models (HilleRisLambers *et al.*, 2013; Jankowski *et al.*, 2013), including those for hummingbirds. This could be problematic for predicting range shifts, because competition is thought to influence hummingbird foraging behaviour (Section IV) and hummingbird community composition (e.g. Graham *et al.*, 2012; Weinstein & Graham, 2016; Weinstein, Graham & Parra, 2017). Moreover, hummingbird existence is ultimately intertwined with nectar resources, but range shifts of plants are generally expected to lag behind changing climatic conditions

(Corlett & Westcott, 2013). If hummingbird range shifts proceed without parallel shifts in plants, hummingbirds are likely to encounter novel flowers as they move into different vegetational zones. For example, Andean communities of hummingbird food plants are generally dominated by Heliconiaceae and Rubiaceae in the lowlands but shift to Campanulaceae, Gesneriaceae, Bromeliaceae, and Ericaceae at higher elevations (Stiles, 2004; Weinstein *et al.*, 2014). The long-term, population-level consequences of novel resource use have not been studied, and the extent to which behavioural plasticity allows hummingbirds to locate and feed from unfamiliar food plants has not been formally tested. However, existing evidence suggests that behavioural plasticity is generally high; hummingbirds are known to visit non-native plants (Maruyama *et al.*, 2016b; Temeles & Bishop, 2019) and routinely visit flowers adapted for insect pollination on islands and/or in nectar-poor habitats (Arizmendi & Ornelas, 1990; Araujo & Sazima, 2003; Dalsgaard *et al.*, 2009; Maruyama *et al.*, 2013). On the other hand, hummingbirds with particularly close relationships with certain plants and/or highly specialized bill shapes may have limited long-term foraging flexibility. For example, hummingbirds that rely heavily on lowland plant lineages, such as hermits and *Heliconia*, have not colonized high-elevation habitats despite the presence of alternative floral resources that seem suitable (Stiles, 2004). Similarly, range expansions of morphologically specialized sicklebill hummingbirds (*Eutoxeres*) into mid-elevation cloud forests – away from the lowland *Heliconia* species with which they probably evolved initially – may have been restricted until the evolution of ornithophily in Andean bellflowers (Campanulaceae) (Lagomarsino *et al.*, 2016; Abrahamczyk *et al.*, 2017). To understand better how biotic interactions might constrain projected range shifts, future research could explore how species-level foraging choices and competitive interactions change across elevational gradients, especially at species range limits and across transitional vegetational zones (HilleRisLambers *et al.*, 2013; Jankowski *et al.*, 2013).

Range shifts may also be constrained if hummingbirds are pushed into unsuitable or non-existent habitat. Using climate envelope models, Marini *et al.* (2009) found that many bird species from the Brazilian Cerrado, including the horned sungem (*Heliactin bilophus*), are expected to shift their ranges toward the country's most urbanized, populated region by 2099. Moreover, in mountainous regions, following climatic niches upslope may be impossible, leading to dramatic range contractions; for instance, by 2060, the climatically suitable range for the hyacinth visorbearer (*Augastes scutatus*) is expected to contract by 95% (Marini *et al.*, 2009). Similarly, the climate envelope for the white-tailed starfrontlet (*Coeligena phalerata*), a Colombian endemic, is expected to disappear entirely by 2050 (Velásquez-Tibata *et al.*, 2012). Such dramatic range contractions are particularly worrisome given that range size is a key predictor of extinction risk.

Elevational range shifts may also expose hummingbirds to physiological stress, particularly while navigating a novel assemblage of competitors. High-elevation flight poses physiological challenges due to reduced oxygen availability and air density (Altshuler & Dudley, 2002), and although hummingbirds are remarkably tolerant to hypoxic environments (Chai & Dudley, 1996; Altshuler & Dudley, 2003; Segre *et al.*, 2016), low air density can compromise their ability to stay aloft while hovering (Chai & Dudley, 1995). For the relatively small range shifts predicted within this century (<1000 m in elevation), hovering requires minimal flight adjustments and introduces negligible energetic costs (Buermann *et al.*, 2011). Hovering, however, is less energetically intense than competitive behaviours requiring short bursts of flight power (e.g. vertical ascents, sharp turns), and these flight manoeuvres are more strongly constrained at high elevation (Altshuler, Dudley & McGuire, 2004; Segre *et al.*, 2016). Constraints on burst power ability influence hummingbird competitive ability at high altitude, and dominance reversals between broad-tailed and rufous hummingbirds occur across just 1000 m in elevation (Altshuler, 2006). Thus, in the novel hummingbird communities created by range shifts, the physiological costs of complex flight behaviour may regulate competitive relationships. To our knowledge, no studies have predicted the competitive dynamics of novel hummingbird assemblages using species traits or explored consequences to species populations (but see Graham *et al.*, 2017).

(ii) Phenological mismatch with floral resources. Changes in temperature and precipitation have been implicated in declines of migratory hummingbirds in recent correlative models of broad-scale bird population trends (Gutiérrez Illán *et al.*, 2014), particularly in the presence of habitat loss (Northrup *et al.*, 2019). Whether such broad-scale declines are due to phenological mismatches or other mechanisms (e.g. increased interspecific competition; Samplonius & Both, 2019) requires further research, but climate change is known to cause temporal mismatches between seasonal floral resources and migratory hummingbird arrival. For example, McKinney *et al.* (2012) used long-term data across the breeding range of broad-tailed hummingbirds to show that flowering of major food plants has advanced substantially in northern areas, but hummingbird arrival has not kept pace. Such phenological mismatches could ultimately result in reduced hummingbird fitness unless behavioural plasticity enables individuals to shift to other flowering plant species or adjust migration timing. Interestingly, adjustment of migration timing has been observed in rufous hummingbirds, which arrive in the Pacific Northwest region of the United States about 1–2 weeks earlier than they did throughout most of the 20th century (Courter, 2017). While these changes are probably due to climate change, there has been no exploration of particular mechanisms such as floral resource availability.

(iii) Extreme weather events. Climate change may also result in a higher frequency and/or intensity of extreme weather events – such as heat waves, hurricanes, and droughts – that could affect hummingbirds directly and indirectly. The direct, physiological effects of rising temperatures on birds are typically thought to be less important than indirect effects on vegetation and have received relatively little attention (Şekercioğlu, Primack & Wormworth, 2012). However, extreme heat events are known to cause mass avian die-offs and are expected to affect smaller birds disproportionately, particularly desert-dwelling species and species that forage in sunny microclimates within tropical lowlands (McKechnie & Wolf, 2010, 2019).

Because hummingbirds inhabit both deserts and humid lowlands, and because nectar-producing plants thrive in sunny microclimates such as canopy gaps and meadows, the direct physiological effects of extreme heat should not be discounted. Moreover, hummingbirds generate large amounts of body heat while hovering and may rely strongly on passive heat dissipation, which requires a temperature differential between the hummingbird and a cooler external environment (Powers *et al.*, 2012, 2017). To achieve this temperature differential in a warming climate, hummingbirds may increasingly depend on microclimatic refugia such as riparian forests. For instance, broad-billed hummingbirds (*Cynanthus latirostris*) in the Arizona desert may already use riparian areas to thermoregulate between foraging flights (Powers *et al.*, 2017). If habitat destruction or further climate change erode these thermal refugia, hummingbirds may be forced to reduce time spent foraging, leading to caloric deficits and eventual population declines.

Extreme weather events can also affect hummingbirds indirectly if nectar plants are destroyed by strong winds, delay their flowering, or reduce nectar production (Wiley & Wunderle, 1993; Calder, 2004). The increasing frequency and intensity of extreme weather events, such as hurricanes, are of particular concern for island species. For example, after Hurricane Maria destroyed much of the understorey vegetation on the island of Dominica in 2017, hundreds of desperate hummingbirds gathered to feed from broken fruits, but only 25% of the purple-throated carib population is thought to have survived the severe loss of nectar resources (Temeles & Bishop, 2019). Similarly, after two consecutive hurricanes hit the Bahamas in the mid-1990s, populations of Bahama woodstars (*Calliphlox evelynae*) declined sharply, leading to pollen limitation and reproductive failure of an endemic shrub (Rathcke, 2000, 2001).

Droughts may also affect hummingbird abundance and behaviour, because water availability can regulate flower number, nectar volume, and nectar concentration (Zimmerman, 1983; Waser & Price, 2016; Gallagher & Campbell, 2017; Phillips *et al.*, 2018). If soil moisture deficits reduce floral resource availability, hummingbirds may repeatedly visit the few available resources, abandon the area, and/or suffer high mortality (Kodric-Brown & Brown, 1978; Smith, 1982; Stiles, 1992; Waser & Price, 2016). For example, many male long-tailed hermits (*Phaethornis superciliosus*) died during a severe drought and nectar shortage in Costa Rica, and the population took 3–4 years to recover (Stiles, 1992). Such a dramatic decline in pollinator abundance could clearly impede pollination, but so could subtle changes in hummingbird behaviour. During drought years, *Ipomopsis aggregata* in the Rocky Mountains received less pollen, despite high hummingbird visitation rates; this unexpected finding could arise if reduced nectar volume shortened hummingbird visit durations and subsequently reduced the amount of pollen transferred per visit (Price *et al.*, 2005; Waser & Price, 2016). Untangling the mechanisms through which drought mediates phenotypic plasticity in plant traits (e.g. nectar properties and corolla length; Gallagher & Campbell, 2017), hummingbird foraging behaviour, and plant reproductive success is certainly an area for future research.

(3) Conservation of plant–hummingbird interactions

Climate change, habitat loss and fragmentation, urbanization, and introduction of non-native species are known to affect pollinator visitation and plant reproduction (Kearns, Inouye & Waser, 1998; Aizen & Feinsinger, 2003; Morales & Traveset, 2009; Geslin *et al.*, 2013; Traveset *et al.*, 2018), but how these conservation concerns influence interactions between hummingbirds and plants remains poorly understood. In this subsection, we briefly outline ways in which these anthropogenic changes may influence plant–hummingbird interaction networks.

One way that climate change may influence plant–hummingbird interaction networks is through its effects on specialization. We know that hummingbird communities from regions experiencing historical climate instability since the Last Glacial Maximum (~21 ka) exhibit less-specialized interactions, possibly because unstable climates prevent partner coexistence over longer, evolutionary timescales (Dalsgaard *et al.*, 2011; Martín González *et al.*, 2015; Sonne *et al.*, 2016). We thus hypothesize that phenological decoupling and associated nectar shortages are likely to erode specialized relationships, particularly if shortages are extreme enough that an entire hummingbird community depends on relatively few shared nectar resources. Studies that capture variability in the resource base, for instance across seasons or elevational gradients, will be key to understanding flexibility in hummingbird foraging choices and species-level specialization (e.g. Petanidou *et al.*, 2008; Benadi *et al.*, 2014; Feinsinger & Swarm, 1982).

Similarly, existing research suggests that hummingbird interaction networks in highly modified habitats such as urban and agricultural areas are less specialized than networks in ecosystems with minimal human influence (Maruyama *et al.*, 2019; Morrison & Mendenhall, 2020), possibly due to lower abundances (or complete loss) of large, long-billed hummingbirds in disturbed habitats (Hadley *et al.*, 2018; Tinoco *et al.*, 2018; Maruyama *et al.*, 2019). Future work could further investigate the mechanisms behind these changes in network structure, as well as the repercussions for hummingbird-pollinated plants. For example, reduced levels of ecological specialization can increase heterospecific pollen transfer and conspecific pollen loss, reducing plant reproduction (Feinsinger, Tiebout & Young, 1991; Morales & Traveset, 2008; Brosi & Briggs, 2013; Briggs *et al.*, 2016; Fonseca *et al.*, 2016).

Less is known about the effects of non-native plants in hummingbird pollination networks, although hummingbirds readily incorporate non-native plants into their diets (Feinsinger *et al.*, 1988; Rodríguez-Flores *et al.*, 2012). In a study analysing more than 20 Neotropical plant–hummingbird networks, Maruyama *et al.* (2016b) found that non-native plant species attracted more hummingbird species than native plants. At the same time, non-native plant species formed exclusive relationships with certain short-billed hummingbird species, which relied on non-native plants to the exclusion of other nectar resources (Maruyama *et al.*, 2016b). To our knowledge, no research has explored whether hummingbird networks that include non-native plants are more specialized overall, whether the presence of non-native plants usurps hummingbird visits from native plant species (Aizen, Morales & Morales, 2008), or whether an influx of non-native pollen compromises pollination success through heterospecific pollen transfer (e.g. Grabas & Laverty, 1999). Alternatively, non-native plants with highly attractive nectar rewards may act as pollinator 'magnets', indirectly increasing visitation rate to nearby native plants (e.g. Molina-Montenegro, Badano & Cavieres, 2008); we anticipate that this effect could be particularly strong for pollen-limited plants in isolated habitat patches, such as forest fragments surrounded by banana plantations.

VI. FUTURE DIRECTIONS IN RESEARCH AND CONSERVATION

In this section, we emphasize major directions for future study, starting with hummingbirds' evolutionary and ecological relationships with plants and concluding with hummingbird conservation. Although hummingbirds have been a focus of western science for more than 50 years (Fig. 2), there are many opportunities to refine, and perhaps revolutionize, how we study plant–hummingbird interactions. These opportunities range from explicitly including pollinator function and individual behaviour to leveraging the potential of genetic techniques, miniaturized tracking devices, and satellite-derived estimates of land cover. Moreover, hummingbirds are not the only taxon of nectar-feeding birds, so future work could apply these research directions to studying their larger-bodied, distant cousins (e.g. sunbirds and honeyeaters). We hope that this section will serve as a reference for researchers designing studies to understand and conserve these magnificent birds and the plants they pollinate.

Within the realm of evolutionary research, increased efforts to quantify the fitness of interacting partners holds great promise for uncovering the intricacies of coevolution between plants and hummingbirds. For example, to apply the geographic mosaic theory of coevolution (Thompson, 2005) to plant–hummingbird interactions, researchers could quantify spatial variation in species traits and fitness (or proxies of fitness) for both interacting partners across their geographical ranges, as has been done for some insect pollinators (e.g. Anderson & Johnson, 2008). Such an endeavour would be a major contribution to evolutionary biology, yet monumental field effort would be required to quantify pollinator effectiveness and nectar extraction efficiency across broad spatial scales; as such, it would be an ideal candidate for a coordinated research effort among researchers across multiple field sites (e.g. Borer *et al*., 2014). As an incentive to participate in such a collaborative effort, we note that quantifying fitness can lead to novel findings and a cascade of additional research directions. For example, many questions remain following the accidental discovery of 'pollinator recognition' in a species of hummingbird-pollinated *Heliconia* (Betts *et al*., 2015); how commonly do plants preferentially accept pollen from certain hummingbirds, what is the role of reproductive assurance, and to what extent is this plant behaviour phylogenetically conserved? Answering these questions about pollinator recognition and quantifying pollinator effectiveness more broadly could further our mechanistic understanding of coevolution in species-rich interaction networks (Section III.1).

As network-based approaches become more common and the need for predicting community responses to unprecedented anthropogenic change intensifies, there is opportunity for future studies of plant–hummingbird interactions to mirror broader trends emerging in the pollination ecology literature. In particular, directions for future research include recognizing intraspecific variation in foraging behaviour, incorporating pollinator contributions to ecosystem functioning, understanding drivers of pollinator declines at landscape and local scales, and making predictions about network stability in response to disturbance (e.g. Kaiser-Bunbury *et al*., 2010; Brosi, 2016; Knight *et al*., 2018; Smith *et al*., 2019).

Pollination networks are typically constructed by aggregating the foraging observations of individual pollinators to the level of species (Section IV.1*c*). However, this approach may obscure the underlying mechanisms of species- and network-level specialization, because a 'generalist' species may in fact comprise individual specialists (Brosi, 2016). Intraspecific variation in floral resource use has not been studied extensively, but existing evidence suggests that hummingbird foraging behaviour can differ considerably among individuals, with consequences for pollination success (Temeles *et al*., 2010; Maglianesi *et al*., 2015a; Volpe *et al*., 2016; Maruyama *et al*., 2016a; Section IV.1*c*). Future research could employ pollinator-focused network sampling approaches, such as identifying pollen grains carried by individual hummingbirds (Table 1; Maglianesi *et al*., 2015a), to investigate whether intraspecific variation in hummingbird bill shape (e.g. between sexes) corresponds to systematic differences in resource use and ecological specialization.

There is also ample room to incorporate ecological function into studies of plant–hummingbird communities. Researchers are increasingly adopting a functional trait perspective when studying hummingbird communities (Maruyama *et al*., 2018; Hadley *et al*., 2018; Tinoco *et al*., 2018), but how variation in functional traits and hummingbird behaviour affect plant reproduction remains poorly understood. For example, additional work is needed to understand how hummingbird territoriality influences pollen dispersal and plant reproduction (Section IV.3*b*). We thus encourage additional studies using fluorescent dye as pollen analogues, or more ambitiously, the landscape genetic approach of Castilla *et al*. (2017): genotyping all plants within a certain area to identify the source of pollen grains delivered to a flower during a single pollinator visit.

Another major contribution to our understanding of plant–hummingbird interactions involves incorporating pollinator effectiveness into plant–hummingbird interaction networks. Effectiveness is best measured as the number of conspecific pollen grains deposited and/or seeds produced from a single pollinator visit (e.g. Ballantyne *et al*., 2015;

Lehmann *et al.*, 2019; Santiago-Hernández *et al.*, 2019; Table 1, Section IV.3*a*). In speciose plant communities, tracking outcomes of single pollinator visits for each plant species requires extensive field effort, but this challenge is not insurmountable; for example, Ballantyne *et al.* (2017) recently constructed single-visit pollen deposition networks for 23 plant species using data from more than 2000 pollinator visits. Networks that incorporate pollinator effectiveness can also highlight the functional importance of certain hummingbird species and guide conservation efforts. For instance, pollen transport networks have emphasized the functional importance of the Endangered colourful puffleg hummingbird, *Eriocnemis mirabilis*, endemic to the Colombian Andes (Ramírez-Burbano *et al.*, 2017). Moreover, pollen deposition networks tend to be more specialized than either visitation or pollen transport networks, which has implications for the structure, function and stability of species-rich hummingbird communities (Ballantyne *et al.*, 2015; Santiago-Hernández *et al.*, 2019).

Another important avenue for future research involves understanding network stability and ecosystem function in response to novel community assemblages created by non-native species invasions, declines of native plants, and/or climate change (Tylianakis & Morris, 2017). For example, to what extent do interactions rearrange in response to disturbance, and what are the consequences for plant reproduction? Can non-native plants buffer against native plant declines? How will competitive dynamics between hummingbirds shift in novel communities created by climate change? Formulating predictions about these scenarios is difficult because pollinator function and the mechanisms underlying pollinator foraging choices are not fully understood. For example, although species traits strongly predict pairwise interaction frequencies (Sonne *et al.*, 2020), they only weakly predict species-level specialization (Dalsgaard *et al.*, 2021 Fig. 6; Section IV.1). Similarly, the precise mechanisms that underlie macroecological patterns of specialization in plant–pollinator networks have not yet been identified (Section IV.2).

There are several ways to study hummingbird foraging responses to changing resource landscapes, the competitive dynamics of novel hummingbird communities, and the consequences for plant reproduction. One approach involves studying how plant–hummingbird interactions change over different spatial scales, environmental gradients, or seasons with varying nectar availabilities and competitive contexts (e.g. Maglianesi *et al.*, 2015a,b; Weinstein & Graham, 2017). Studies at geographical range boundaries will also be informative to predict how biotic interactions, such as competition with other hummingbird species or turnover in plant communities, might constrain range shifts (HilleRisLambers *et al.*, 2013; Jankowski *et al.*, 2013). More directly, researchers could design manipulative experiments that add or remove species to quantify how interaction networks 're-wire' as hummingbird foraging choices shift. Although experimental manipulations of nectar resources are common in studies of hummingbird territoriality (Kodric-Brown & Brown, 1978; Ewald & Carpenter, 1978; Hixon *et al.*, 1983; Eberhard & Ewald, 1994; Temeles *et al.*, 2004), to our knowledge, only one study has quantified changes in hummingbird resource use following experimental reductions in nectar availability (Hazlehurst & Karubian, 2018).

Finally, our understanding of how landscape-level habitat loss and fragmentation affect plant–hummingbird interactions remains limited, especially with respect to long-term responses and/or responses that are challenging to measure in the field (e.g. hummingbird population dynamics, plant reproduction, hummingbird movement behaviour). Although hummingbirds are generally assumed to be resilient to disturbance (Section V.2*a*), a major challenge to hummingbird conservation is the lack of long-term population monitoring data. Hummingbirds have historically been omitted from systematic bird banding efforts (Wethington, Russell & West, 2005), and data are often insufficient to assess hummingbird population trends, even *via* indirect proxies such as habitat loss (Tables S2 and S3; IUCN, 2020a). Further, only a few studies have quantified reproductive success (e.g. Gleffe *et al.*, 2006), documented changes in historical gene flow, or tracked individual-level movements (e.g. Hadley & Betts, 2009), all of which may unveil species' responses to changing land cover and climate. As tracking devices become smaller and lighter, future studies of hummingbird movement may not only elucidate latitudinal and altitudinal movements, but also allow researchers to identify habitats within human-altered landscapes important for reproduction (*versus* opportunistic foraging) and detect behavioural changes overlooked by standard biodiversity metrics. We also recommend that researchers studying patterns of hummingbird diversity include both landscape and local measures of habitat and/or nectar availability to pinpoint the mechanisms driving observed patterns more effectively (e.g. Hadley *et al.*, 2018; Tinoco *et al.*, 2018). Long-term hummingbird monitoring efforts, such as those led by the Hummingbird Monitoring Network in western North America, would allow better detection of hummingbird population changes. Similarly, long-term studies of plant phenology (McKinney *et al.*, 2012) could help untangle the mechanisms underpinning recent range expansions, arrival times, and declines in some migratory hummingbird species (Sauer *et al.*, 2014; Courter, 2017; Greig *et al.*, 2017).

VII. CONCLUSIONS

(1) Despite close associations between plants and hummingbirds, acquiring evidence for coevolution between hummingbirds and plants (*versus* one-sided adaptation) is difficult because it requires data on fitness outcomes for both partners. Moreover, researchers are still grappling with how coevolution

proceeds in species-rich communities, in which a diversity of hummingbird visitors appear to exert conflicting selection pressures. These conflicting pressures may be reconciled by examining differences in pollinator effectiveness or testing for the existence of hummingbird functional groups with internally similar morphologies and foraging behaviours. Intensified efforts to quantify hummingbird and plant fitness using proxies (e.g. feeding efficiency and seed set) hold great promise in demonstrating plant–hummingbird coevolution and can be used to test the geographic mosaic theory of coevolution if applied across broad spatial scales.

(2) Over the past decade, network approaches have increasingly been applied to the study of plant–hummingbird interactions. Studies of pairwise interaction frequencies within these networks suggest that hummingbirds interact more frequently with plant species whose flower lengths correspond to their bill length. Spatial and phenological overlap between partners is also important in determining interaction frequencies, and all of these mechanisms are more important than neutral, probabilistic processes based on partner abundance. On the other hand, local abiotic and biotic context (e.g. nectar availability, competition, and hummingbird abundance) seem to be more important than hummingbird traits for determining whether hummingbird species form specialized relationships with their plant partners. The ecological specialization of individuals within hummingbird species warrants further study, particularly given large variation in individual foraging choices and widespread sex differences in hummingbird bill morphology and plumage coloration.

(3) At macroecological scales, the specialization of plant–hummingbird interaction networks increases with species richness, topographic heterogeneity, historically stable climates, and precipitation. The importance of these climatic and topographic variables – all of which typify species-rich, tropical communities in mountainous regions – suggests that interspecific competition and partner persistence over evolutionary time intensify network-level niche partitioning. Additional work at finer spatial scales and organizational levels is needed to understand fully the mechanisms underlying these patterns.

(4) Linking plant–hummingbird interactions to plant reproduction is not only a major avenue for future coevolutionary work, but also critical for enhancing our understanding of the ecological dependencies between plants and hummingbirds. For example, when studies have implications for plant conservation, it is important to distinguish between hummingbird visitors that only consume nectar and those that contribute to fruit and seed production by depositing pollen onto conspecific stigmas. Further work is also needed to confirm the generality of the often-assumed link between hummingbird foraging strategies and pollen dispersal distance; in our analysis of studies using fluorescent dye as pollen analogues, we found that pollen is generally dispersed over shorter distances when the source plant is defended by territorial hummingbirds, but there tends to be substantial overlap in the dispersal curves for defended and undefended plants.

(5) We used conservation assessment data from the IUCN to model hummingbird extinction risk as a function of various morphological and natural-history traits. We found that small range size and high reliance on forests were the most important predictors of a hummingbird being listed as threatened (Vulnerable, Endangered, or Critically Endangered) and/or having a decreasing population trend. These results suggest that forest conservation efforts are a key strategy for ameliorating hummingbird declines.

(6) Habitat loss and climate change pose the greatest threats to hummingbird populations. Although hummingbirds are commonly viewed as resilient opportunists that thrive in brushy habitats, very few studies have explicitly quantified hummingbird reproductive success across a range of expected habitat quality. Moreover, studies of hummingbird communities and foraging movements in disturbed habitats indicate that loss of native vegetation cover leads to movement limitation and reduced abundance of large and morphologically specialized hummingbirds, such as sicklebills and hermits. Climate change is expected to cause geographical range shifts into higher latitudes and elevations, phenological mismatches between migratory hummingbirds and their food plants, and, possibly, mass mortality during extreme weather events such as heat waves, hurricanes, and droughts. Additional research is needed to understand potential constraints and costs associated with hummingbird range shifts, such as novel assemblages of competitors, absence of coevolved plant partners, and reduced competitive performance due to physiological limitations of high-elevation flight.

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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. Data sets and code used for analyses of pollen dispersal and hummingbird extinction risk are available in Zenodo at https://doi.org/10.5281/zenodo.5787072.

Appendix S1.

Supplementary Methods

(1) Mapping total, threatened, and range-restricted species richness (Fig. 1).

(2) Estimating numbers of publications over time (Fig. 2).

(3) Summarizing number of species per category of IUCN extinction risk (Fig. 3).

(4) Literature survey of pollen dispersal (Fig. 7, Table 2).

(5) Analysis of IUCN extinction risk and hummingbird traits (Fig. 8).

Supplementary Figures

Fig. S1. Amount of overlap between subcategories of plant–hummingbird interaction research, visualized using a quantitative alternative to a Venn diagram.

Supplementary Tables

Table S1. Search terms used to find publications related to plant–hummingbird interactions in the *Web of Science* database.

Table S2. Summary of IUCN extinction risk for each extant hummingbird clade.

Table S3. Summary of IUCN extinction risk and forest dependency for extant hummingbirds.

Table S4. Replication of dye dispersal experiments in the hummingbird literature.
Table S5. Results of dye dispersal experiments in the hummingbird literature.
Table S6. Description of variables included in phylogenetic logistic regression.
Table S7. Average bill length for 336 hummingbird species.
Table S8. Variance inflation factors for phylogenetic logistic regression models.
Table S9. Summary of phylogenetic logistic regression models testing how morphological, ecological, and anthropogenic variables affect hummingbird extinction risk.

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