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REVIEW

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Stefan Abrahamczyk · Michael Kessler

Abstract Hummingbirds are the most specialised nectarivorous birds and show close ecological relationships to their food plants. Their small body size, bright colors, and unique behaviour have fascinated generations of naturalists. In this review, we investigate the morphological and behavioural adaptations of hummingbirds to feed on nectar and arthropods, and explore their diffuse co-evolution with their food plant species. Further, a list of plant genera including species mainly pollinated by hummingbirds is presented. Summarising the existing knowledge on hummingbird feeding ecology, we find that much of the variability in morphology and behaviour of hummingbirds is determined by their unique feeding mode and the constraints set by their food plants. Based on the existing literature, we developed a hierarchical system explaining how different environmental factors have shaped the current richness of hummingbirds, and their morphological and behavioural diversity. We propose that climatic stability within and between seasons and days determines the constancy of food availability, which in turn is the most important factor for species richness in hummingbird assemblages. However, the assemblage composition of hummingbirds is also influenced by phylogenetic factors, especially under harsh environmental conditions. Unsurprisingly, the highest morphological and behavioural diversity is observed in the most species-rich assemblages. This diversity may have at least partly evolved to reduce inter- and intraspecific competition. Independently of which morphological character we consider, the 360 different hummingbird species have evolved a large morphological variability to adapt to their individual feeding niches.

Keywords food plant species · Nectar · Arthropods · Competition · Assemblage composition · Co-evolution

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Zusammenfassung

Morphologische und Verhaltensanpassungen um Nektar zu fressen: Wie die Nahrungsökologie den Artenreichtum und die Zusammensetzung von Kolibrigemeinschaften bestimmt

Kolibris sind die am höchsten spezialisierten, Nektar fressenden Vögel und zeigen enge ökologische Anpassungen an ihre Futterpflanzen. Ihre geringe Körpergröße, ihre leuchtenden Farben und ihr einzigartiges Verhalten haben Generationen von Naturliebhabern fasziniert. In dieser Literaturübersicht untersuchen wir die morphologischen und Verhaltensanpassungen von Kolibris, um sich von Nektar und Arthropoden zu ernähren und erkunden die diffuse Koevolution mit ihren Futterpflanzen. Außerdem präsentieren wir eine Liste von Pflanzengattungen, in denen Arten vorkommen, die hauptsächlich kolibribestäubt sind. Indem wir das vorhandene Wissen über die Nahrungsökologie von Kolibris zusammengefassten, zeigen wir, dass die Variabilität in der Morphologie und dem Verhalten von

Kolibris größtenteils durch ihre einzigartige Art der Nahrungsaufnahme und den Beschränkungen verursacht werden, die ihre Futterpflanzen vorgeben. Basierend auf der vorhandenen Literatur haben wir ein hierarchisches System entwickelt, das erklärt, wie unterschiedliche Umweltfaktoren den aktuellen Artenreichtum sowie die morphologische und Verhaltensvielfalt von Kolibris geformt haben. Wir postulieren, dass klimatische Stabilität innerhalb und zwischen Jahreszeiten und Tagen die kontinuierliche Verfügbarkeit von Nahrung bestimmt, was wiederum den wichtigsten Faktor für den Artenreichtum einer Kolibrigemeinschaft darstellt. Allerdings ist die Zusammensetzung von Kolibrigemeinschaften ebenfalls von phylogenetischen Faktoren abhängig, besonders unter harschen Umweltbedingungen. Wenig überraschend ist, dass die größte Vielfalt von morphologischer und Verhaltensvielfalt in den artenreichsten Kolibrigemeinschaften zu finden ist. Diese Diversität entstand vermutlich zumindest teilweise, um inter- und intraspezifische Konkurrenz zu vermeiden. Unabhängig davon welche morphologische Eigenschaft wir berücksichtigen, haben die etwa 360 bekannten Kolibriarten eine enorme morphologische Vielfalt entwickelt, um sich an ihre ökologischen Nischen anzupassen.

Introduction

The diversity and abundance of animal assemblages depends, among other factors, on the availability of food resources (Johnson and Sherry 2001; Turchin and Batsli 2001; Bleher et al. 2003). Birds are probably the best-studied major group of animals, and the factors influencing the relationship between bird assemblages and their food resources has been the focus of a large number of studies. Influencing factors are, on the one hand, morphological, physiological, and behavioural characters of the birds and, on the other hand, the type and composition of food resources and their temporal and spatial distribution. For many bird groups, the availability of food resources is difficult to measure, but nectarivorous birds and their food plants represent an exceptionally easy system to study the impact of food resources on the ecology and anatomy of birds because their food resources are relatively homogeneous and easy to quantify (Feinsinger and Colwell 1978; Dearborn 1998). Additionally, the feeding ecology of nectarivorous birds and in particular of hummingbirds has always fascinated naturalists. Therefore, a large amount of ecological data on nectarivorous bird-food plant interactions are available to date, especially from the Americas (summarised, e.g. in Stiles 1981, 1985; Schuchmann 1999; Fodgen and Fodgen 2006).

Since Darwin's (1871) and Wallace's (1891) times, generations of ecologists have studied different aspects of the feeding ecology of hummingbirds (e.g. Snow and Snow 1972; Feinsinger et al. 1979, 1985; Stiles 1995; Altshuler 2006). Hummingbirds and the flowers visited by them present a unique example of plant–animal interactions because, with about 360 species and a predominance of nectar as food source, hummingbirds are the most specialised and diverse group of nectar-feeding birds worldwide (Stiles 1981; Fleming and Muchala 2008). Hummingbirds cover 85–90 % of their daily energy demand by nectar (Gass and Montgomerie 1981) and show numerous ecological, morphological, and physiological adaptations to their main food resource (e.g. Martinez del Rio and Karasov 1990; McWhorter et al. 2003; Temeles et al. 2002; Araujo and Sazima 2003). In parallel with this amazing species richness and morphological diversity of hummingbirds, thousands of plant species evolved in the Americas that exclusively or mainly rely on hummingbirds for pollination (Schuchmann 1999; Fleming and Muchhala 2008).

Between Alaska and Tierra del Fuego, ∼7,000 angiosperm species from 404 genera belonging to 68 families are dependent on hummingbirds for pollination (see Table S1). Several species-rich genera of entirely or mainly hummingbird-pollinated species such as *Columnea* (Gesneriaceae, 270 spp.), *Centropogon* (Campanulaceae, 220 spp.), *Heliconia* (Heliconiaceae, 200 spp.) or *Palicourea* (Rubiaceae, 200 spp.; Mabberley 2008) contribute to the enormous plant diversity of the Neotropics, especially in montane forests and páramos, open heathland above the treeline in the northern Andes where insect pollinators are handicapped due to adverse climatic conditions (Cruden 1972; Stiles 1981; Kessler and Krömer 2000). Hummingbird-pollinated plant species have evolved several morphological and physiological features that document the tight adaptation to hummingbird pollination (Stiles 1981). Typical traits of hummingbird food plants include brightly coloured, scentless, solitary or loosely clustered flowers with long, often thickened corolla tubes, and large amounts of fluid, sucrose-rich nectar (Stiles 1981; Stiles and Freeman 1993; Sazima et al. 1996; Nicolson 2002). Most hummingbird-pollinated plant species are herbs, epiphytes, vines, shrubs or small trees. Only a few canopy trees are known to rely on hummingbird pollination, for example some species of the genus *Erythrina* (Fabaceae; Stiles 1981). However, this result may be biased by the small number of studies on pollination ecology in the canopy of tropical forests. Additionally, hummingbirds also visit many non-native plant species from the Old World, planted as ornamentals or escaped from gardens, such as *Agave* (Agavaceae) or *Melia* (Meliaceae) (Martinez del Rio and Eguiarte 1987; Mendonça and dos Anjos 2005).

The species number and abundance of hummingbirds at a given site is strongly dependent on the continuous and predictable availability of nectar (Cotton 2007;

Abrahamczyk and Kessler 2010). Therefore, the temporal and spatial distribution of nectar has a strong impact on the hummingbird assemblages. Several authors (e.g. Des Granges 1978; Feinsinger et al. 1985; Araujo and Sazima 2003; Abrahamczyk et al. 2011) have documented strong seasonal differences in assemblage composition and species diversity correlated with flower abundance. Further, these authors emphasised that, on the large scale, the morphological diversity, i.e. the variability of body size or bill morphology in hummingbird assemblages, is negatively correlated to climatic seasonality, defined as the mean variability of temperature and precipitation.

During the last 30 years, several reviews have summarised our knowledge on the ecology of hummingbirds. These reviews studied in detail the hummingbird–food plant co-evolution (Stiles 1981), the impact of flight physiology on the ecology and morphology of hummingbirds (Altshuler and Dudley 2002), and arthropods as food resources for hummingbirds (Stiles 1995). Further, Schuchmann (1999) published a general introduction to the ecology of hummingbirds, while Paton and Collins (1989) and Collins and Paton (1989) compared the bill and body morphology of nectarivorous birds between continents. However, all these reviews are over a decade old and none of them analysed the mechanisms that determine total species richness or morphological diversity of hummingbird assemblages, even though this knowledge is essential to the understanding of the evolutionary processes that may have shaped hummingbird assemblages. Therefore, taking into account the recent literature, in the present review we investigate the morphological and behavioural adaptations of hummingbirds to feed on nectar and arthropods. We start with a short introduction into the relationship between hummingbirds and their food plants. Then, we address (1) what may drive the co-evolution between hummingbirds and their food plant species and (2) which morphological and environmental factors influence the hummingbirds feeding on arthropods. Moving into more detailed aspects, we then ask (3) which morphological and energetic constraints limit the set of available food recourses. Finally, we discuss whether (4) food availability is a driver of hummingbird diversity and assemblage composition and whether morphological and behavioural adaptations exist to separate feeding niches between (5) hummingbird species and (6) sexes of one hummingbird species, as this is a basic prediction when assemblage diversity increases.

What has driven the co-evolution between hummingbirds and their food plant species?

Hummingbirds visit a large number of plant species of a wide array of plant families from the whole angiosperm tree of life, including such disparate families as Heliconiaceae, Cactaceae, Elaeocarpaceae, and Acanthaceae. For a list of genera containing hummingbird-pollinated species, see Table S1. Although the number of phylogenetic studies is limited, there is an indication that hummingbird-pollinated plant clades may have higher species numbers than their insect-pollinated sister clades (Schmidt-Lebuhn et al. 2005). Therefore, hummingbirds may be a vector driving plant diversification (Kay et al. 2005).

For a long time, the relationship of hummingbirds and their food plant species was seen as a classical example of narrow co-evolution, where all hummingbird species were believed to feed on several plant species but where many food plant species had only one pollinator species (Grant and Grant 1968; Snow and Snow 1980; Snow and Teixera 1982). Thus, hummingbirds were seen as major forces for the evolution of their food plants and vice versa. Today, we know that most plant species are visited by several hummingbird species and that all hummingbird species feed from a more or less wide array of plant species. Therefore, the idea of a narrow co-evolution between a certain hummingbird species and its food plant species has been replaced by the notion that hummingbird–plant mutualisms are best described as diffuse co-evolution (Janzen 1980; Feinsinger 1983) between co-occurring functional groups on the population level (Thompson 1999; Fenster et al. 2004). This idea has been supported by Tripp and McDade (2013), who showed that the hummingbird-pollinated Ruellia (Acanthaceae) species, which are pollinated by a large array of short-billed hummingbird species, are evolutionarily younger than their pollinators. Thus, the evolution of these species was partly stimulated by the pre-existing hummingbird species. In contrast, focussing on the West Indies as an entire biogeographic region, Abrahamczyk et al. (2014a) showed that the oldest hummingbird clades and their food plant clades have roughly the same age.

Despite the generally rather loose co-evolution, the number of hummingbird species that pollinate a given plant species is generally speaking negatively correlated with the length and curvature of the plant's corolla tube (Walther and Brieschke 2001). This can be interpreted as a negative relationship between the diffuseness of coevolution and the difficulty of accessing the nectar and the adaptations necessary to do so (G.F. Stiles, personal communication). A few plant species indeed have just a single hummingbird pollinator species and could have coevolved with this species. These are, firstly, species with extremely long or curved corolla tubes, for which only one hummingbird species can act as efficient pollinator. Examples are *Passiflora mixta* (Passifloraceae) that is only pollinated by the Sword-billed Hummingbird *Ensifera ensifera* (Snow and Snow 1980), and some members of the genus *Centropogon*

(Campanulaceae), pollinated only by the two Sicklebill Hummingbird species (*Eutoxeres*) (Stein 1992). Of course, these hummingbird species occasionally feed on flowers with much shorter or less curved corolla tubes, but their main food source are the flowers with which they co-evolved (Stein 1992; Büchert Lindberg and Olesen 2001). Recently, Abrahamczyk et al. (2014b) further supported the idea of narrow co-evolution of these morphologically extreme taxa by showing that *Passiflora* section *Tacsonia* (to which *P. mixta* belongs) has a similar age as *Ensifera ensifera*, of which *Tacsonia* species represent one of the main food resources. Secondly, there are endemic plant and hummingbird species that have co-evolved on small oceanic islands, e.g. *Rhaphithamnus venustus* (Verbenaceae) and *Dendroseris litoralis* (Asteraceae) with *Sephanoides fernandensis* on the Juan Fernandez-Islands (Sun et al. 1996) or *Heliconia bihai* (Heliconiaceae) and *Eulampis jugularis* on the Lesser Antilles (Temeles et al. 2005; Temeles and Kress 2003). Thirdly, species like the western North American *Ribes speciosum* (Grossulariaceae) and the central Andean *Chuquiraga spinosa* (Asteraceae) that flower during the winter each interact with just a singe hummingbird species, in North America with *Calypte anna* (Stiles 1973) and in the Andes with *Oreotrochilus estella* (Carpenter 1978). These plant species occur in high latitudes or high elevations in the tropics, flower during the coldest season, and are mutually dependent on a single hummingbird species. Fourthly, whether plant species that only occur at the northern and southern borders of the hummingbird distribution, where only one hummingbird species is present, co-evolved with their pollinator species is likely, but needs to be shown. Indeed, *Castilleja coccinea* (Orobanchaceae) is exclusively pollinated by *Archilochus colubris,* the only hummingbird species of eastern North America (Williamson 2001), and *Tristerix corymbosus* (Loranthaceae) is exclusively pollinated by *Sephanoides sephanoides* (Aizen 2005), the only hummingbird species of southern Patagonia. However, whether other, regionally extinct, hummingbird species were present in the area when these hummingbird-pollinated plant species evolved, or whether these plant species evolved in a different geographical region and later became restricted to their current range, is unknown.

The notion that hummingbird–plant mutualisms are best described as diffuse co-evolution between functional groups is supported by the fact that hummingbirds and their food plant species rarely show broadly overlapping distribution areas (Baltosser 1989). However, the above-mentioned extreme morphological and ecological cases, as well as the mutualisms of some island endemics (Carpenter 1978; Stein 1992; Sun et al. 1996), clearly show that narrow co-evolution can occur between individual hummingbird species and their food plant species. Determining co-

evolution is difficult, and further research is necessary to show reciprocal selection. Further, detailed dated phylogenies of both partners could give important evidence of the temporal development of these narrow mutualistic relationships.

To what extents do hummingbirds feed on arthropods?

More than 70 % of all bird species, including hummingbirds, need to consume arthropods from time to time to survive (Klasing 1998). Indeed, while hummingbirds are able to produce by themselves about half of the amino acids that they need, the other half has to be obtained from their food (Klasing 1998). Nectar and especially nectar of hummingbird-pollinated species contains amino acids only in low quantities (Hainsworth and Wolf 1972; Baker and Baker 1982), and while pollen grains contain substantial amounts of amino acids, hummingbirds are not able to digest the resilient wall of sporopollenin surrounding the grains (Brice et al. 1989). Therefore, hummingbirds have to regularly feed on arthropods. Hummingbirds use two main techniques to catch arthropods: gleaning (picking arthropods from a surface) and hawking (catching flying insects) (Stiles 1995). It is possible to further subdivide these two categories by specifying how hummingbirds forage (hovering, sallying) and where (at spider nets, in the open air, inside the vegetation, at leaves or at bark). Most hummingbird species belonging to the subfamily Phaethornithinae have curved bills and are hover-gleaners, taking spiders from webs or leaves, whereas many members of the subfamily Trochilinae, with their straight bills, take flying insects, mainly flies from the air, although several exceptions exist (Stiles 1995). Straight bills are used in both modes of arthropod capture, while strongly curved bills are virtually always gleaners—although very slightly curved bills may also function in fly catching (Yanega 2007).

Stiles (1995) stated that wing morphology is more related to the way hummingbirds catch arthropods and only indirectly to the foraging behaviour at flowers, distinguishing between trapliners that forage over large areas and visit specific flowers only a few times per day versus territorials that stay in small territories which they often defend aggressively. This opinion is questionable, because wing and bill morphology are correlated in hummingbirds (Feinsinger et al. 1979) and bill morphology is strongly related to the nectar-feeding ecology of hummingbirds (see previous section). Additionally, wing morphology also varies with elevation (Feinsinger et al. 1979), feeding habit (hovering vs. perching), and male aggressive behaviour (Feinsinger and Chaplin 1975). Further, hummingbirds gain their energy mainly from nectar (Powers et al. 2010) and only a small but variable amount from arthropods (see

below). Therefore, it is more reasonable to assume that different factors, such as nectar-feeding ecology or habitat-determined wing morphology, constrain both the way in which arthropods are caught and the different kinds involved.

The ratio of arthropods in the diet of hummingbirds has long been under discussion. In earlier times, some authors suggested that at least those hummingbird species occurring at high elevations or in dry forest mainly feed on arthropods (e.g. Wallace 1891; Wagner 1946; Wolf 1970), because they only found parts of arthropods but no nectar in the stomachs of collected birds. However, these authors were not aware that nectar is digested very quickly whereas arthropods are retained in the stomach much longer and are thus easier to detect (Hainsworth and Wolf 1972). Using more extensive ecological and physiological information, Stiles (1995) stated that all hummingbird species mainly live on nectar, requiring 85–90 % of the daily foraging time (Gass and Montgomerie 1981). Even breeding females that need high amounts of protein to produce eggs and to feed their offspring, mainly feed on nectar (65–70 % of the foraging time). Thus, they breed during the peak of the flowering season, which is related to the local rainfall pattern, rather than during the peak of arthropods availability (Stiles 1995). However, the foraging time, especially for territorial species, may underestimate arthropod consumption since the "search" phase may be subsumed in perch time for monitoring territories (G.F. Stiles, personal communication).

Today, it is common sense that hummingbirds have comparatively low requirements of nitrogen (McWhorter et al. 2003), but that the amount of arthropods in their diet varies throughout their annual life cycle (Yanega 2007). Arthropod consumption increases during reproduction (Murphy 1996), moult (Fraser et al. 2010), stopovers during migration (Stiles 1995; Yanega 2007), and periods of low nectar availability (Chávez-Ramírez and Down 1992). Further, hummingbirds consume more arthropods in arid regions, while in humid areas the consumption of arthropods increases with elevation (Remsen et al. 1986). This is reasonably because higher elevations increase the general effects of climatic seasonality, and the frequency and regularity of seasonal movements by the birds, both within high-elevation habitats and altitudinal movements increases (G.F. Stiles, personal communication). Thus, an increase in feeding on arthropods reduces the effects of nectar shortage and can be seen as an adaptation to colonising climatically more seasonal habitats in higher latitudes and elevations. Additionally, Sandlin (2000) speculated that, within the same habitat, trapliners consumed more arthropods than territorial species. However, in a detailed study, Powers et al. (2010) were not able to support this hypothesis by comparing the feeding ecology

of the trapliner *Eugenes fulgens* and the territorial *Lampornis clemenciae* (both flycatching species) in southeastern Arizona.

Besides the seasonal component of the amount of feeding arthropods, there is also a daily component. Wheeler (1980) found that hummingbirds feed less on arthropods on days with sunny weather than on rainy days. On sunny days, hummingbirds feed mainly on arthropods during the hottest hours of the day, between 11:00 am and 3:00 pm. During this time, plants often reduce their nectar production to save water or, especially in more open flowers, evaporation increases the sugar concentration of the nectar to a point that it may change the bird's food preference (Tamm and Gass 1986). Further, diurnal flower-visiting insects are most active during the hottest hours and then compete with the hummingbirds for nectar (Brown et al. 1981).

Thus, we can conclude that arthropods are a small but essential part of the hummingbirds diet, which can vary depending on the circumstances of each individual bird. However, there is no convincing evidence for special morphological adaptations to catch arthropods, e.g. in bills and wings. More reasonably, existing bill adaptations to feed on nectar, as well as wing adaptation, depending on the feeding ecology and habitat, determine the way in which hummingbirds catch arthropods and the kinds of arthropods that are consumed. In future studies, it would be important to test experimentally that hummingbirds compensate for nectar shortages by an increased consumption of arthropods. Further, it should be investigated in detail to which degree species with different feeding strategies within a hummingbird assemblage use arthropods or tree sap to compensate for nectar shortages.

Which morphological and energetic constraints limit the set of available food recourses?

Most food plant species of hummingbirds exhibit a more or less elongated corolla tube such as in *Aechmea* (Bromeliaceae), *Sinningia* (Gesneriaceae), or *Fuchsia* (Onagraceae) species, although some also have open flowers, such as many Malvaceae or Fabaceae. Many studies have found close relationships between the bill length of a hummingbird species and the corolla-tube length of its food plants (e.g. Sazima et al. 1996; Vasconcelos and Lombardi 2001; Walther and Brieschke 2001). Exceptions from this rule only exist in areas with high climatic seasonality, in which the few occurring hummingbird species primarily feed on short-tubed, often insect-pollinated, plant species because long-tubed flowers occur in lower abundances (Araujo and Sazima 2003). Besides flower length, the curvature of the flower also plays an important role because it excludes

smaller hummingbirds with short, straight bills (Temeles et al. 2009). Larger-bodied hummingbirds have longer, often curved bills and regularly feed from a higher number of long-tubed hummingbird-pollinated plant species than short-billed species (Cotton 1998a; Lasprilla and Sazima 2004). Often, plant species with long corolla tubes produce more nectar than plant species with short corolla tubes (Colwell 2000). Smaller flowers are thus not able to cover the energy demand of larger hummingbird species (Colwell 2000), unless they occur in dense aggregations (G.F. Stiles, personal communication).

Smaller hummingbird species with straight, short to medium-sized bills instead are able to efficiently use small flowers and even typically insect-pollinated plant species on a regular basis if they are abundant (e.g. Snow and Snow 1972; Araujo and Sazima 2003; Abrahamczyk and Kessler 2010). Thus, these species are adapted to use a high number of food plant species and can be ranked as less specialised (Snow and Snow 1972; Walther and Brieschke 2001). Most of the hummingbird species occurring in dry forest and savanna habitats belong to this group (Araujo and Sazima 2003; Abrahamczyk and Kessler 2010). Especially in these climatically seasonal habitats, on small oceanic islands, or for small hummingbird species in species-rich, highly competitive assemblages, insect-pollinated plant species can account for high proportions of food plant species (Araujo and Sazima 2003; Dalsgaard et al. 2009; Abrahamczyk and Kessler 2010; Rodrigues and Araujo 2011). In such a seasonal habitat in the Brazilian Cerrado, hummingbirds mainly use the flowers of the melitophilous shrub *Styrax ferrugineus* (Styracaceae) during the cool morning hours when few insects are active and the small flowers offer a larger amount of nectar (Maruyama et al. 2012). However, this is not a general pattern because hummingbirds can use insect-pollinated flowers throughout the day as long as sufficient nectar is offered and not too many other nectar sources are available (S. Abrahamczyk, unpublished data). Instead, in areas with a less strongly developed climatic seasonality, even the larger resident hummingbirds are known to visit insect-pollinated flowers mainly as a last resource when more nectar-rich, hummingbird-pollinated flowers are scarce (Stiles 1978, 1980; Cotton 1998a).

As mentioned before, a close relationship exists between bill length and the corolla length of the food plants. However, in several cases, hummingbirds are known to feed on plants with corollas markedly longer or shorter than their bills or on brush-like flowers with no corolla at all, e.g. on *Calliandra* or *Inga* (both Fabaceae) (Temeles 1996). Larger hummingbirds with medium-sized to long bills rarely feed on small flowers due to the small amount of nectar on offer, which does not fulfil the energy demands of the birds (Snow and Snow 1972). Only if such short-

tubed flowers are very abundant and productive, as in large *Inga* trees, can one regularly find larger hummingbirds feeding on these flowers (Koptur 2000). Instead, smaller hummingbirds regularly use larger flowers as long as they are able to reach the nectar (Snow and Snow 1972; Temeles et al. 2002). Especially, plant species with wide, tubular, straight flowers such as *Campsis radicans* (Bignoniaceae) provide access to the nectar to small, straight-billed hummingbird species by enabling the hummingbird to put its entire head into the flower (Temeles et al. 2002). Yet, even if small hummingbird species are able to use these large flowers, they are not able to feed from them with the same speed and efficiency as large hummingbird species (Temeles et al. 2009).

Another way in which short-billed hummingbirds illegitimately get access to the nectar of long-tubed plants is to pierce the flowers at the bottom (Pelayo et al. 2011). Some short-billed hummingbird species such as *Heliothryx barroti* have even been classified as highly specialised nectar parasites (Skutch 1954). These species mainly feed by piercing flowers that are adapted to hummingbirds with larger bills (Colwell 1973; Stiles 1985). Ornelas (1994) hypothesised that *Heliothryx barroti* even shows morphological adaptations to flower piercing, such as a serrate bill. If this is the case, or if the serrate bill helps in catching insects, has not yet been investigated.

Thus, not taking into account the effects of inter- and intraspecific competition, which will be discussed below, we can conclude that two mechanisms exist that limit the availability of food plant species to each individual hummingbird: (1) bill morphology that only allows efficient access to flowers with a fitting corolla length and curvature, and (2) energetic constrains that do not allow large, long-billed species to feed efficiently on small flowers with low nectar quantities. Especially in dry and climatically highly seasonal habitats or on oceanic islands, the latter mechanism appears to be strong and limits the morphological diversity of the occurring hummingbird species because these species have to be able to feed efficiently from small, insect-pollinated flowers, which only offer small amounts of nectar. This constrains their morphology to small to medium-sized bodies with short to medium-sized bills.

Is food availability a driver of hummingbird diversity and assemblage composition?

Several studies have found a strong relationship between hummingbird species richness and nectar availability (e.g. Araujo and Sazima 2003; Cotton 2007; Abrahamczyk and Kessler 2010). These authors hypothesised that hummingbird species richness of an assemblage is positively related to a continuously high availability of food resources

throughout the year, which is dependent on a continuously humid and moderately warm climate, as typical for mountain cloud forests. Based on these hypotheses, we analysed a range of studies from temperate North America to temperate South America and found evidence for such relationships (Table S2). The total number of hummingbird species within an assemblage is determined by the amount of flowers during the time of the year when flower availability is lowest, normally the dry season or winter (Fig. 1a). Additionally, the minimum amount of flowers available to a hummingbird assemblage during a year is negatively related to temperature seasonality (Fig. 1b). Thus, climatic seasonality has a strong but indirect influence on hummingbird diversity.

Along a climatic seasonality gradient in lowland Bolivia, Abrahamczyk and Kessler (2010) showed that the geographical decline in species richness is not gradual but abrupt as soon as the climate gets strongly seasonal, including an intensive dry season or very low temperatures. Outside of regions with a moderate climatic seasonality, only the least specialised hummingbird species can occur during the dry season, when nectar is scarce (Araujo and Sazima 2003; Machado et al. 2007). More specialised, often slightly larger and longer-billed, hummingbird species migrate into strongly seasonal areas only during the

rainy season, when many flowers are available, to utilise this seasonally rich resource and leave the area as soon as flower availability decreases (Araujo and Sazima 2003; Machado et al. 2007; Abrahamczyk and Kessler 2010). Similarly, in humid, warm regions, the most dominant, large, and long-billed hummingbird species only occur during the peak flowering season and leave the assemblage when the nectar resources decrease (e.g. Arizmendi and Ornelas 1990; Cotton 2007). These species have the highest energy requirement and can only feed energetically efficiently from large flowers offering large amounts of nectar (Arizmendi and Ornelas 1990).

Analysing a number of hummingbird assemblages, Daalsgard et al. (2011) showed that the food webs of these assemblages in the tropics are generally more specialised than those of hummingbird assemblages occurring in the subtropics or temperate zones. This suggests that hummingbird species occurring around the equator have more finely separated, individual feeding niches than hummingbird species occurring in higher latitudes. However, most studies conducted in tropical and subtropical areas observed that the number of food plant species used by a hummingbird species tend to vary seasonally (e.g. Feinsinger 1976, 1978; Feinsinger and Swarm 1982; Abrahamczyk and Kessler 2010). This raises the question of

Fig. 1 Correlation analyses between a hummingbird species richness and the amount of flowers during the time of the year when flower availability is lowest, normally the dry season or winter; b the amount of flowers during the time of the year when flower availability is lowest and temperature seasonality taken from WorldClim (Hijmans et al. 2005; Table S2); c hummingbird species richness and the variance of exposed culmen length of male individuals per assemblage; d hummingbird species richness and the variance of body mass of male individuals per assemblage. Data of hummingbird species richness and the amount of flowers during the time of the year when flower availability is lowest as well as data for culmen length and body mass of hummingbirds were taken from publications listed in Table S2
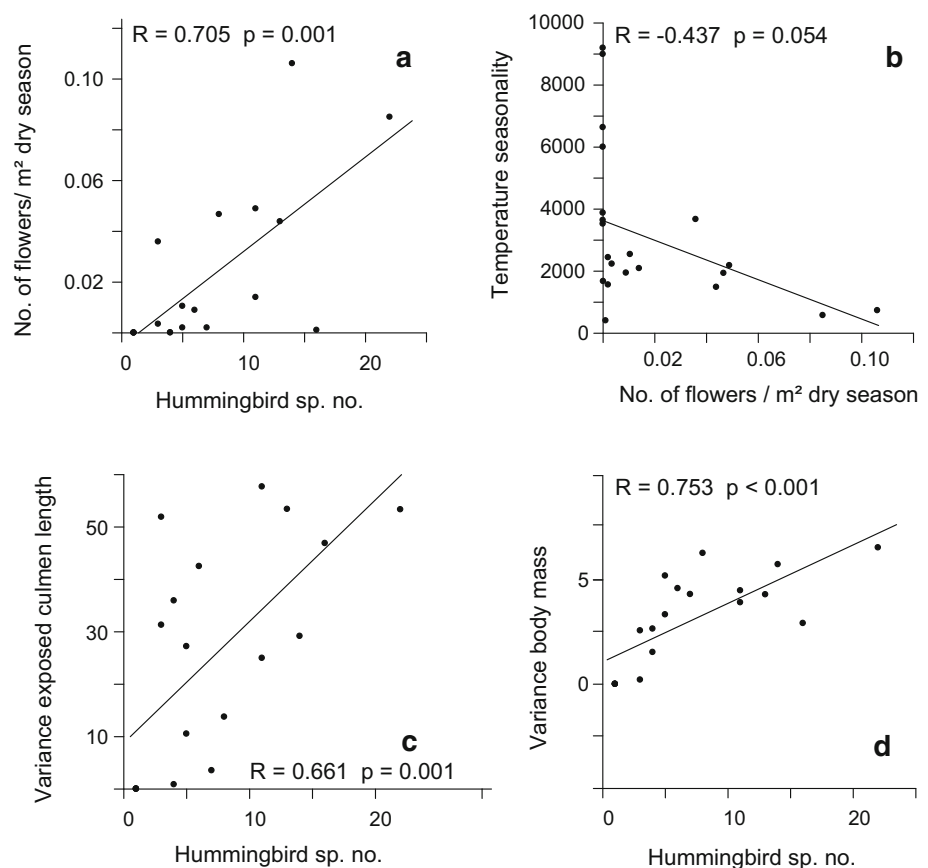
what happens when only the diversity of food plant species decreases but not the abundance of flowers or the amount of nectar on offer.

The above-mentioned studies provide evidence that, when a large number of abundant food plant species are available, hummingbirds preferentially forage on those food plant species that best fit their morphological traits. In these cases, the food niche overlap between hummingbird species is low (Feinsinger and Swarm 1982; Cotton 1998c). This resource sharing between species is interpreted as a way to reduce interspecific competition (Feinsinger and Colwell 1978; Lara 2006), but of course it is also evolved by the plants to reduce the amount of non-conspecific pollen on the stigma (G.F. Stiles, personal communication). Naturally, the degree of food niche overlap within species and sexes is also dependent on the number of hummingbird species present in the assemblage, and the amount and diversity of flowers available for each species (Feinsinger and Swarm 1982; Berns and Adams 2010). In contrast, when the number of food plant species decreases but the few remaining plant species still provide an abundant amount of nectar, the number of hummingbird species within the assemblage can remain surprisingly high (Abrahamczyk and Kessler 2010). Often, these species are small to medium-sized with short to medium-sized bills, which enables them to opportunistically utilise a large number of plant species. Feinsinger and Swarm (1982) reported that, during the dry season, the flower morphology of the available food plant species does not perfectly match the bill morphology of the hummingbird species utilising them. During these periods, the dominant hummingbird species feed in the centre of the remaining flower clumps, where the highest number of flowers (i.e. the largest amount of food resources) is concentrated, whereas the less dominant species are forced to feed at the margins or range more widely to exploit small clumps with few flowers (Lara et al. 2009; Abrahamczyk and Kessler 2010).

In conclusion, we state that food availability is an important and perhaps even the main driver for species richness of hummingbird assemblages (Fig. 1a). Food availability itself is strongly affected by the intensity of climatic seasonality (Fig. 1b), which may also have direct effects on hummingbird species richness if the range of tolerance for example in temperature is exceeded seasonally. The most diverse hummingbird assemblages occur in continuously humid and moderately warm continental, tropical mountain areas (Rahbek and Graves 2000). On oceanic islands, species richness of hummingbirds is strongly reduced due to island effects, whereas at high elevations it is negatively affected by low nocturnal temperatures and the low air density which require special physiological and morphological adaptations. In addition to food availability, the diversity of nectar resources also plays a role for the assemblage composition of hummingbirds. However, the diversity of the hummingbird assemblage appears not to be related to the width of the food niche of the individual species.

More studies analysing the phenological patterns of hummingbirds and their food plant species and comparing them between assemblages, for example along an elevational or latitudinal gradient, would help to further increase our knowledge on the balance between flower availability, diversity of hummingbird assemblages, and food niche separation between species. Therefore, based on the high mobility especially of larger hummingbird species, it would be interesting to track the regional movements of hummingbirds over the year and maybe over large distances to understand which areas they cover to fulfil their high energetic demands. These data could help to define conservation strategies for tropical as well as temperate hummingbird species.

Which morphological and behavioural adaptations exist to separate feeding niches between hummingbird species?

Hummingbirds exhibit a wide range of morphological characters. They vary in body length (6–22 cm) and mass (2–24 g; Schuchmann 1999), and also differ in bill length and curvature, wing size and shape, and foot length. All these morphological characters in combination with behavioural differences allow hummingbirds to exploit a wide range of ecological niches. Primarily, these characters are adaptations to the feeding ecology of the species, but presumably the variation in morphology also helps to reduce interspecific competition (Brown and Bowers 1985). While these traits are inherited and show clear phylogenetic patterns, they are not necessarily related to the phylogenetic structure of the hummingbird assemblages (Graham et al. 2012).

Several studies have shown that, within hummingbird assemblages, morphological diversity, for example in bill length and body mass, increases with increasing species richness (Snow and Snow 1986; Berns and Adams 2010). By relating the absolute species number of an assemblage against the variance of exposed culmen length or body mass, we can support this hypothesis (Fig. 1c, d). The differences in morphological characters enable the individual hummingbird species to fill different feeding niches (Snow and Snow 1986). By presenting a couple of examples, we will illustrate how (1) hummingbirds living under different ecological conditions and (2) individual higher hummingbird taxa have managed to decrease interspecific competition:

1. A classical example of this phenomenon are hummingbird assemblages occurring on the Caribbean Islands. Within the same habitat on one island, two hummingbird species usually co-occur, a small, short-billed and a large, longer-billed one (Lack 1973). These two species always have well-separated feeding niches and do not compete with each other for food (Kodric-Brown et al. 1984). Where more than two hummingbird species occur on the same island, such as on Puerto Rico or Hispaniola, species from the same size and bill category replace each other geographically or elevationally (Lack 1973).

2. Another group of species-poor and often phylogenetically clustered communities are hummingbird assemblages occurring at high elevations (Graham et al. 2009). Hummingbirds of only two clades can occur above 4,000 m (individual species reaching up to 5,200 m) in the Andes where air density is low (Schuchmann 1999). In these extreme habitats, hummingbirds need to reduce their energy expenses during flight. One adaptation to the low air density is an increase in wing length and area, which reduces energetic costs while hovering at flowers (Feinsinger et al. 1979; Stiles 2004, 2008). Additionally, at high elevations, hummingbirds hover less frequently and tend to perch while drinking nectar, often even hanging upside down at the inflorescences (Yanega 2007; Stiles 2008). The species occurring at high elevations therefore tend to have larger and stronger feet than species that rarely perch while drinking nectar (Feinsinger and Colwell 1978; Stiles 2004). At high elevations in the Andes, the larger, longer-billed hummingbird species often feed on the nectar-rich *Puya* spp. (Bromeliaceae), while the smaller, shorter-billed species use less abundant nectar resources (Kraemer et al. 1993). In general, the bills of hummingbirds occurring in the páramo tend to be shorter than the bills of species that live in mountain forests due to the high abundance of small flowers in the páramo (Schuchmann 1999). Often, the páramo hummingbirds even walk on the ground and feed from insect-pollinated flowers, such as *Gentianella spp.* (Gentianaceae) (Schuchmann 1999), but always with wings "idling" for balance (G.F. Stiles, personal communication). Therefore, these species not only need strong feet but they also need strong legs to walk from one plant to another.

3. In contrast to the previous examples, morphological characters in species-poor continental hummingbird assemblages at low elevations can be surprisingly similar (Graham et al. 2012). In climatically strongly seasonal habitats, such as the Chaco or the Cerrado region in central South America, or temperate meadows and forests in North America, the few occurring hummingbird species all tend to be medium-sized and have straight, medium-sized bills (e.g. Brown and Kodric-Brown 1979; Araujo and Sazima 2003; Abrahamczyk and Kessler 2010). In these extreme areas, the number of hummingbird-dependent plant species is rather low and the occurring hummingbird species therefore have to feed on a large number of insect-pollinated plant species. Thus, ecological filtering (i.e. the constraints given by harsh environmental conditions) can lead to a surprising homogeneity of morphological characters within an assemblage, independent of their phylogenetic relatedness (Graham et al. 2012).

4. Except at high latitudes and elevations or on small oceanic islands, hummingbird assemblages are often relatively species-rich, for example containing up to 28 species syntopically in montane cloud forests at around 2,000 m (Rahbek and Graves 2000; Graham et al. 2009). Towards higher and lower elevations, the species richness of the assemblages decreases. In the hermits of the subfamily Phaethornithinae, comprising 38 species of more or less specialised, often curve-billed, feeders on flowers with long corolla tubes in the lowest strata of lowland rainforests, only one species from the same size categories occurs within an assemblage (Hinkelmann 1990). This means that, maximally, four hermit species can occur syntopically. However, the composition of hermit assemblages varies on a local scale, depending on the microhabitat. Therefore, a high number of species show overlapping distribution areas on a larger geographical scale, but on a smaller scale morphologically similar species are well separated (Hinkelmann 1990). Aside from the hermits, lowland hummingbird assemblages contain up to ten species from the subfamily Trochilinae (Cotton 1998a). In most highland assemblages above 2,500 m, only species of Trochilinae occur (Schuchmann 1999). Similar to Phaethornithinae, the Trochilinae are also structured into four to five body-size categories. However, the Trochilinae show a higher morphological diversity in wing and bill shape than the Phaethornithinae (Schuchmann 1999; Stiles 2004). Therefore, Stiles (1985) categorised hummingbird species within rainforest communities by their bill length and the vegetation layer in which they feed. He differentiated long-billed specialists from medium- to short-billed generalists and divided the long-billed specialists further, depending on whether they feed in the canopy or in the forest understory. More commonly, hummingbird assemblages are subdivided into territorial species and trapliners, which search a large area for plants, often epiphytes, herbs and small shrubs

that produce few flowers for a relative long time (Feinsinger 1976). These trapliners are further separated into two groups, depending on whether they use high- or low-reward flowers. This segregation is often correlated with body size and bill length (Feinsinger 1976).

As mentioned above, hummingbird species tend to be morphologically well adapted to their ecological niches. Normally, the largest, strongest, and most aggressive species dominate and structure the assemblage (e.g. Powers and McKnee 1994; Cotton 1998b; Mendonça and dos Anjos 2005). Males of these species defend territories at shrubs or trees with the most abundant nectar resources against con- and interspecific intruders by vocalisation and chasing behaviour (Wolf et al. 1976). Smaller species and females are forced to establish territories at plants with less abundant nectar resources, to trapline, or to steal nectar from occupied territories (Mendonça and dos Anjos 2005). Further, smaller hummingbird species often arrive earlier at newly flowering rich stands than large ones (Cotton 1998a; Lara et al. 2009).

Normally, dominant species have a higher wing loading, the ratio between wing disc area and body mass (Feinsinger and Chaplin 1975). Further, dominant species show a higher wing beat frequency, which leads to a higher burst of power output compared with less dominant and traplining species (Altshuler 2006).Therefore, dominant hummingbird species are more maneuverable and faster than less dominant and traplining species, which increases the chances of the dominant species of winning aggressive encounters (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978). Dearborn (1998) found that the frequency of chasing behaviour increases with increasing difference in body size between the dominant and the intruder species because the chance of winning a fight increases. However, the intensity and length of chasing increases the more similar are the two birds in body size (G.F. Stiles, personal communication). Additionally, the abundance of chasing behaviour increases with increasing resource availability in the territory, which is equivalent to increasing territory quality (Dearborn 1998). Therefore, territories with high and persistent resource availability are often held for the longest periods of time (Lyon 1976).

Territorial hummingbird species with shorter wings spend more energy hovering at flowers, the most energy-consuming way of flying (Weis-Fogh 1972). Therefore, when the resource availability decreases, territory defence becomes too costly and is given up (Cotton 1998a). Instead, for traplining species, which fly longer distances to search for nectar with lower speed than territorial species, it is more important to reduce energy expenses during the energy-intensive hovering at flowers (Feinsinger and

Chaplin 1975). Therefore, traplining species like many Phaethornithinae have relatively long and narrow wings. In contrast to larger hummingbird species, independently of whether they are territorial or trapliners, small hummingbird species are constrained by the need to use small flowers efficiently (Daalsgard et al. 2008). They commonly use insect-pollinated flowers and to a smaller extent small, hummingbird-adapted plant species (Dalsgaard et al. 2009). Additionally, they also steal nectar from occupied territories of larger hummingbird species (Feinsinger and Colwell 1978) or use resources that are only defended during parts of the day (Ornelas et al. 2002).

Competition with other groups of organisms has been less well studied. Hummingbirds are known to defend their territories against large, nectar-feeding insects, e.g. moths, butterflies or bumblebees, and subordinate them to the territory margins (Primack and Howe 1975; Boyden 1978; Carpenter 1979). Only if insects become too numerous, do hummingbirds stop chasing them (Carpenter 1979). In contrast, perching songbirds are rarely seen as competitors and are thus rarely chased (Martinez del Rio and Eguiarte 1987). There is no direct competitive interaction between hummingbirds and nectarivorous bats due to the segregation of their foraging times. However, there appears to be indirect competition between them in that, in habitats suitable for nectarivorous bats (with high nocturnal temperatures and year-round nectar supply), a certain proportion of animal-pollinated plants have adapted to bats as pollinators. These species reduce the diversity and abundance of food plants for hummingbirds by shifting nectar production to the night (Kessler and Krömer 2000; Krömer et al. 2006). On the other hand, bat-pollinated flowers may provide some nectar for hummingbirds especially early in the morning, even if hummingbirds do not pollinate the flowers (Aguilar-Rodriguez et al. 2014). The same argument may apply to insect-pollinated plants.

In summary, hummingbirds have developed a wide range of morphological and behavioural adaptations to fill individual feeding niches. This separation is so effective that up to 28 species can co-occur in the same spot at a given point in time and up to 35 over the course of a year (Rahbek and Graves 2000; Graham et al. 2009). Although competition between hummingbird species is hard to measure directly, we can conclude that, taking into account interspecific competition, bill and flower morphology, and the available amount of nectar per flower, hummingbird species tend to use those plant species at which they can feed most efficiently (Wolf et al. 1976; Cotton 1998a). However, this set of food plant species, and especially the number of visits per flowering species, would be different if no competing species were present, except possibly for the most dominant species. Thus, besides flower morphology, interspecific competition appears to be an

important factor shaping the feeding niches of most hummingbird species. Thus, studies quantifying and comparing interspecific competition between hummingbird species within different assemblages are necessary to evaluate the impact of interspecific competition in the evolution of hummingbirds.

Do morphological and behavioural adaptations exist to separate feeding niches between sexes of one hummingbird species?

Like most groups of birds, many hummingbird species show sexual dimorphism in size, body weight, wing length, bill morphology or coloration (Temeles et al. 2010). Bleiweiss (1999) hypothesised that social dominance is a driving factor for the evolution of sexual dimorphism because morphological differentiation reduces intraspecific competition and enables the sexes of the same species to have separated feeding niches (Temeles et al. 2009). Sexual dimorphism within the same species is often more pronounced in species-poor hummingbird assemblages (Feinsinger and Swarm 1982; Berns and Adams 2010). The most famous case of sexual dimorphism in hummingbirds is documented for *Eulanpis jugularis* from the Lesser Antilles. One of the main food resources of this species is *Heliconia bihai* (Heliconiaceae), which has two flower morphs, a more or less strait-tubed, red-green one and a curve-tubed, green one (Temeles et al. 2005, 2009, 2010; Temeles and Kress 2010). The dominant, heavier, and more straight-billed males of *Eulampis jugularis* are only able to feed from the red-green morph, which produces a higher volume of nectar (Temeles et al. 2005). Females instead mainly use the curve-tubed, green morph of *Heliconia bihai* and occasionally steal nectar from the males' territories (Temeles et al. 2005). Thus, their special bill morphology enables females of *Eulampis jugularis* to fill a feeding niche that is free from male competitors.

Similar to *Eulampis jugularis*, females of most hummingbird species have longer bills than males (Bleiweiss 1999). In these species, females are subordinated by the more aggressive, larger males and have to feed at more widely dispersed, but more nectar-rich, long-tubed flowers or from small flower clumps, which are both unattractive for males (Wolf 1969; Temeles 1996). Instead, the short bills of the territorial males enable them to feed from short-tubed flowers with higher efficiency (Temeles 1996). With increasing intersexual bill dimorphism, intersexual dichromatism also increases, and species with a stronger intersexual dichromatism also have shorter bills than species with a less strong dichromatism (Bleiweiss 1999). In some of these monochromatic species, both sexes defend territories during the non-breeding season (Stiles and Wolf 1969; Wolf 1969). These observations show that morphology and coloration are often correlated with the ecology and the behaviour of hummingbirds (Bleiweiss 1999). Possibly, a bright coloration in dichromatic species is, among other characters, a signal for intraspecific dominance of one sex and helps to reduce intersexual encounters.

In a few hummingbird species, females have shorter and more curved bills than males, even though they are not larger in body size (Temeles et al. 2010). This is especially true in hummingbird species in which the males display in groups (leks) at traditional display sites; for example, in many Phaethornithinae, females often have shorter and more curved bills than males (Bleiweiss 1999; Temeles et al. 2010). During mating time, Phaethornithinae males, which are all trapliners, have increased competition for food due to their mating system. Therefore, these species may have evolved larger bills in males to increase the effectiveness of drinking from large, high-reward flowers and to increase the number of potentially usable flowers to reduce intraspecific competition at least with females (Bleiweiss 1999; Temeles et al. 2010). An additional explanation for the longer bills might also be the increase in their chances of winning male–male aggressive encounters in the leks (G.F. Stiles, personal communication), although this remains to be tested.

A similar situation exists in species in which females nest colonially and defend feeding territories around their nests, including the richest feeding areas, such as in *Oreotrochilus estella* (Carpenter 1976) or in *Topaza* spp. (Bleiweiss 1999). In these species, females also often have shorter bills than males and subordinate males during the breeding season (Bleiweiss 1999). Additionally, these species often show a strong dichromatism. Thus, males of species in which females dominate during the breeding season may have evolved longer bills to reduce competition (Bleiweiss 1999). This parallels the system in which males dominate and females have developed longer bills, and may underline the trend that most hummingbird species have developed strategies to reduce intraspecific competition, independent from sex dominance and mating system. The reduction of intraspecific competition is also independent from the species richness of the hummingbird assemblage because it occurs in species-poor assemblages on oceanic islands (on which, e.g., *Eulampis jugularis* occurs) or at high elevations (in which, e.g., *Oreotrochilus estella* occurs) as well as in assemblages with a higher hummingbird species richness in Amazonia (in which, e.g., *Topaza* and *Phaethornis* species occur). More detailed studies similar to those of Temeles and coauthors conducted on *Eulampis jugularis*, involving hummingbird species with different intersexual dominances and feeding strategies, are needed to evaluate the impact of intraspecific competition on the evolution of hummingbirds.
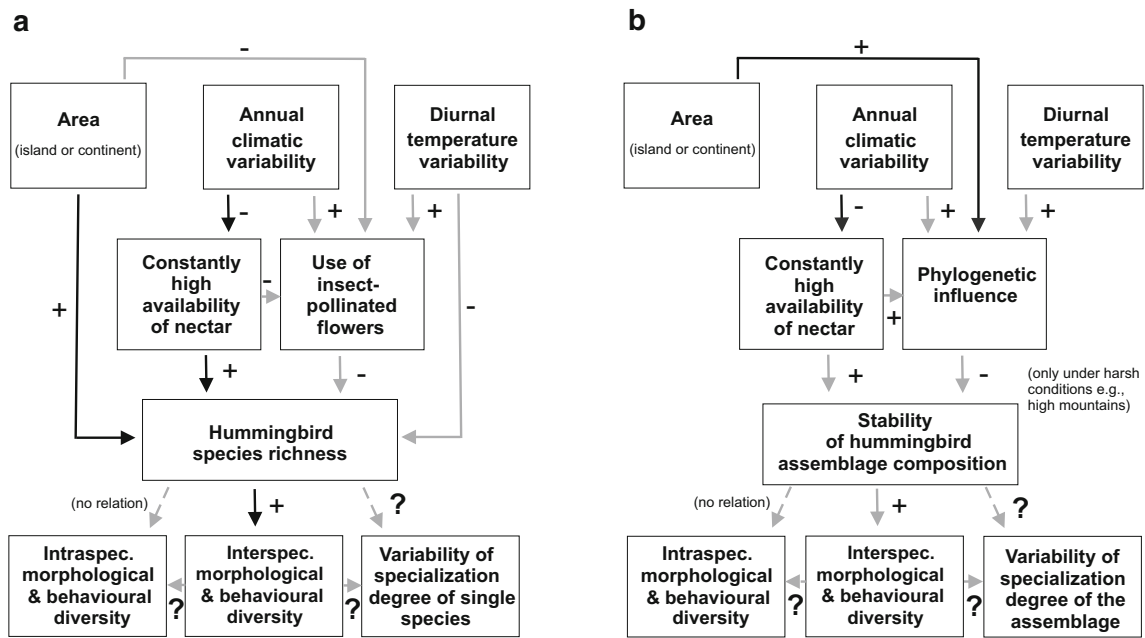
a

b

Fig. 2 Hierarchical model explaining how hummingbird species richness (**a**) and temporal stability of assemblage composition (**b**) are related to climatic conditions, morphological diversity and other ecological factors. The +(positive) and −(negative) signs shows the relationship between two factors; *question mark* indicates relationships that have to be studied in more detail. *Black arrows* show already supported relationships, *grey arrows* presumed relationships

Conclusions

Hummingbirds have evolved a high species richness in combination with a fascinating variability in morphology and behaviour to adapt to their environment. Much of this is determined by their unusual feeding mode and the constraints set by their food plants. Based on the existing extensive literature on the feeding ecology of hummingbirds, we here propose a hierarchical system explaining how different environmental factors have shaped the current species richness of hummingbirds and their morphological and behavioural diversity (Fig. 2). Some of these relationships can be supported by the available data. Thus, we have shown that the minimum availability of flowers, which is determined by climatic seasonality, is related to hummingbird species richness and that more species-rich assemblages are also morphologically more diverse (Fig. 1). However, we are aware that the relationships between several other biotic and abiotic factors in connection with the feeding ecology of hummingbirds have not been exhaustively investigated. Thus, Fig. 2 provides a summary of proven and presumed relationships and should be seen as a source from which new hypotheses can be developed to test these relationships. Further studies are necessary to understand in detail the presumed relationships.

Up to now, much of the published research has focused on the niches of single hummingbird species or the species within selected hummingbird assemblages. To understand how the fascinating morphological diversity of hummingbirds has evolved, it is now necessary to focus on how changes in the availability of food resources, which are related to the intensity of climatic seasonality, influence the feeding niches and specialisation of all members of different hummingbird assemblages as well as the morphological diversity of these hummingbird assemblages. Further, it would be interesting to investigate how interspecific morphological and behavioural diversity have influenced the evolution of intraspecific morphological and behavioural diversity. Another interesting question is how interspecific morphological and behavioural diversity are related to temporal variability of the specialisation of species and assemblages.

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