The Use of Biogeographical Patterns to Assess Key Adaptations in Two Families of Birds

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Abstract

Adaptations can be thought of as evolutionary technologies that allow organisms to exploit their environment. Like human technologies, adaptations can be 'progressive', increasing in their ability to accomplish a task. Progressive adaptations which also fundamentally alter the rules of trade-offs are known as key adaptations. Key adaptations allow a taxon to expand its niche space thereby radiating to larger species numbers and spread beyond its original range. If so, then of two otherwise ecologically equivalent taxa, the one with the greater geographical range may have a key adaptation. We tested this hypothesis by comparing the global biogeographic patterns of hummingbirds (Trochilidae) and sunbirds (Nectariniidae), ecologically equivalent families with distinct evolutionary technologies. Though many species of both families feed on nectar, hummingbirds also possess adaptations permitting hovering flight. We analyzed each family's species diversity with latitude and elevation, charting how they decline with movement towards poles and peaks. Hummingbirds persist into higher elevation and more extreme latitudes than sunbirds, reaching their 50% species richness value at 22.14º and 2087 m versus 18.92º and 2533 m for sunbirds. Looking at morphology, the evolution of hovering is likely the constraint breaking adaptation that allowed hummingbirds to radiate into more species and inhabit more extreme climes than sunbirds. Comparing the biogeography of ecologically-equivalent taxa has the potential to reveal insights into the species adaptations and niche expansion.
The traits possessed by a species govern the types of environments it can exploit – its fundamental niche. Evolution by natural selection shapes the traits of species to optimize fitness by tailoring an organism’s morphology, physiology, and behavior to their environments (Darwin, 1859). Such traits – or adaptations – can be thought of as “evolutionary technologies” that allow an organism to operate within an environment. An organism’s adaptations add up to a suite of technologies that allows it to persist in its fundamental niche. As many habitats across the world display remarkable similarity in environmental condition, species within these similar habitats have evolved similar adaptations, a process known as convergent evolution (Mooney and Dunn, 1970). If the full suite of evolutionary technologies of multiple different species are similar enough to each other and the species exist within similar niches, the species are deemed to be ecological equivalents, species that occupy a similar fundamental niche space and fulfill similar functional roles (Biggins et al., 2011). Examples are found within taxa as diverse as weasels (Biggins et al., 2011), desert snakes, rodents (Montgomery, 1989; Mares, 1975), and epiphytes (Bennet, 1986).

Like human technologies, evolutionary technologies are not perfect in their ability to accomplish a task, these imperfections relaying costs to the organism. The costs may be concrete – such as the energy and material needed to maintain the adaptation – or abstract – such as the lack of information that comes from a less than perfect adaptation (Kotler and Mitchell, 1995). The costs derived from evolutionary technologies lead to trade-offs that a species must negotiate if it is to optimize its fitness. Yet like human technologies, evolutionary technologies can be progressive, increasing their ability to accomplish a specific task (Dawkins, 1997). If an adaptation is not only progressive but also fundamentally changes the rules of the trade-offs, it is
known as a key adaptation (Rosenzweig and McCord, 1991; Galis, 2001). An example of a key adaptation would be the evolution of wood. To grow taller, plants must accumulate tissue to support the extra weight. Wood, a non-living tissue, allows plants to grow taller without the need to maintain the tissue. Trade-offs are not eliminated – it takes much longer to create wood compared to living tissue – but instead altered such that woody plants are favored in environments with infrequent disturbance.

Looking across evolutionary history, the evolution of a key adaptation often leads to the radiation of a new, more speciose clade – now defined by its synapomorphy – often replacing the older, ecologically-equivalent clade from which it came. This replacement process – known as incumbent replacement – has been seen in turtles (Rosenzweig and McCord, 1991), native and introduced marsh snails (Berman and Carlton, 1991), spiriferacean brachiopods (McGhee, Jr., 1981) and more. More importantly, the evolution of adaptations which reduce the cost of trade-offs allow the clade to expand niche space and corresponding biogeographical range (Holt et al., 1997). This effect can be seen with the *Peromyscus* and *Apodemus* genera of mice. *Peromyscus* has a better and more widely used torpor state which allows species within the genera to inhabit colder, more arid, and elevationally higher habitats compared to the ecologically equivalent genus *Apodemus* (Morhardt, 1970; Walton and Andrews, 1981; Motngomery, 1989). With this relationship of key adaptations leading to more speciose clades with a larger geographical extent, it may imply the reverse: among ecologically equivalent clades, the one with the greatest species richness and biogeographical range should possess superior evolutionary technologies.

One test of the presence of key adaptations within a clade has been to compare the species richness between taxa (Galis, 2001). However, of the two properties of species richness and biogeographical extent that define a clade, biogeographical extent is theoretically more
useful when comparing strength of evolutionary technologies: the larger the biogeographical extent, the greater the range of environmental and ecological variables with which a clade has to deal in most cases. Therefore, any comparison between taxa based upon biogeographical extent more explicitly compares the strength of the evolutionary technology within the clades and the possibility of key adaptations versus simple species richness alone. Comparing biogeography should work best when comparing extant, non-sympatric, ecologically equivalent taxa due to an incomplete fossil record and the possibility of competition otherwise.

While there is extreme variation in many biogeographic patterns, latitudinal and elevational gradients in species richness are robust geographic patterns found among nearly all taxa (Terborgh, 1977; Graham, 1983; Rosenzweig, 1995; Kaufman, 1995; Sánchez-Cordero, 2001; Sanders, 2002; Hillebrand, 2004). Generally, as one moves from low latitudes or elevations towards the poles and higher elevations respectively, the species richness of a taxon declines. Numerous properties change along the two gradients. Both gradients show declines in productivity and temperature averages and increases in seasonal temperature variation. Only species with superior evolutionary technologies are able to mitigate the costs of colder temperatures and reduction of exploitable resources (Buckley et al., 2012). Elevational gradients also include the properties of declining atmospheric pressure, an especially critical resource for metazoans, and increasing daily temperature variation. These additional factors mean that taxa should show a clearer response to elevation dependent upon their evolutionary technologies.

To this end, we analyzed at the latitudinal and elevational distribution of two convergent families of nectarivorous birds, hummingbirds (Trochilidae) and sunbirds (Nectariniidae), to see if and what their biogeography can tell us about the strength of their adaptations. Both families show adaptations to a nectarivorous environment, namely elongated bills and tongues with
lamellae-like structures, with the hummingbirds displaying a stronger mutualistic co-adaptation
with flowers compared to sunbirds, suggesting the presence of a key adaptation within the taxon
(Johnsgard, 1997, Cheke and Mann, 2001). These features, combined with the hemispheric
separation and differences in species richness, indicate that hummingbirds and sunbirds are well-
suited for biogeographic comparisons to determine key adaptation strength. In this study, we
seek to ask several questions. Do hummingbirds extend farther latitudinally and elevationally
than sunbirds? What does the shape of their distribution tell us about their interactions with the
environment? And more generally, will a difference in biogeography and species richness
between ecologically equivalent taxa indicate the presence of a key adaptation in one of the taxa?

Materials and Methods

Study Families

Hummingbirds (order Apodiformes, family Trochilidae) and sunbirds (order
Passeriformes, family Nectariniidae) are two families of nectarivorous birds. There are
approximately 365 hummingbird species all located in the New World (BirdLife International,
2015) with a latitudinal extent from Alaska to Argentina. Hummingbirds are the most specialized
of all the nectar feeding birds, all feeding almost exclusively on nectar and only supplementing
protein intake by eating small insects (Yanega and Rubega, 2004). Due to this tight co-
adaptations between food and forager, hummingbirds have evolved distinct anatomical and
morphological features suited to nectar foraging. Such features include elongated bills and
extensile, bifurcated, tubular tongues that acts as micro-pumps for reaching and gathering nectar,
large breast muscles (30% of body weight) and specialized wings giving them the ability to
hover and fly backwards, and a dense erythrocyte count delivering a steady supply of oxygen to
feed extremely active muscles (Johnsgard, 1997; Rico-Guevera and Rubega, 2011; Rico-Guevera
et al., 2014).

One-hundred-twenty-four sunbird species (family Nectariniidae) exist worldwide (BirdLife International, 2015). All of them occur in the Old World, specifically Africa, mainland Asia, the Indonesian Archipelago, and much of Australasia. Their latitudinal range stretches from the southern tip of Australia to as far north as Lebanon and the Himalayas. Though the family of sunbirds contain a large number of nectar feeders, the co-adaptation between food and forager is not as tight as hummingbirds. Many species will supplement their diet with insects, seeds, fruit, and flower heads. As expected, there is large variation in morphology based on each species’ relationship with nectar. Sugarbirds and most true sunbirds have long bills with some adapted specific flower species and long, tubular, bifurcated tongues with serrated edges similar to hummingbirds. Flowerpeckers and the *Hedydipna* and *Hypogramma* sunbirds have broad, flat tongues as they are less specialized to nectar feeding. Though some species can hover in front of flowers when feeding, sunbirds generally lack the breast muscle architecture found in hummingbirds with most perching to feed; those less specialized to nectar feeding will typically nectar-rob, entering the flower through the side rather than the front (Cheke and Mann, 2001).

**Methods**

To determine the presence of key adaptations within the family of hummingbirds, we assessed the latitudinal and elevational gradients of both families. Besides the expected relationship with the strength of adaptations, latitudinal and elevational gradients have many features that make particularly useful for this analysis. Firstly, the commonality of latitudinal and elevational gradients of species richness brings a robustness and consistency to the analysis by standardizing the comparison. Secondly, spatial comparisons over a wide geographic range are better able to indicate the presence of key adaptations as they cover many environmental
variables – reducing the chance of a false negative – but are not inherently correlated to the
adaptation in question – preventing false positives. (Admittedly, spatial analysis does not tell us
what the key adaptation is or what it is adapted towards, something which looking at a suite of
environmental variables would indicate). Additionally, elevational comparisons offer a stronger
comparison between families. This is because a purely random process of range size and position
determination within a bounded geographical space of a group of species will generate a hump-
shaped gradient resembling, but not similar to, latitudinal gradients (Willig and Lyons, 1998).
Elevational gradients occur in bounded geographical space but present a skewed distribution
indicating the lack of random processes. Therefore, any difference between the families is almost
definitely an effect of their natural histories.

To create latitudinal and elevational gradients with which compare the two families, we
used the latitudinal and elevational range of each species. Elevational ranges were taken from a
database on the ecology and biogeography maintained by Çağan H. Şekerçioğlu and used as is.
Two different latitudinal gradients were analyzed: latitude as is and “polewardness,” a measure
of distance from the equator. Latitudinal ranges of the families were taken from shapefiles
downloaded from BirdLife International (2015) – data extracted using R – and used for the first
measure as is except for converting southern latitudes to negative values. To create the second
measure of polewardness, the maximal and minimal latitudinal range of each species was
extracted and rounded up and down respectively to the nearest integer. For example, the
hummingbird species *Amazilia amabilis* which ranges from 14.17N to 3.98S would have its
range modified to 15N and 4S. If the range then crossed the equator, then the range was taken to
be from 0 to the maximum distance from the equator, effectively ‘folding’ the range at the
equator. In the previous example, this would mean the poleward range would be 0 to 15 degrees.
A species which exists only in the Northern or Southern hemisphere would simply have its poleward range as the absolute value of its latitudinal range.

With the latitudinal, poleward, and elevational ranges, we analyzed the families in two ways. First, we compared several empirical cumulative distribution functions (ECDFs) based upon the three geographical properties (elevation, latitude, and polewardness) for each family. To create the ECDFs, we assumed a species to be present depending upon three different points in the range: the minimum, maximum, and central points. Central points were usually determined by taking the midpoint of each range which assumes a symmetrical abundance distribution. Since polewardness had the folding property, we created an extra measure of centrality, expected polewardness. For species whose ranges crossed the equator, we assumed that abundance was stacked creating a new distribution (abundance was assumed to be uniform for easier calculation). We then calculated the expected value of this stacked uniform distribution seen in eq. (1) where \( \text{min} \) and \( \text{max} \) stand for the absolute value of minimum and maximum latitude respectively.

\[
\frac{1}{2} \cdot \frac{\text{min}^2 + \text{max}^2}{(\text{min} + \text{max})}
\]  

(Equation 1)

This lead to ten different ECDFs for each family: minimum elevation, maximum elevation, midpoint elevation, minimum latitude, maximum latitude, midpoint latitude, minimum polewardness, maximum polewardness, midpoint polewardness, and expected polewardness. Each type of ECDF was then compared between families using two different minimum difference estimation (MDE) tests, the Kolmogorov-Smirnov and Anderson-Darling tests, with the assumption that of hummingbird ECDF is less than the sunbird ECDF (one-tailed tests). We feel that the ECDFs based upon central points were most accurate as they were neither under nor
over conservative. This method of analysis tells us with statistical certainty whether the distributions differ, though not necessarily how they differ.

Second, to characterize each family’s distribution, we intervals of 5 degrees for polewardness and half kilometers for elevation and counted the number of species for each family in each interval. If a species’ range was the cutoff point of the interval, it would be considered as present in the lower interval but not in the upper interval due to previous rounding.

In the example with A. amabilis, this would mean that the species would exist in the 10 to 15 degree interval but not the 15 to 20 degree interval. With the data on the two families’ species richness vs the two ranges, the data were then normalized such that the interval with the highest number of species became 1 to remove the effect of species richness. This gave us four sets of data based on a 2x2 factorial: sunbird and hummingbird vs. latitude and elevation. A logistic function (eq. 2) was then fitted onto each of the four sets of data – the proportional species richness, $S_p$, per interval vs. the midpoint of each interval – with variables $a$ and $b$ determining position and steepness respectively.

$$S_p = \frac{1}{1+ae^{bx}}$$  \hspace{1cm} (Equation 2)

With each function characterized, we then found the specific inflection points (eq. 3), which corresponded to the point at which species richness was half of maximum species richness, and the roots of the third derivative (jerk points) (eq. 4) and points of maximum magnitude of curvature (MMC points), both of which corresponded to the start and end of the decline of species richness. Since MMC points have no explicit solution, we instead estimated them by searching over the positive number line with R. Using these points, we characterized how species richness declines in each family with elevation and polewardness.
This second method of analysis with functions and points now characterize the shape of each family’s gradient.

**Results**

Broadly, our results show that hummingbirds extend further poleward and higher in elevation than sunbirds. Hummingbirds extend from as far north as 62 degrees to as far south as 56 degrees and up to 5000m in elevation. Sunbirds, on the other hand, extend only from 36 degrees north to 40 degrees south and up to 4880m in elevation (Table 1). Both families show the same general pattern of initial increase in species richness from the equator and sea-level, both reaching their maximum in the 5-10 degree and 500-1000m intervals, before declining (Fig. 2). Inspecting the figures, we can see that hummingbirds are able to maintain proportional species richness at higher levels than sunbirds but in different ways with regards to elevation and latitude.

**ECDF Results**

The ECDF results broadly show that hummingbird and sunbird distributions differed across all measures (Table 2). The only measures that returned values of non-significance were the measures based upon the maximum latitude of each species’ range. The centrality based ECDFs all returned significant values. Elevational ECDFs gave the greatest degree of difference and the smallest p-values, followed by poleward ECDFs, then simple latitude ECDFs. With the confirmation of difference in elevational and latitudinal distributions between hummingbirds and sunbirds, we turn to characterizing the differences.
Both hummingbirds and sunbirds reach approximately the same maximum elevation, around 5000m (Table 1a, Fig. 2a). With our fitted functions, we see that even though both hummingbirds and sunbirds extend to roughly the same elevation, hummingbirds are able to maintain higher proportional species richness at higher elevations compared to sunbirds. For sunbirds, the relationship with elevation is $S_P = \frac{1}{1 + 0.006546e^{2.409634\cdot ELEV}}$; for hummingbirds, $S_P = \frac{1}{1 + 0.02024e^{1.53943\cdot ELEV}}$ (Table 3). Looking at the inflection points, we see that sunbirds reach 50% of maximum species richness at 2087m in elevation with hummingbirds reaching theirs at 2533m. Sunbirds and hummingbirds both start their decline around the same elevation – 1540m and 1678m respectively using the jerk, 1764 and 1898m using MMCs – but sunbirds end their decline at a lower elevation compared to hummingbirds – 2634m vs. 3385m respectively according to the jerk, 2410m vs. 3458m according to the MMCs – indicating a more gradual decline in proportional species richness for hummingbirds (Table 4, Fig 2b.).

Unlike the case of elevation, hummingbirds reach further from the equator than sunbirds, 60-65 degrees vs. 35-40 degrees respectively (Table 1b, Fig. 2b). Also unlike elevation, hummingbird proportional species richness is at its greatest divergence from sunbird proportional species richness at mid-latitudinal ranges. For hummingbirds, the relationship equation is $S_P = \frac{1}{1 + 0.019757e^{0.177253\cdot ELEV}}$ and for sunbirds, $S_P = \frac{1}{1 + 0.077829e^{0.134976\cdot ELEV}}$ (Table 3). Hummingbirds reach 50% $S_P$ at 22.14 degrees latitude, later than the 18.92 degrees of sunbirds. Hummingbirds also begin their declines later than sunbirds – 14.71 and 9.16 degrees respectively using the jerk, 14.99 and 9.44 degrees using
MMC. Both stop the decline around the same latitude – 29.57 vs. 28.67 degrees according to the jerk, 29.29 vs. 28.39 degrees according to the MMC – confirming the steeper but later decline of hummingbirds (Table 4, Figure 2d).

Discussion

Sunbirds and hummingbirds are two convergent nectarivorous families of birds with various evolutionary technologies for their feeding operations. While hummingbirds are extremely specialized to their nectar feeding diet, sunbirds vary in specialization ranging from the hummingbird-like sugarbirds to the passerine-like flowerpeckers (Johnsgard, 1997; Cheke and Mann, 2001). These differences in evolutionary technologies should reflect differences in the respective families’ distribution and biogeography. Species richness of hummingbirds show greater resilience compared to sunbirds as one moves higher in elevation and away from the equator. With regards to elevation, hummingbirds and sunbirds extend to the same elevational height, approximately 5000m, but proportional hummingbird species richness holds up much better at higher elevations when compared with sunbirds, declining at a slower rate until they reach the same species richness at 5000m. With regards to latitude, though not as striking a difference, hummingbirds do show greater robustness compared to hummingbirds, especially noting that hummingbirds extend further north and south than sunbirds. Our results give additional evidence to the correlation between a taxa’s species richness and geographic range.

One potential hypothesis for the differences in biogeography between hummingbirds is dispersal limitation. In the Old World, many of the mountain ranges run along the east-west axis while New World mountains run in a north-south manner. The Old World mountains may form barriers which prevent sunbirds from extending as far north as hummingbirds; certainly, lack of land prevents sunbirds from extending as far south. We, though, reject the dispersal limitation
argument on two key grounds. Firstly, hummingbirds are still more speciose than sunbirds. Of
the 365 species, only 15 hummingbirds are found in the latitudinal range where sunbirds are not.
Even if we assume that expansion into the northern latitudes led to the creation of all 15 species,
it still only accounts for approximately 4% of hummingbird species. Clearly the differences in
species richness of the families are not due to range expansion. This implies that greater
geographic range followed greater speciosity and not vice-versa if dispersal limitation were a
factor. Secondly, hummingbirds are able to deal well with mountains. Not only do hummingbirds
maintain species richness at higher elevations as our study showed, they have higher species
richness in the mountains of western North and South America compared to the flat-lying eastern
regions and frequently migrate along these routes. Instead, we feel that the evidence is highly
suggestive of one or more key adaptations in hummingbirds.

There are many similarities between hummingbirds and highly specialized sunbirds,
making them ecological equivalents, but they do differ in specific areas. It is within these
differences where hummingbirds’ key adaptation should lie. Likely, the key adaptation deals with
the manner of foraging, specifically feeding and flight. With regard to feeding, one possibility for
hummingbirds’ key adaptation may be their unique tongues. The tongues of hummingbirds have
recently been shown to act as micropumps, a way of quickly and efficiently gathering nectar
from flowers versus the previous assumption of capillary action (Rico-Guevera and Rubega,
2011; Rico-Guevera et al., 2014). This unusual method of nectar-gathering may allow
hummingbirds to more efficiently gather nectar compared to sunbirds. Not enough is known
about sunbird tongues though to see how the two taxa compare in nectar gathering abilities.
Studies indicate that hummingbirds and sunbirds gather nectar at seemingly comparable rate
suggesting that the amount gathered is not the key difference (Hainsworth, 1973; Schlamowitz et
al., 1976; Paton and Collins, 1989; Rico-Guevera et al., 2014 [pers. calc.]). If the tongue is the key adaptation, then it will be for the fact that micropumping requires no energy expenditure on the part of hummingbirds – removing a cost – while sunbirds apparently intake nectar through suction – a potentially energetically expensive system (Liversidge, 1967; Downs, 2004). Much more research needs to be done on the tongues of sunbirds to see how they compare with the tongues of hummingbirds.

Another possibility of the key adaptation that separates hummingbirds and sunbirds is the hummingbird’s ability to hover and fly in all directions more efficiently (Johnsgard, 1997). Adaptations for a hovering lifestyle include shortened arm bones (humerus, ulna, and radius) and longer hand bones, a relatively fixed V-shaped arm position, a shallow ball-and-cup joint between the coracoid and sternum, a large sternum with a deep keel onto which large breast muscles – pectoralis and supracoracoideus – attach, and red-blood cells and hemoglobin adapted for higher-oxygen affinity and carrying capability (Schuchmann, 1999; Chantler, 1999; Warrick et al., 2012; Zusi, 2013). All these anatomical features are adaptations to stiff-winged flight and seen to a lesser extreme within other bird families of the order Apodiformes (Schuchmann, 1999; Chantler, 1999; Zusi, 2013). What truly differentiates the flight of hummingbirds is the axial rotation of the humerus and wrist bones during flight (Zusi, 2013). Hummingbirds are able to create lift on the upstroke – in addition to the downstroke seen in all birds – due to wing inversion caused by axial rotation of the wrist (Warrick et al., 2012). Wrist flexibility comes from changes in carpal structure and deletion of key ligaments and is seen in birds outside of Apodiformes (Ros et al., 2011; Zusi, 2013; Parslew, 2015). In addition, additional power to each downstroke and upstroke comes from axial rotation of humerus, driven by the pectoralis, supracoracoideus, and other muscles (Hedrick et al., 2012; Warrick et al., 2012; Zusi, 2013). The
humerus is able to rotate up to 180° due to a unique humeroscapular joint (Ingram, 1978; Schuchmann, 1999). The key adaptation of this joint is the placement of the humeral head along the axis of the shaft instead of the terminal position, a feature only seen in hummingbirds (Karhu, 1999; Videler, 2006). Together, this suite of adaptations allows hummingbirds to hover effectively when foraging.

It is currently unknown what the benefits to hovering may be. We speculate three possible reasons. Firstly, hummingbirds may be able to exploit the nectar of plants without perches, potentially opening up a new resource for them. As most nectarivorous birds need to perch while feeding, flowers without perches may represent a relatively abundant and constant resource without competition from other similar species. Evolution of hovering in this scenario may be a virtuous cycle as other hovering becomes more efficient at high nectar volumes which occur in the absence of competition (Dreisig, 1997). Secondly, hummingbirds may be able to escape predation due to their unique flying abilities. With the ability to fly in all directions, hummingbirds may be easily avoid predators, a useful ability especially when feeding at a flower with blocked sightlines (Lima, 1993). Finally, while hovering is energetically costly, it is also time efficient (Hainsworth, 1986). Hovering birds spend less time gathering resources at flowers than birds which rely on perches. This means that hovering becomes more energetically efficient compared to perching when birds feed within clustered flower patches (Pyke, 1981; Wolf and Hainsworth, 1983). The suite of evolutionary technologies may also benefit hummingbirds in secondary ways. For example, hummingbirds are able to sustain flight more efficiently at higher altitudes, likely due to their denser erythrocyte count, expanding their fundamental niche to higher elevations (Berger, 1974). What is clear though is that a hummingbird’s adaptations for hovering – in particular, the movement of the humeral head from a terminal to axial position –
fundamentally changes the rules of their nectarivory; they exist as a new type of bauplan while
sunbirds are still effectively a fancy passerine (Rosenzweig and McCord, 1991; Vincent and
Brown, 2005). Coupling the fact that almost no hummingbird species is not a highly specialized
nectarivore while many sunbirds range in their specialization with species richness and
biogeographic data suggest hummingbirds have incumbently replaced their ancestral-type that
was less specialized to nectar feeding.

There could be many reasons why hummingbirds developed their key adaptation.

Hummingbirds underwent an expansive radiation during the uplift of the Andes beginning
around 10mya (McGuire et al., 2014). Living in such harsh conditions could have necessitated
the evolution of a more efficient foraging system. As mentioned earlier, greater oxygen capacity
is beneficial to both hovering and living in low oxygen conditions. There is also the possibility
that the rise of the Andes freed up niche space that would have otherwise been taken up by a
competing family like hawkmoths (Sphingidae), a sort of ecological and evolutionary constraint
(Halloway et al., 201X). Furthermore, sunbirds may face their own internal constraints, genetic
or otherwise, preventing them from evolving a key adaptation (Arnold, 1992). Whatever the case
may be, the evolution of this adaptation allowed hummingbirds to more efficiently take
advantage of a resource and expand their species number and geographical range.

By comparing the biogeography of two convergent families of organisms, we can gain
insight into the difference in evolutionary technologies between them. A taxon with higher
species richness and a larger geographical range than its equivalent sister taxa is likely to have a
key adaptation that allows it to achieve such species numbers and range extent. One possible
example could be the American and European earthworms. European earthworms, having been
introduced to North America, have colonized parts of North America that are farther north than
their American counterparts (Frelich et al., 2006). Both earthworms are ecological equivalents and have convergent features to fill the role of soil turners. This greater range could potentially mean that the European earthworms have some superior evolutionary technology that allows them to expand their range farther north than the native North American species.

Great insights into the nature of adaptations of ecologically equivalent taxa may be deduced from comparison of their geographic ranges. Our study provides a proof-of-concept for this hypothesis.
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Table 1a: Proportional species richness per elevation interval of sunbirds and hummingbirds

| Elevation (meters) | Sunbirds      | Hummingbirds |                  |
|-------------------|---------------|--------------|-----------------|
| [ 0 , 500 ]       | 0.967741935  | 0.883040936 |                 |
| (500 , 1000]      | 1             | 1            |                 |
| (1000 , 1500]     | 0.924731183  | 0.947368421 |                 |
| (1500 , 2000]     | 0.677419355  | 0.760233918 |                 |
| (2000 , 2500]     | 0.376344086  | 0.543859649 |                 |
| (2500 , 3000]     | 0.172043011  | 0.421052632 |                 |
| (3000 , 3500]     | 0.107526882  | 0.292397661 |                 |
| (3500 , 4000]     | 0.053763441  | 0.140350877 |                 |
| (4000 , 4500]     | 0.043010753  | 0.058479532 |                 |
| (4500 , 5000]     | 0.021505376  | 0.005847953 |                 |

Table 1b: Proportional species richness per latitudinal interval of sunbirds and hummingbirds

| Latitude (degrees) | Sunbirds      | Hummingbirds |                  |
|-------------------|---------------|--------------|-----------------|
| [ 0 , 5 ]         | 0.904761905  | 0.76953125  |                 |
| (5 , 10]          | 1             | 1            |                 |
| (10 , 15]         | 0.80952381   | 0.86328125  |                 |
| (15 , 20]         | 0.495238095  | 0.6953125   |                 |
| (20 , 25]         | 0.380952381  | 0.37109375  |                 |
| (25 , 30]         | 0.314285714  | 0.25         |                 |
| (30 , 35]         | 0.2           | 0.15234375  |                 |
| (35 , 40]         | 0.00952381   | 0.05859375  |                 |
| (40 , 45]         | 0             | 0.03515625  |                 |
| (45 , 50]         | 0             | 0.02734375  |                 |
| (50 , 55]         | 0             | 0.0234375   |                 |
| (55 , 60]         | 0             | 0.01171875  |                 |
| (60 , 65]         | 0             | 0.00390625  |                 |
Table 2: The results of the ECDF comparisons between families. *Italicics* indicate the centrality based ECDFs. **KS** stands for Kolmogorov-Smirnov and **AD** stands for Anderson-Darling. **NS** indicates that the result was non-significant.

| ECDF Type               | Hbird Num | Sbird Num | KS D-statistic | KS Significance | Standardized AD Criterion | AD Significance |
|-------------------------|-----------|-----------|----------------|----------------|---------------------------|----------------|
| Minimum Elevation       | 309       | 119       | 0.331783199    | p<0.001        | 31.482                    | p<0.001        |
| Maximum Elevation       | 309       | 119       | 0.163280846    | p<0.05         | 3.2666                    | p<0.01         |
| *Midpoint Elevation*    | 309       | 119       | 0.214598461    | p<0.001        | 8.685                     | p<0.001        |
| Minimum Latitude        | 365       | 124       | 0.234423332    | p<0.001        | 10.207                    | p<0.001        |
| Maximum Latitude        | 365       | 124       | 0.069443217    | NS             | 0.49404                   | NS             |
| *Midpoint Latitude*     | 365       | 124       | 0.156407424    | p<0.05         | 1.7652                    | p<0.05         |
| Minimum Polewardness    | 365       | 124       | 0.242222713    | p<0.001        | 14.455                    | p<0.001        |
| Maximum Polewardness    | 365       | 124       | 0.073486522    | NS             | 0.71488                   | p<0.1          |
| *Midpoint Polewardness* | 365       | 124       | 0.14719399     | p<0.05         | 1.4571                    | p<0.05         |
| Expected Polewardness   | 365       | 124       | 0.13121962     | p<0.05         | 1.8851                    | p<0.05         |
Table 3: The values of $a$ and $b$ for each of the models along with their significance. RSS is the residual sum of squares for each model and RSE is the residual standard error. It should be noted that all residuals fall between 0 and 1, and therefore the sum of squares are smaller than the sum of the absolute values of the residuals.

| Model      | a       | b       | RSS     | RSE     |
|------------|---------|---------|---------|---------|
| NectarElev | 0.00655d| 2.40963a| 0.010254| 0.035802|
| TrochElev  | 0.02024c| 1.53943a| 0.022979| 0.053594|
| NectarLat  | 0.04133c| 0.15735a| 0.04463 | 0.063696|
| TrochLat   | 0.02318 | 0.17739a| 0.054938| 0.070671|

a: p<0.001, b: p<0.01, c: p<0.05, d: p<0.1
Table 4: The Inflection point, the jerk points, and MMC points for each of the models.

| Model     | Inflection | Jerk #1 | Jerk #2 | Curve #1 | Curve #2 |
|-----------|------------|---------|---------|----------|----------|
| NectarElev| 2.087005   | 1.540442| 2.633544| 1.441369 | 2.73264  |
| TrochElev | 2.533536   | 1.678043| 3.389003| 1.608667 | 3.458399 |
| NectarLat | 20.24934   | 11.87956| 28.61911| 11.872   | 28.62667 |
| TrochLat  | 21.22319   | 13.7989 | 28.64747| 13.79037 | 28.656   |
Fig. 1 A plot of the four main ECDFs used to compare hummingbird and sunbird distribution. Solid lines indicated the sunbirds and dashed lines indicate hummingbirds. One can see that the hummingbird ECDFs are almost entirely below and reach the 1 at much a higher latitude and elevation compared to the sunbird ECDFs. One can also see that the deviation between the elevation-based ECDF is significantly larger than the deviations of the latitudinal based ECDFs.

Fig. 2 A plot of the proportional species richness $S_p$ of hummingbirds and sunbirds, along with the fitted line, for elevation (a,c) and latitude (b,d). Hummingbirds are denoted by the triangles and dashed lines while sunbirds are denoted by the circles and solid lines. One can see that hummingbirds sustain their species richness at higher elevations and mid-latitudinal ranges, and extend farther latitudinally than sunbirds. The calculated inflection (non-diagonal cross), jerk (diagonal cross), and MMC points (asterisks) also are shown for elevation (c) and latitude (d). As seen in the figures inflection points come later in hummingbirds than sunbirds, confirming that hummingbirds hold up better than sunbirds. We also see that hummingbird $S_p$ and sunbird $S_p$ start their elevational decline at the same spot but eventually separate by the end of the decline, while with latitude, sunbird $S_p$ declines earlier but hummingbird $S_p$ quickly declines until the declines end at roughly the same point.
Fig. 1

Midpoint Elevation

Midpoint Latitude

Midpoint Polewardness

Expected Polewardness
