Distribution of iridescent colours in hummingbird communities results from the interplay between selection for camouflage and communication

Hugo Gruson[a], Marianne Elias[b], Juan L. Parra[c], Christine Andraud[d], Serge Berthier[e], Claire Doutrelant[a], and Doris Gomez[a,e]

[a]CEFE, Univ Montpellier, CNRS, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France
[b]ISYEB, CNRS, MNHN, Sorbonne Université, EPHE, 45 rue Buffon CP50, Paris, France
[c]Grupo de Ecología y Evolución de Vertrebados, Instituto de Biología, Universidad de Antioquia, Medellín, Colombia
[d]CRC, MNHN, Ministère de la Culture et de la Communication, CNRS, Paris, France
[e]INSP, Sorbonne Université, CNRS, Paris, France

Abstract

Identification errors between closely related, co-occurring, species may lead to misdirected social interactions such as costly interbreeding or misdirected aggression. This selects for divergence in traits involved in species identification among co-occurring species, resulting from character displacement. On the other hand, predation may select for crypsis, potentially leading co-occurring species that share the same environment to have similar appearance. Few studies have explored these antagonistic processes at the community level. Here, we assess colour clustering and overdispersion in multiple hummingbird communities across Ecuador and identify the processes at stake by controlling for species phylogenetic relatedness. In hummingbirds, most colours are iridescent structural colours, defined as colours that change with the illumination or observation angle. Because small variations in the underlying structures can have dramatic effects on the resulting colours and because iridescent structures can produce virtually any hue and brightness, we expect iridescent colours to respond finely to selective pressures. Moreover, we predict that hue angular dependence – a specific aspect of iridescent colours – may be used as an additional channel for species recognition. In our hummingbird assemblages in Ecuador, we find support for colour overdispersion in specific body patches at the community level even after controlling for the phylogeny, especially on iridescence-related traits, suggesting character displacement among co-occurring species. We also find colour clustering at the community level on patches involved in camouflage, which may counter-balance the effect of character displacement.

Keywords: Reproductive Character Displacement, Agonistic Character Displacement, Camouflage, Structural Colours, Angle-Dependent Colouration, Community structure, Ecuador

Colour is a complex communication channel widespread among various taxa and involved in many ecological and evolutionary processes [1]. It can be described by multiple variables, including hue (colour in its common sense, such as red, green, blue, etc.) and brightness (average level of grey of a colour, i.e. whether the object is light or dark). Colours can be produced by two non-mutually exclusive means: pigmentary colours are produced by the selective absorption of incoming light by pigments, while structural colours are produced by the interaction of incoming light with nanostructures, causing diffraction, interferences or scattering [2]. Among structural colours, iridescent colours are characterised by a shift in hue with changes in illumination or observation angle [3]. Iridescent colours are found in many bird families such as Anatidae (ducks) Phasianidae (fowls), Sturnidae (starlings), or Trochilidae (hummingbirds), and thought to be involved in numerous adaptations [4]. But evolution of iridescent colours at the community level remains poorly understood. Yet, they may display evolutionary patterns that differ from non-iridescent colours. Indeed, as opposed to other types of colours, iridescent colours can produce virtually any hue and are expected to respond more readily and finely to selection, because large changes of hue can be achieved by small changes in the underlying structures [5]. They can also result in directional colours only seen at specific angles, as well as highly reflective colours [6].

Because colours are involved in many different ecological processes, they are subject to multiple selection pressures, often with opposite effects [7]. For example, colour can reduce predation risk via crypsis or aposematism or serve as a means of species identification. In this case, two opposite evolutionary forces act on colours: (i) On the one hand, species living in the same environment are likely experiencing similar selective pressures, such as predation. The environment is characterised by ambient light and vegetation, which both influence greatly which colours are poorly detectable and which colours are highly detectable [8, 9]. We thus expect co-occurring species to converge in coloration and harbour poorly detectable colours as this would decrease the risk of being detected by predators. Colour clustering can result from convergence between sympatric species (evolutionary process), from environmental filtering (ecological process), i.e. species assortment locally according to the traits they harbour, or a mixture of the two (detailed in table S1). (ii) On the other hand, sympatric closely-related species are more likely to face problems of species recognition, eventually resulting in reproductive interference - a phenomenon where an individual courts or mates with individuals of another species, producing no offspring or low fertility hybrids, leading to costly inter-breeding [10]. Species misidentification can also lead to misdirected aggression and costly fighting when individuals compete over resources or territories. Hence, any feature that would enhance species recognition is expected to be selected for. In this context, closely related species living in sympatry should be under strong selective pressure to diverge in traits involved in communication, if divergence enhances species recognition. Divergence can result from a process called character displacement (RCD for reproductive character displacement, ACD for agonistic character displacement; evolutionary process) [11–13] or from species assortment (ecological process). For ACD, it is worth noticing that traits are expected to diverge only in case of moderate ecological competition, they should converge in case of high competition [13, 14]. Multiple empirical studies have shown character displacement for songs (e.g. Gerhardt [15] in frogs and Grant and Grant [16] in birds), or olfactory signals [17]. However, fewer studies have looked at divergence in colour patterns (but see Sætre et al. [18], Naisbit et al. [19], Lukhtanov et al. [20], Martin et al. [21], Doutrelant et al. [22], and Hemingson et al. [23]). Almost all these studies were at the species level, and at best involved comparison between closely related species. Many of them also did not use objective spectrometry measurements and instead relied on human vision, which is likely to have biased their results [24, 25].

In birds, it has been argued that colouration is under different selective pressures depending on the body patch location: dorsal patches are mainly involved in camouflage while ventral and facial patches are mainly involved in communication [7, 26]. In this study, we test this hypothesis for iridescent colours at the community level by looking at phenotypic structure in hummingbird local assemblages across different body parts. Accordingly, we predict that co-occurring hummingbird species should display similar hues on dorsal patches, leading to phenotypic clustering of hues (i.e. co-occurring species are more similar than expected by chance, prediction 1) and different hues on ventral patches, resulting in a phenotypic overdispersion pattern (i.e. co-occurring species are more dissimilar than expected by chance, prediction 2). For brightness, we can formulate two alternative predictions: on the one hand, it might evolve in the same way as hue, also because of reproductive character displacement and selection for camouflage, leading to the same outcome as for hue (prediction 3, equivalent to predictions 1 and 2 but for brightness). On the other hand, because brightness level positively correlates with signal conspicuousness, poorly detectable signals have similar brightness, and highly detectable signals have similar brightness. Hence, we may instead expect that species co-occurring should converge for brightness on all patches (prediction 3bis) if the same patches are involved in the same ecological process (communication or camouflage).

Compared to other types of colouration, iridescent colours might enable species recognition on another dimension in the sensory space. Two species can have the same hue or brightness at a given angle but can differ at another angle, via an additional variable we call "hue shift". Because hue shift cannot be seen at large distances, it may allow species to diverge without interfering with camouflage against predators [4]. Accordingly, we predict overdispersion for hue shift not only on ventral patches, but also on dorsal patches (prediction 4). However, hue shift is often highly correlated with hue due to the optics underlying iridescence (Dakin and Montgomerie [27] for example reported $R^2 \geq 0.95$ for the correlation between hue and hue shift). We test this correlation with the data from this article and discuss how it may impact our results.

At the community level, we predict that community colour volume (also known as functional richness `FRic` in functional ecology [28]) and brightness range increase with species richness more than expected in a random species assemblage (null model) because co-occurring species would use different colours (hue or brightness) (prediction 5).

Here we test our five predictions by quantifying both iridescent and non-iridescent colours of 189 hummingbird assemblages in Ecuador that include 112 species and span a large variety of habitats, and by assessing the phenotypic structure (clustering, random distribution, overdispersion of colours) and correct that for the expectation given species phylogenetic relatedness within these assemblages. Comparing the uncorrected and the phylogenetically-corrected phenotypic structure of hummingbird communities will allow us to identify which mechanisms (character displacement, species assortment with mutual exclusion of similar species, environmental filtering; as detailed in table S1) underlie the community structure of iridescent colours in hummingbirds.

Materials and methods

Community data

Hummingbirds are particularly suited as a study system to explore the possible effect of reproductive character displacement on iridescent colours because (i) they display a large variety of hues [29] and all species harbour some iridescent patches, many of which have a very strong angular dependence, rapidly shifting from pink to green or black [30, 31] (but note that many hummingbirds species also have non-iridescent, pigmentary, patches), (ii) they belong to a very speciose family whose phylogeny is well established and readily available [32, 33], (iii) they live only in the Americas, especially in the tropics where numerous species can coexist locally [29] and (iv) almost all species are available in museum collections and their colour can be objectively measured using spectrometric measurements [34].

Presence/absence data for hummingbird assemblages at 189 sites in Ecuador (see map in fig. S3) were compiled from data in peer-reviewed papers and reports from environmental organisations [35]. These sites cover a large variety of elevation ranges (fig. S3) and habitats [35, 36]. This dataset was previously thoroughly reviewed by comparing the observations with the known elevational and geographical ranges of each species [36] and includes observations of 112 of the 132 hummingbirds species found in Ecuador [37].

Colour measurements and analyses

For each one of the 112 species, we borrowed one male from either the Museum National d'Histoire Naturelle (MNHN) in Paris or the Musée des Confluences, in Lyon (full list in Online Supplementary Information). When multiple subspecies were living in the area where presence was recorded, we randomly picked one of them. We consistently took spectral reflectance measurements on the 8 following patches (described in fig. S1): crown, back, rump, tail, throat, breast, belly, wing. We also made additional measurements on patches that visually differed in colouration from these 8 main ones, as in Gomez and Théry [7] and Doutrelant et al. [22].

We measured reflectance using a setup similar to Meadows et al. [38], relying on the use of two separate optical fibres. Light was conducted from an Oceanoptics DH-2000 lamp emitting over the 300-700 nm range of wavelengths to which birds are sensitive [39] to the sample through an illuminating FC-UV200-2-1.5 x 100 optical fibre (named illumination fibre). Light reflected by the sample was then collected by a second identical optical fibre (named collection fibre) and conducted toward an Oceanoptics USB4000 spectrophotometer (used with the SpectraSuite 2.0.162 software). This setup allows for a precise independent rotation of the illumination and the collection fibres, necessary for the measurements of iridescent colours [6]. For more details about the measurement conditions as recommended in White et al. [40], see SI.

For every patch, we recorded a first reflectance spectrum at the position of the fibres which maximised total reflectance. To measure hue angle dependency (iridescence), we then moved both fibres 10° away from the previous position and recorded a second spectrum, as in Meadows et al. [41]. More recent measurement methods revealed that it would be more accurate to keep the angular span between the illumination and collection fibres constant [42]. We however confirmed that this did not impact our results by running our analyses once with all data and once with only data at a given angular span (which represented 94 % of the total data). All measurements were performed in a dark room with temperature control. Recorded spectra were normalised by an Avantes WS-1 white standard and a measurement with the lamp shut down (dark reference) and integration times were determined for each sample as to maximise the intensity of the signal without saturating the spectrometer.

Final values were averaged over 5 consecutive measurements and spectra were smoothed using a loess algorithm and interpolated every 1nm and negative values were set to zero using the R package `pavo` [43].

We analysed spectra using Endler and Mielke [44] model with relative quantum catches Q_i (without Fechner's law). All birds are tetrachromats and can see light with wavelengths from 300 to 700 nm, which includes ultra-violet light (UV) [45]. But different bird species vary in their sensitivity [46]: some are called UV-sensitive (UVS) while others are violet-sensitive (VS). Literature on colour vision in hummingbirds suggests that both types are found within the family (see Chen and Goldsmith [39] and Herrera et al. [47] for UVS species and Ödeen and Håstad [48] for VS species). Because we did not have enough information to compute ancestral states and vision type for all species in our study and because it was found to have little influence in previous studies [7], we ran our analyses as if all species were VS, using the spectral sensitivities of a typical VS bird, *Puffinus pacificus* [49]. We used different illuminants defined in Endler [8], depending on the habitat of the species described in Stotz et al. [50] (detailed in SI): "large gaps" illumination was used for species living in the canopy while "forest shade" was used for species living in the understory. Hue was a tridimensional variable defined by the position (x, y and z) of the reflectance spectrum in the tetrahedron representing bird colour vision space [44] and brightness was defined as in Endler and Mielke [44] (perceived intensity of colour, also sometimes referred to as luminance). We ensured that all indices were repeatable (table S2) using the `rptR` R package [51]. We add another variable to describe iridescence: hue shift, defined as the difference between hue at maximum reflectance and hue at 10° away from maximum reflectance, in a similar fashion to Dakin and Montgomerie [27]. Because it is the difference of two tridimensional variables (hue at the position where reflectance was maximum and hue at 10° away), hue shift is tridimensional as well. Dakin and Montgomerie [27] found a high correlation between hue and hue shift at the intraspecific level in the peacock *Pavo cristatus*, we also report a high correlation at the interspecific level in hummingbirds by performing a linear regression in $\mathbb{R}^3$ between hue and hue shift ($R^2 = 0.51$, $F(3; 1372) = 469.7$, $p < 0.0001$). New measurement methods have since been developed and propose a new definition for hue shift which is not correlated to hue but they were not available at the time of this study [42].

We analysed the colour volume for each species by measuring the convex hull volume of all colour patches on the bird, as suggested in Stoddard and Prum [52].We compared the relationship between the colour volume of a community and the number of species within this community relative to a null model (prediction 5) obtained by creating random assemblages from a species pool containing all species from all communities.

However, the colour volume does not differentiate the different patches on the bird, raising several concerns. First, two species could use the same colour but at different places on their body. They would then look different to an observer but not identified as such in this analysis. Additionally, we expect different evolutionary signals on different patches, that could even each other out, and blur the outcome at the bird level. For these reasons, we also performed our analyses separately for each one of the following eight patches: crown, back, rump, tail, throat, breast, belly, wing (locations shown in fig. S1).

Trochilidae phylogeny and comparative analyses

A distribution of 100 phylogenetic trees of the Trochilidae family was downloaded from birdtree.org [32] to take into account phylogenetic uncertainty in the comparative analyses [53]. The 112 species included in this study constitute a fairly even sampling of the hummingbird phylogeny (fig. S2).

We used the method developed by Hardy and Senterre [54] and Baraloto et al. [55] to analyse respectively the phylogenetic (Π_{ST}) and phenotypic (τ_{ST}) structures of the hummingbird communities of Ecuador (clustering or overdispersion). This method relies on computing indices inspired by the Simpson index and the fixation index F_{ST}, comparing the observed diversity within and between the communities. For phylogeny, Π_{ST} can reveal phylogenetic clustering ($\Pi_{ST} > 0$) or phylogenetic overdispersion ($\Pi_{ST} < 0$) within communities. Likewise, for phenotypic traits, τ_{ST} can reveal phenotypic clustering ($\tau_{ST} > 0$) or phenotypic overdispersion ($\tau_{ST} < 0$) within communities. Statistical significance of overdispersion or clustering is obtained from comparing the observed value to that obtained from 1000 random communities (created by drawing from the total species pool, using algorithm `1s` from Hardy [56], which keeps the local species richness per site constant). This approach compares the phenotypic structure to what would be expected by chance.

To disentangle the relative effect of ecological (species assortment) and evolutionary mechanisms (selection), we also perform our analyses by taking into account the phylogenetic relationships between species. If the species in the community are more clustered or overdispersed than expected given their phylogenetic relationships, this is taken as evidence that the trait has not evolved in a Brownian fashion (detailed in table S1). To this end, we used the `decouple` function [57], which returns phylogenetically predicted and residual trait values by performing a linear regression of individual trait values explained by the phylogeny. We computed the value of τ_{ST} on trait values decoupled from the phylogeny. This value is hereafter denoted $dc\tau_{ST}$. Similarly to the classical τ_{ST}, the sign of $dc\tau_{ST}$ indicates phenotypic clustering ($dc\tau_{ST} > 0$) or overdispersion ($dc\tau_{ST} < 0$) once the effect of the phylogenetic structure of the communities has been removed.

Analyses performed on a tree distribution (Π_{ST} and $dc\tau_{ST}$) with n trees return a distribution of n statistics values and n p-values p_i. We summarised this information by computing the median of the statistics and the overall p-value p by using Jost's formula [58]:

$$p = k \sum_{i=0}^{n-1} \frac{(-\ln(k))^i}{i!} \qquad \text{where } k = \prod_{i=1}^{n} p_i \tag{1}$$

Results

We find a strong phylogenetic clustering within communities ($\Pi_{ST} = 0.062 > 0$, $p < 0.0001$), indicating that co-occurring species are more closely related than expected by chance.

Phenotypic structure of the communities (predictions 1 - 4)

When looking at the bird entire body (when all patches are included simultaneously) by computing the overlap of the colour volumes, we did not find any phenotypic structure.

When the different major patches (crown, back, rump, tail, throat, breast, belly and wing) are examined separately (table 1 and table S3), we find clustering ($\tau_{ST} > 0$) in hue and hue shift on the back, rump, tail, belly and wing. Once we remove the effect of the shared evolutionary history with the `decouple` function, we find clustering on the crown and the back ($dc\tau_{ST} > 0$) but overdispersion on the belly for both hue and hue shift ($dc\tau_{ST} < 0$). Hue shift is also overdispersed on the rump and the tail ($dc\tau_{ST} < 0$). There is no phenotypic structure on the throat, breast or wing for hue and hue shift nor on the rump or the tail for hue.

We find no phenotypic structure (neither clustering nor overdispersion) for brightness on any patches before phylogenetic correction. After phylogenetic correction, brightness values for the throat, breast and belly are clustered among co-occurring species ($dc\tau_{ST} > 0$) but show no phenotypic structure for the crown, the back, the wing and the tail.

Effect of community species richness on colour characteristics (prediction 5)

We found that the brightness range within a community increased in the same way as a null model built from random species assemblages (fig. 1b). For colour volume, we find some outliers with a higher colour volume than expected for community with the same number of species (fig. 1a).

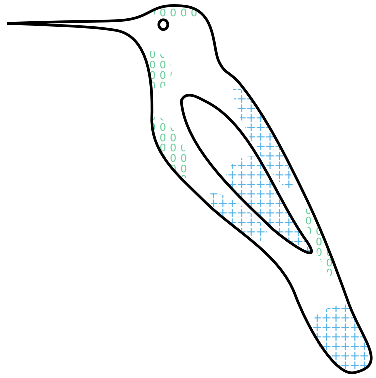
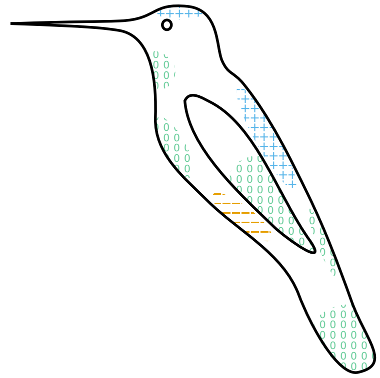
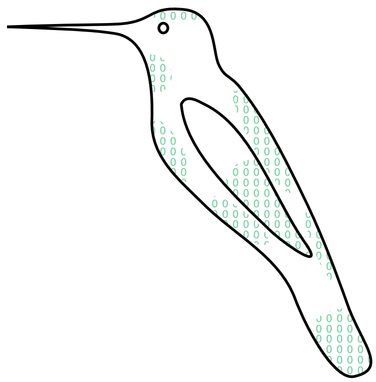
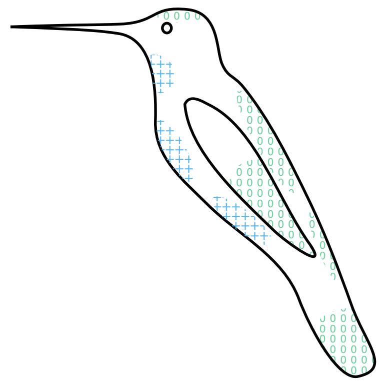
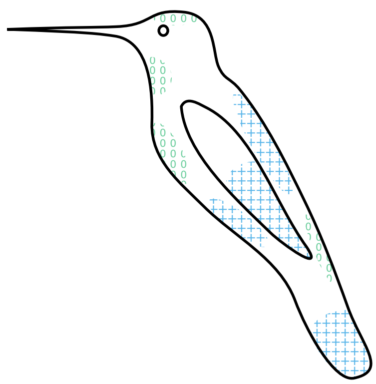
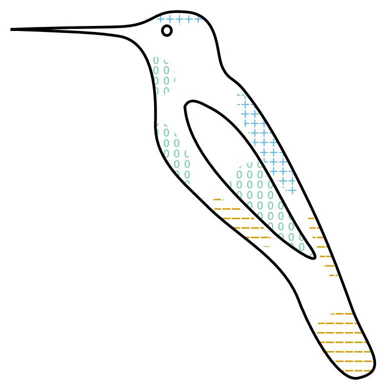
Variable	Phenotypic structure (τ_{ST})	Decoupled phenotypic structure ($dc\tau_{ST}$)
Hue		
Brightness		
Hue shift (=iridescence)		

Table 1: Phenotypic structure of hummingbird communities for different variables (hue, brightness and hue shift) on the patches studied (crown, back, rump, tail, throat, breast, belly, wing; names and locations illustrated in fig. S1). Hue is a tridimensional variable defined by the reflectance spectrum position x, y and z in the tetrahedron representing avian colour space. Blue plus sign + patterns indicate significant phenotypic clustering (τ_{ST} or $dc\tau_{ST} > 0$), orange minus sign – indicate significant phenotypic overdispersion (τ_{ST} or $dc\tau_{ST} < 0$), and green zero 0 patterns represent the absence of phenotypic structure. The left column shows the raw phenotypic structure of the community, which may be influenced by the phylogenetic structure while the right column shows the phenotypic structure of the community, decoupled from all effects caused by the phylogeny. Exact values for the statistics are available in table S3.

Discussion

Our findings suggest that colour structure within hummingbird communities results from a trade-off between selection for camouflage (leading to phenotypic clustering) and species recognition (leading to phenotypic overdispersion). This balance between selective pressure acting in opposite directions produces a complex phenotypic structure when looking at different patches on the body.

Evidence for different evolutionary scenarios depending on patch location

At the entire bird level (i.e. when pooling together all patches), we did not find any phenotypic structure

As predicted in our prediction 5, community colour volume (as estimated by the convex hull of hue and brightness range within a community) increases slightly faster with the number of species in the community than predicted by a null model. This suggests that co-occurring species in these communities tend to use less different colours than expected by chance. However, this is not the cause for the majority of communities, where co-occurring species do not use more nor less similar colours than expected by chance. This is further confirmed by the absence of phenotypic structure on the colour volume and the brightness when the effect of the phylogeny is not removed.

This could be the consequence of similar selective pressures between the communities we studied, leading colours in all assemblages to be randomly determined. This is however not very likely because the communities we studied differ a lot in both their vegetation background and therefore in the pressure for crypsis [35] and in their species composition. A more likely hypothesis is that co-occurring species tend to use the same colours but not necessarily on the same patches. This is confirmed by our analysis patch by patch, where we find either clustering or overdispersion depending on the location of the patch.

Selection for convergence and phenotypic clustering

In accordance with our predictions, co-occurring hummingbird species tend to have similar hues on patches more likely dedicated to camouflage (back, rump, tail, wing; prediction 1) but not on patches more likely used in communication (crown, throat, breast; prediction 2), as shown in table 1 and table S3. This new result for iridescence colours matches what has been previously described for non-iridescent colours [7]. The phenotypic clustering observed for hue on the rump, the tail and the wing vanishes after removing the clustering effect due to phylogenetic structure. This means that phenotypic clustering of hue on the rump, the tail and the wing is not caused by convergent evolution of co-occurring species but by environmental filtering, leading related, similar-looking species to live in the same area (as explained in table S1). This is confirmed by the high value of phylogenetic clustering. Using different methods on the same dataset, Graham et al. [35] also found significant phylogenetic clustering in 37 communities and overdispersion in only one. This phylogenetic clustering may be caused by a strong niche conservatism but our study cannot discriminate whether such niche conservatism involves colour or other ecological traits. However, hummingbirds' costly hovering flight at high elevation [59–61] and high foraging specialisation [62] likely contribute to this pattern. Alternatively, phylogenetic clustering could also be caused by a very low dispersal ability of hummingbirds.

Contrary to our prediction 2, we also find clustering of hue on the belly before the use of the `decouple` function. However, the fact that it turns into overdispersion after the use of the `decouple` function, and not simply into a random phenotypic structure (as opposed to the rump, the tail and the wing mentioned just before), suggests this initial clustering is mainly caused by environmental filtering on another trait. This other trait may be the colour of another patch or other ecological traits, as we explained previously.

We found a significant clustering of brightness on the throat, breast and belly after controlling for the phylogeny, indicating that brightness on those patches is more similar than expected given the phylogeny among co-occurring species (prediction 3bis). This suggests that the same patches have been selected to be involved either in communication or in camouflage among species living in the same environment. This is seen after controlling for the phylogeny and it is therefore not caused by the phylogenetic relatedness of co-occurring species. Two main hypotheses can explain why co-occurring species tend to communicate (or camouflage themselves) using the same patches: (i) There may be selective pressures for the use of specific patches in camouflage in a given environment (e. g., patches that are more exposed to predators' sight). (ii) Convergence in patches used in communication may be selected because it improves competitor identification in the case of a strong ecological niche overlap (convergence by agonistic character displacement as shown in Grether et al. [13] and Tobias et al. [63]).

All those results suggest a strong effect of the environment in the evolution of colour in agreement with McNaught and Owens [64] who found that bird plumage colour was due to the light environment and not to reproductive character displacement in Australian birds. However, we do not find clustering on all patches, which means that the effect of habitat pressure is somehow limited or counterbalanced by reproductive or agonistic character displacement. On the contrary, for some patches, we found patterns that are likely the result of character displacement.

Character displacement and phenotypic overdispersion

In agreement with our prediction 2, after removing the effect of the phylogeny, there is overdispersion of hue on the belly, likely caused by character displacement (table S1). At a completely different taxonomic scale, focusing on a single hummingbird genus (*Coeligena*) with 11 species, Parra [26] also found that the belly was always involved in the difference in hue between subspecies. It was sometimes even the only patch causing those differences, as for example between *Coeligena torquata fulgidigula* and *Coeligena torquata torquata*. This suggests that the interspecific divergence we found on the belly at the community level on the whole Trochilidae family can be observed at different geographic and taxonomic scales, and even between subspecies of the same species.

As predicted, we also find more phenotypic overdispersion for hue shift than hue after removing the effect of the phylogeny, for example, on the rump and on the tail (prediction 4). It is possible that hue shift is less sensitive to selection for convergence because it may vary without disturbing camouflage efficacy. However, we did not find the expected relaxing of clustering on hue shift on patches such as the back. This is likely caused by the fact that hue shift is highly correlated with hue, as found in this study and in Dakin and Montgomerie [27], who used the same indices to quantify iridescence. This correlation is due to the optics controlling iridescence, meaning that species that display similar hues should also display the same hue shift if they use the same underlying multilayer structures. The fact that the correlation is not perfect and that we nonetheless get different phenotypic patterns for hue and hue shift on some patches suggests that co-occurring species use different multilayer structures, which can produce different iridescent effects while displaying the same hue (functional convergence on hue).

Against our prediction 2, we did not find phenotypic overdispersion on any of the colour variables on patches such as the throat or the crown, that are thought to be sexually selected and often used in courtship displays [65, 66]. Several hypotheses can explain this fact: (i) The overdispersion on some patches (hue on the belly and hue shift on the rump and tail) is sufficient to enable species recognition. (ii) The current phenotypic structure, which is neither overdispersed nor clustered, on those patches is sufficient to enable species recognition. Indeed, the absence of phenotypic overdispersion does not mean that species look the same. It simply means that colour differences between species living in the same community and species in different communities occur in similar ranges. This difference may be sufficient to relax the selective pressure towards reproductive character displacement. (iii) The pressure towards overdispersion is balanced by habitat filtering (for both ventral and dorsal patches), resulting in no apparent phenotypic structure. The latter hypothesis was also a candidate explanation of the pattern found by Martin et al. [21], where sympatric closely related species are more divergent than allopatric ones, but only when the range overlap is limited. They suggested that local adaptation could hinder divergence when species ranges was exactly the same.(iv) Species recognition is achieved by additional means and divergence occurs on others traits, such as modified feathers [67], song [68, 69] or non-vocal noises [70–72] and size. Notably, different species of hummingbirds can have very different courtship behaviour: leks for hermits [73, 74], dives and shuttle displays for bees [71, 75, 76], for instance.

Taken together, our results suggest that hummingbird iridescent colours are determined by different evolutionary mechanisms depending on their location. Within a community, co-occurring hummingbird species tend to use the same hue on dorsal, large, patches probably because of the evolutionary pressure for camouflage, causing phenotypic clustering at the community level. This phenotypic clustering does not seem to be caused by adaptive convergence on colours but rather by environmental filtering perhaps linked to other ecological traits such as elevation tolerance or flight ability. In spite of such environmental filtering, character displacement leads to overdispersion for hue on the belly and hue shift on the rump and the tail. Iridescence may therefore enable species recognition without affecting camouflage efficacy of birds, by opening up a new dimension in the sensory space: hue shift.

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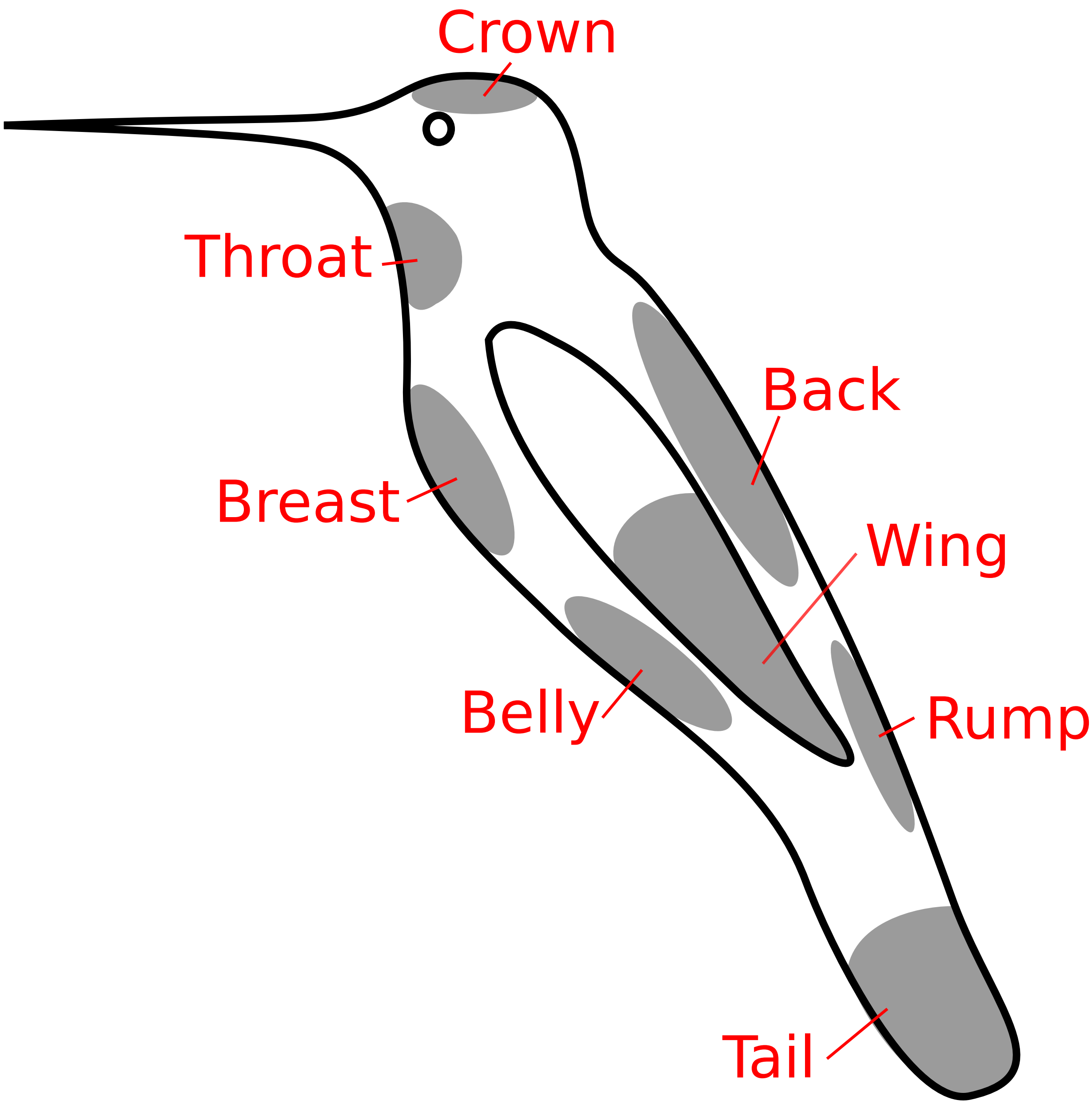


Supplementary figure 1: Locations and names of the 8 patches measured on all species. Additional patches were measured for each species as soon as they differed from one of the 8 patches listed here for a human observer, as detailed in the methods section and as in Gomez and Théry [7].

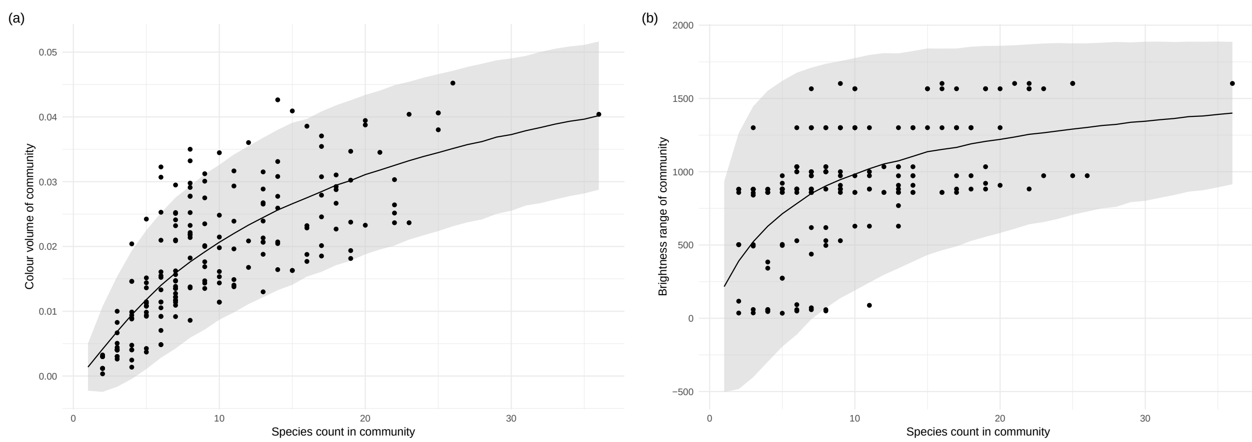


Figure 1: (a) community total colour volume and (b) brightness range increase with the number of species within the community. Each point is a community. The black solid line represents the mean value of (a) colour volume or (b) brightness range from 10 000 random communities with a given species count (null model) and the gray ribbon represents two standard deviations from the mean of the null model.

	$\tau_{ST} < 0$ **Phenotypic overdispersion**	$\tau_{ST} = 0$ **No community structure**	$\tau_{ST} > 0$ **Phenotypic clustering**
$dc\tau_{ST} < 0$ **Character displacement (divergence):** co-occurring species are more dissimilar than expected given their phylogenetic relationships, which means they evolved towards dissimilarity in their colours.	Co-occurring species are less similar than expected by chance because of character displacement.	Co-occurring species are nor more neither less similar than expected by chance despite character displacement because closely related species co-occur more often than expected at random (phylogenetic clustering; $\Pi_{ST} > 0$).	Co-occurring species are more similar than expected by chance despite character displacement because closely related species co-occur more often than expected at random (phylogenetic clustering; $\Pi_{ST} > 0$).
$dc\tau_{ST} = 0$ **Brownian trait evolution**	**Competitive exclusion**: co-occurring species are more dissimilar than expected by chance because distantly-related (and therefore dissimilar) species co-occur more often than expected at random (phylogenetic overdispersion; $\Pi_{ST} < 0$).	Co-occurring species are not more similar nor more different than expected by change or than predicted given their phylogenetic relationships.	**Environmental filtering**: co-occurring species are more similar than expected by chance because closely-related (and therefore similar) species co-occur more often than expected at random (phylogenetic clustering:$Pi_{ST} > 0$).
$dc\tau_{ST} > 0$ **Evolutionary convergence** : co-occurring species are more similar than expected given their phylogenetic relationships, which means they evolved towards similarity in their colours.	Co-occurring species are less similar than expected by chance despite evolutionary convergence because distantly-related species co-occur more often than expected at random (phylogenetic overdispersion; $\Pi_{ST} < 0$).	Co-occurring species are neither more nor less similar than expected by chance despite evolutionary because distantly-related species co-occur more often than expected at random (phylogenetic overdispersion; $\Pi_{ST} < 0$).	Co-occurring species are more similar than expected by chance because of evolutionary convergence.

Supplementary table 1: Summary of the different evolutionary and ecological scenarios and their results in terms of values of τ_{ST} and decoupled $dc\tau_{ST}$.

Table 2: List of species with their provenance (Confluences = Musée des Confluences, Lyon, France, MNHN = Muséum National d'Histoire Naturelle, Paris, France) and strata. Strata data were extracted from Stotz et al. [50] and used in vision models.

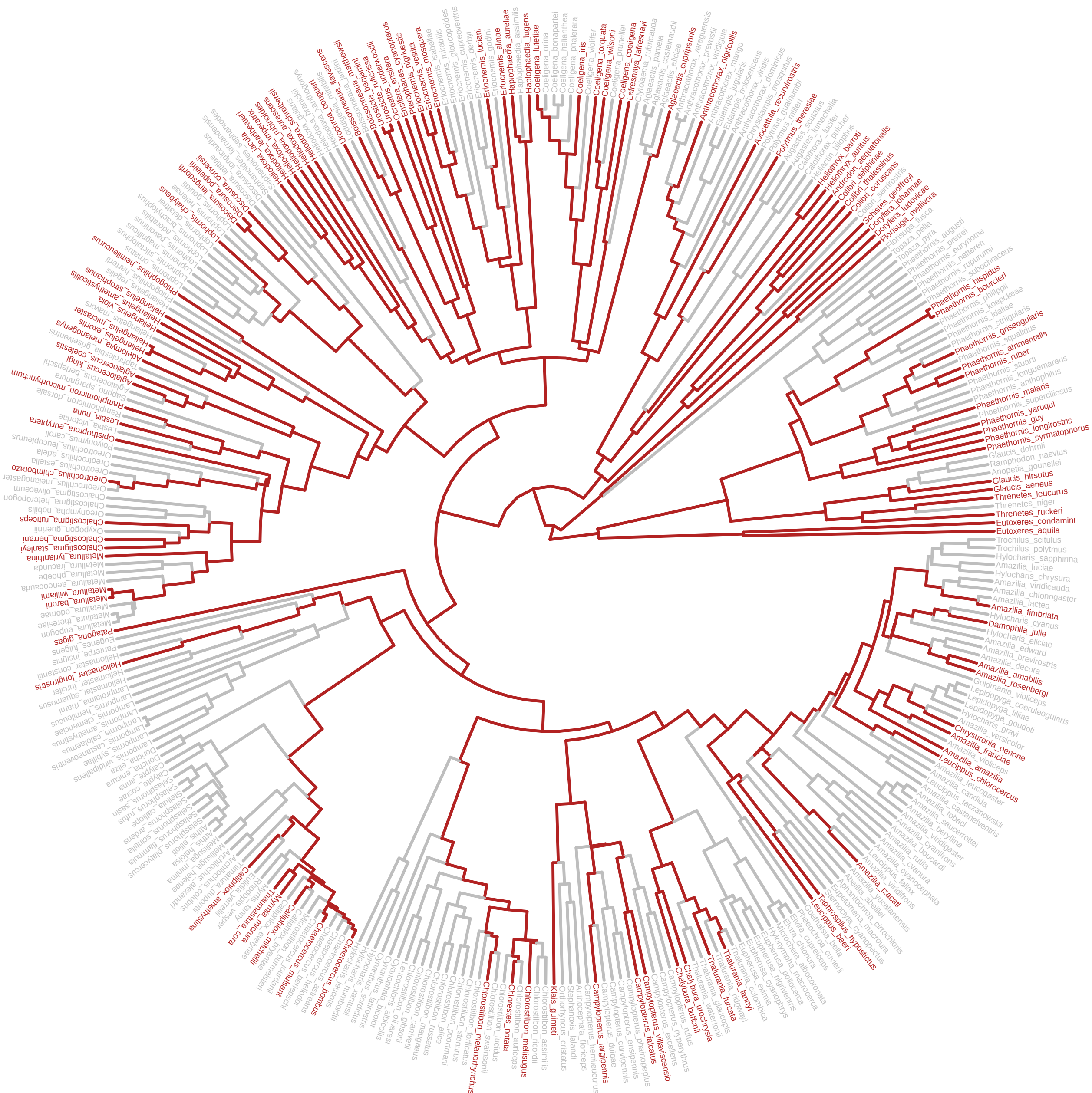
Species	Clade	Provenance	Strata
Adelomyia melanogenys	Coquette	Confluences	Understory
Aglaeactis cupripennis	Brilliant	MNHN	Canopy
Aglaiocercus coelestis	Coquette	MNHN	Canopy
Aglaiocercus kingi mocoa	Coquette	MNHN	Canopy
Amazilia amabilis	Emerald	MNHN	Understory
Amazilia amazilia	Emerald	MNHN	Understory
Amazilia fimbriata fluviatilis	Emerald	MNHN	Canopy
Amazilia franciae	Emerald	MNHN	Canopy
Amazilia grayi meridionalis	Emerald	MNHN	Canopy
Amazilia rosenbergi	Emerald	MNHN	Understory
Amazilia sapphirina	Emerald	MNHN	Canopy
Amazilia tzacatl jucunda	Emerald	MNHN	Canopy
Androdon aequatorialis	Mangoe	MNHN	Understory
Anthracothorax nigricollis	Mangoe	MNHN	Canopy
Avocettula recurvirostris	Mangoe	Confluences	Understory
Boissonneaua flavescens	Brilliant	MNHN	Canopy
Boissonneaua matthewsii	Brilliant	MNHN	Canopy
Calliphlox amethystina	Bee	MNHN	Canopy
Calliphlox mitchellii	Bee	Confluences	Canopy
Campylopterus falcatus	Emerald	MNHN	Understory
Campylopterus largipennis	Emerald	MNHN	Understory
Campylopterus villaviscensio	Emerald	MNHN	Understory
Chaetocercus bombus	Bee	MNHN	Canopy
Chaetocercus mulsant	Bee	MNHN	Understory
Chalcostigma herrani	Coquette	MNHN	Canopy
Chalcostigma ruficeps	Coquette	Confluences	Understory

Species	Clade	Provenance	Strata
Chalcostigma stanleyi stanleyi	Coquette	MNHN	Canopy
Chalybura buffonii intermedia	Emerald	Confluences	Understory
Chalybura urochrysia urochrysia	Emerald	Confluences	Understory
Chlorestes notata obsoletus-puruensis	Emerald	Confluences	Canopy
Chlorostilbon melanorhynchus	Emerald	MNHN	Understory
Chlorostilbon mellisugus phoeopygus	Emerald	Confluences	Understory
Chrysuronia oenone	Emerald	MNHN	Canopy
Coeligena coeligena	Brilliant	MNHN	Understory
Coeligena iris hesperus	Brilliant	MNHN	Understory
Coeligena iris iris	Brilliant	MNHN	Understory
Coeligena lutetiae	Brilliant	MNHN	Understory
Coeligena torquata fulgidigula	Brilliant	MNHN	Understory
Coeligena torquata torquata	Brilliant	MNHN	Understory
Coeligena wilsoni	Brilliant	MNHN	Understory
Colibri coruscans	Mangoe	MNHN	Canopy
Colibri delphinae	Mangoe	MNHN	Canopy
Colibri thalassinus	Mangoe	MNHN	Canopy
Damophila julie	Emerald	MNHN	Understory
Discosura conversii	Coquette	MNHN	Canopy
Discosura langsdorffi	Coquette	Confluences	Canopy
Discosura popelairii	Coquette	MNHN	Canopy
Doryfera johannae	Mangoe	MNHN	Understory
Doryfera ludovicae	Mangoe	MNHN	Understory
Ensifera ensifera	Brilliant	MNHN	Understory
Eriocnemis alinae	Brilliant	MNHN	Understory
Eriocnemis luciani	Brilliant	MNHN	Understory
Eriocnemis mosquera	Brilliant	Confluences	Understory
Eriocnemis nigrivestis	Brilliant	MNHN	Understory

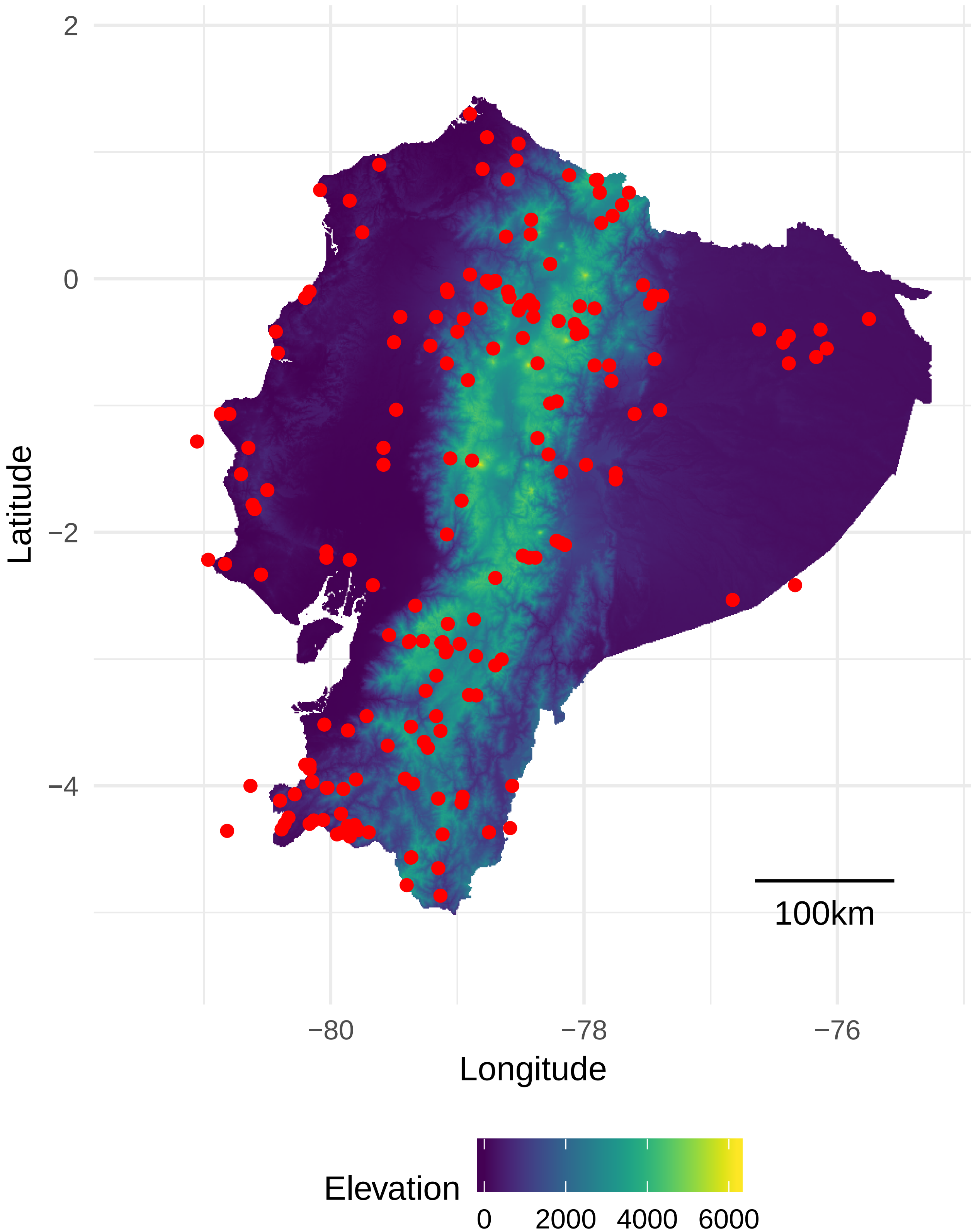
Species	Clade	Provenance	Strata
Eriocnemis vestita smaragdinicollis	Brilliant	MNHN	Understory
Eutoxeres aquila	Hermit	MNHN	Understory
Eutoxeres condamini	Hermit	Confluences	Understory
Florisuga mellivora	Topazes	MNHN	Canopy
Glaucis aeneus	Hermit	MNHN	Understory
Glaucis hirsutus affinis	Hermit	MNHN	Understory
Haplophaedia aureliae russata	Brilliant	Confluences	Understory
Haplophaedia lugens	Brilliant	Confluences	Understory
Heliangelus amethysticollis laticlavius	Coquette	Confluences	Understory
Heliangelus exortis	Coquette	MNHN	Understory
Heliangelus exortis	Coquette	MNHN	Understory
Heliangelus micraster	Coquette	MNHN	Understory
Heliangelus strophianus	Coquette	MNHN	Understory
Heliangelus viola	Coquette	MNHN	Understory
Heliodoxa aurescens	Brilliant	MNHN	Understory
Heliodoxa imperatrix	Brilliant	MNHN	Understory
Heliodoxa jacula jamesoni	Brilliant	MNHN	Understory
Heliodoxa leadbeateri	Brilliant	MNHN	Understory
Heliodoxa rubinoides aequatorialis	Brilliant	MNHN	Understory
Heliodoxa schreibersii	Brilliant	MNHN	Understory
Heliomaster longirostris	MtGem	MNHN	Canopy
Heliothryx auritus	Mangoe	MNHN	Canopy
Heliothryx barroti	Mangoe	MNHN	Canopy
Klais guimeti	Emerald	MNHN	Understory
Lafresnaya lafresnayi gayi	Brilliant	Confluences	Understory
Lesbia nuna gracilis	Coquette	MNHN	Canopy
Leucippus baeri	Emerald	Confluences	Understory
Leucippus chlorocercus	Emerald	Confluences	Canopy

Species	Clade	Provenance	Strata
Lophornis chalybeus verreauxi	Coquette	MNHN	Canopy
Metallura baroni	Coquette	MNHN	Canopy
Metallura tyrianthina tyrianthina	Coquette	MNHN	Understory
Metallura williami primolina	Coquette	MNHN	Canopy
Myrmia micrura	Bee	MNHN	Canopy
Ocreatus underwoodii melanantherus	Brilliant	MNHN	Understory
Opisthoprora euryptera	Coquette	Confluences	Understory
Oreotrochilus chimborazo chimborazo	Coquette	MNHN	Understory
Oreotrochilus chimborazo jamesonii	Coquette	MNHN	Understory
Patagona gigas	Patagona	MNHN	Canopy
Phaethornis atrimentalis atrimentalis	Hermit	Confluences	Understory
Phaethornis bourcieri	Hermit	MNHN	Understory
Phaethornis griseogularis	Hermit	MNHN	Understory
Phaethornis griseogularis	Hermit	MNHN	Understory
Phaethornis guy	Hermit	MNHN	Understory
Phaethornis hispidus	Hermit	Confluences	Understory
Phaethornis longirostris	Hermit	Confluences	Understory
Phaethornis malaris	Hermit	Confluences	Understory
Phaethornis ruber	Hermit	Confluences	Understory
Phaethornis syrmatophorus columbianus	Hermit	MNHN	Understory
Phaethornis yaruqui yaruqui	Hermit	MNHN	Understory
Phlogophilus hemileucurus	Coquette	MNHN	Understory
Polytmus theresiae leucorrhous	Mangoe	MNHN	Understory
Pterophanes cyanopterus	Brilliant	MNHN	Understory
Ramphomicron microrhynchum	Coquette	MNHN	Canopy
Schistes geoffroyi	Mangoe	MNHN	Understory
Taphrospilus hypostictus	Emerald	MNHN	Understory
Thalurania fannyi verticeps	Emerald	MNHN	Understory

Species	Clade	Provenance	Strata
Thalurania furcata viridipectus	Emerald	MNHN	Understory
Thaumastura cora	Bee	Confluences	Canopy
Threnetes leucurus cervinicauda	Hermit	Confluences	Understory
Threnetes ruckeri	Hermit	MNHN	Understory
Urochroa bougueri	Brilliant	Confluences	Understory
Urochroa bougueri leucura	Brilliant	Confluences	Understory
Urosticte benjamini	Brilliant	MNHN	Understory
Urosticte ruficrissa	Brilliant	Confluences	Understory



Supplementary figure 2: Phylogenetic coverage of the *Trochilidae* family in our dataset (species and lineages in red).



Supplementary figure 3: Study sites locations (red dots) plotted on an altitudinal map of Ecuador. Communities outside the borders of the map are on islands or close enough to Ecuador borders to be taken into account in our study.

Variable		R	p-value
	x	0.925	<0.0001
Hue	y	0.951	<0.0001
	z	0.940	<0.0001
Brightness		0.373	0.04

Supplementary table 2: We quantified the repeatability R (intra-class coefficient ICC) and the related p-value by boostraping using the `rptR` R package [77] of indices used in this study by performing the same measurements twice on two patches for 12 species (*Coeligena torquata*, *Colibri coruscans*, *Doryfera ludovicae*, *Heliangelus strophianus*, *Heliodoxa jamesonii*, *Heliothryx barroti*, *Juliamyia julie*, *Lesbia nuna*, *Metallura tyrianthina*, *Ramphomicron microrhynchum*, *Schistes albogularis*, *Urosticte benjamini*). Patches were selected to be of similar hue from a human point of view.

variable	value	Crown	Back	Rump	Tail	Throat	Breast	Belly	Wing
Hue	τ_{st}	-0.0073	0.055	0.055	0.044	0.027	0.03	0.05	0.058
	$p_{\tau_{st}<0}$	0.4	1	1	1	0.9	0.9	1	1
	$p_{\tau_{st}>0}$	0.6	**0.01**	**0.01**	**0.03**	0.09	0.06	**0.005**	**0.006**
	$dc\tau_{st}$	0.0099	0.026	-0.0021	0.0034	-0.0021	-0.0032	-0.01	0.00073
	$p_{\tau_{st}<0}$	1	1	0.8	1	0.9	0.3	**<0.0001**	1
	$p_{\tau_{st}>0}$	**<0.0001**	**<0.0001**	1	0.2	1	1	1	1
Brightness	τ_{st}	-0.021	0.0078	0.0032	-0.0064	0.00015	0.0041	-0.0031	0.0091
	$p_{\tau_{st}<0}$	0.1	0.7	0.6	0.5	0.5	0.6	0.5	0.6
	$p_{\tau_{st}>0}$	0.9	0.3	0.4	0.5	0.5	0.4	0.5	0.4
	$dc\tau_{st}$	-0.0014	0.0028	0.00037	0.00068	0.013	0.023	0.007	-0.0058
	$p_{\tau_{st}<0}$	0.3	1	0.9	1	1	1	1	0.2
	$p_{\tau_{st}>0}$	0.8	0.7	0.7	0.8	**<0.0001**	**<0.0001**	**0.002**	1
Hue shift	τ_{st}	-0.007	0.051	0.052	0.043	0.027	0.029	0.049	0.058
	$p_{\tau_{st}<0}$	0.4	1	1	1	0.9	0.9	1	1
	$p_{\tau_{st}>0}$	0.6	**0.01**	**0.01**	**0.03**	0.08	0.06	**0.006**	**0.006**
	$dc\tau_{st}$	0.0087	0.0059	-0.0068	-0.006	-0.0033	0.0023	-0.0098	-0.0018
	$p_{\tau_{st}<0}$	1	1	**0.005**	**0.01**	0.6	1	**<0.0001**	1
	$p_{\tau_{st}>0}$	**<0.0001**	**0.03**	1	1	1	0.9	1	1

Supplementary table 3: Numerical values for τ_{st} and decoupled τ_{st} (denoted $dc\tau_{st}$). P-values were computed by comparison of the actual value with the null distribution (obtained by randomisation of the communities using method `1s` of Hardy [56]). Significant p-values are in bold and green. Positive values of $dc\tau_{st}$ indicate phenotypic clustering whereas negative values indicate overdispersion.