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## Research



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# Back in black: melanin-rich skin colour associated with increased net diversification rates in birds

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Evolutionary biologists have long been interested in understanding the factors that promote diversification in organisms, often focussing on distinct and/or conspicuous phenotypes with direct effects on natural or sexual selection such as body size and plumage coloration. However, multiple traits that potentially influence net diversification are not conspicuous and/or might be concealed. One such trait, the dark, melanin-rich skin concealed beneath the feathers, evolved more than 100 times during avian evolution, frequently in association with white feathers on the crown and UV-rich environments, suggesting that it is a UV-photoprotective adaptation. Furthermore, multiple species are polymorphic, having both light and dark skin potentially aiding occupation in different UV radiation environments. As such these polymorphisms are predicted to occur in species with large latitudinal variation in their distribution. Furthermore, by alleviating evolutionary constraints on feather colour, the evolution of dark skin may promote net diversification. Here, using an expanded dataset on bird skin coloration of 3033 species we found that more than 19% of species had dark skin. In contrast to our prediction, dark skinned birds have smaller distribution ranges. Furthermore, both dark skin and polymorphism in skin coloration promote net diversification. These results suggest that even concealed traits can influence large scale evolutionary events such as diversification in birds.

## 1. Introduction

Evolutionary biologists have long been interested in understanding the factors that promote net diversification (i.e. speciation minus extinction) in organisms. Such factors include traits involved in natural selection such as body size, nest type and tooth complexity [1,2,3], but also traits involved in sexual selection such as plumage [4,5]. Regardless of the underlying mechanism, most previous work has focussed on distinct and/or conspicuous phenotypes with a clear link with selection. How less conspicuous traits, with more indirect effects on selection, influence net diversification remains unclear.

Previous work has shown that colours of birds vary not only in the plumage, but also in other integumentary structures [6–9]. One such example is skin melanization [9,10], which likely evolved over 100 times in birds from an unmelanized ancestor [9]. As in other vertebrates, including humans, dark skin is produced by the deposition of eumelanin [11,12]. UV irradiation (300–400 nm) is normally absorbed by feathers with eumelanin, and thus passes through to the skin when feathers are light-coloured or absent. Thus, that dark-skinned birds inhabit high irradiation regions (including the tropics), and tend to be bald and/or have white feathers, suggests that dark skin in birds protects against harmful UV light. However, as in humans, dark skin in low UV radiation environments may come at a cost, such as problems with producing vitamin D [13]. For species with high latitudinal variation

(and thus variation in UV radiation), conflicting selective pressures might select for the evolution of polymorphisms, where species can have both dark and light skin colours, depending on the environment.

By protecting skin against UV damage, the evolution of dark skin might alleviate selection against the evolution of light feathers (and/or loss of feathers), and thereby enhance the potential for lighter feathers to evolve in response to other selective pressures such as predation, the need for sexual and social signalling or establishment in a new niche. For example, white crown feathers (where dark skin is most distinct), are often used in display (e.g. in white-crowned manakins), and camouflage (e.g. many desert birds) [14], but might come at the cost of decreased UV protection. Similarly, the evolution of naked skin helps vultures consuming carrion, but also exposes them to UV irradiation [15]. Should dark skin provide any release from selection against white feathers, then the evolution of dark skin might result in increased net diversification rates. Similarly, polymorphism, i.e. having both dark and light skin colour in the same species, might increase net diversification as it allows more flexibility in heterogeneous environments and/or distributions [16]. This is particularly true when integumentary colour modification (i.e. in skin and feathers) is independent and can change at different times in function of different selective pressures. Indeed, in lizards and birds, skin and plumage colour polymorphisms, respectively, act as motors of diversification [17,18] but see [19].

Here we use an expanded dataset of bird skin colours comprising all but five genera and 3033 species (compared to the 2247 before [9]) to investigate whether and how the evolution of dark skin influenced net diversification.

## 2. Methods

### (a) Data collection

Methods follow Nicolai *et al.* [9]. We examined skin on the back of the head, near the neck region (this time excluding ventral coloration as ventral dark skin is much rarer than dorsal dark skin). To do so we lifted, or moved away, feathers to expose a skin section and registered whether the skin was melanized (i.e. black) or not. In species with large areas of naked skin (e.g. Cathartidae and Threskiornithidae) we scored the skin colour based on the exposed skin patch. Naked and exposed patches near the face (i.e. areas around the eye and bill) were not used to assess skin colour. We collected data from adult specimens when possible and tried to collect data for at least one male and one female specimen. We screened all available specimens of each species for polymorphism: when we sampled at least two specimens of a species and found both dark and light skin (regardless of the sex), we classified the species as polymorphic. This means that, in some cases, polymorphism is the result of sexual dichromatism. Furthermore, this does not mean that a single specimen has to have both dark and light skin (which sometimes happen, e.g. in *Picathartes*). For polymorphic species we collected additional information from all available specimens, with a maximum of five specimens per sex, to investigate geographical influences on polymorphism. However, the geographical information turned out to be too incomplete or unspecific for analyses. All new data (i.e. excluding data from [9]) are from the natural history collection of the Royal Belgian Institute for Natural Sciences (RBINS, permission granted by Olivier Pauwels) unless reported otherwise. In total we examined 11 702 specimens from 3033 (extinct and extant) species. New specimens (relative to [9]) were collected following three

priority criteria: (1) sampling additional species from large genera where previously only one or few species were sampled, (2) species with white crown feathers and (3) sampling genera with known dark-skinned species. This last criterion resulted in a large increase in the number of species with dark skin (e.g. in *Icterus* and *Cinnyris*).

### (b) Choice of phylogenetic tree

All phylogenetic analyses were run on the complete Bayesian maximum clade credibility species-level avian phylogeny from the Bird Tree Project [20], built based on both genetic and taxonomic information and the higher-order relationship backbone from Hackett *et al.* [21]. Taxonomy follows Clements [22]. We had an overlap between data and the phylogenetic tree of 2995 species for skin colour data and 2010 species for polymorphism data (differences mostly being explained by extinct species and recently split subspecies). For the reduced Jetz *et al.* [20] tree, i.e. that for which taxa without genetic information were excluded. Previously we showed that this phylogeny produced similar results as using a genes-only tree, nonetheless we tested for phylogenetic robustness by re-running analyses on 100 different trees randomly selected from the posterior distribution [9]. Furthermore, since this might influence state-dependent diversification analyses in particular, we also ran a second set of analyses using a MCC genes-only tree for these analyses. We had an overlap of 2319 species for skin colour data and 1854 species for polymorphism data.

### (c) State-dependent diversification analyses

To test for associations between dark skin/polymorphism and diversification we used the *HiSSE* (Hidden State Speciation and Extinction) package [23] in R v. 4.1 [24]. We ran two sets of SSE models, one where the tested trait was dark skin and another where the tested trait was skin colour polymorphism. More specifically, we used the Binary State Speciation and Extinction (BiSSE) [25] and *HiSSE* framework. First, we implemented a BiSSE null model that assumes that net diversification rates were similar in lineages with or without dark skin, regardless of transition rates associated with it. Next, we implemented a BiSSE model that tests whether net diversification rates differ between lineages when dark skin is absent/present. However, unmeasured and co-distributed factors might influence net diversification as well. As such we also implemented a character-dependent *HiSSE* model which allows differential net diversification between the absence/presence dark skin, but also differential net diversification associated with a hidden, unobserved state. Finally, we implemented two additional null-models CID-2 and CID-4 that do not include skin colour but rather investigated whether or not differential net diversification is associated with two (CID-2) or four (CID-4) hidden states [23].

To exclude the potential that polymorphism was a third state (in addition to dark and non-dark skin) we ran four Mk models (implemented using *fitMk* in *phytools*) [26] to simulate the evolution of skin colour: (1) ER (equal transition rates), (2) SYM (symmetrical transition rates), (3) ARD (all transition rates different) and (4) an intermediate model where there is no direct evolution between dark and non-dark skin but where an intermediate evolutionary state (i.e. polymorphism) is necessary.

### (d) Phylogenetic comparative analyses

We previously found that dark skin is more prevalent at lower latitudes with higher ambient UV radiation, while being less frequent at higher latitudes [9]. Thus, species with wider geographical distributions encounter more diverse UV radiation regimes across their range. Therefore, we predicted that species occurring both in the tropics and at higher latitude, i.e. species

**Table 1.** Results of different SSE models show that both dark skin and polymorphic skin colour promote net diversification. We ran two sets of analyses, once on the full Jetz *et al.* [20] and once on the genes only tree.

	LnI	AICc		LnI	AICc
<b>dark skin (<i>n</i> = 2995) full tree</b>			<b>dark skin (<i>n</i> = 2319) genes only tree</b>		
null	−12251.08	24510.18	null	−9676.818	19361.65
BiSSE	−11769.95	23549.92	BiSSE	−9166.562	18343.15
HiSSE	<b>−11391.87</b>	<b>22803.82</b>	HiSSE	−9092.124	18204.34
CID2	−11817.51	23647.05	CID2	−9258.008	18528.05
CID4	−11627.39	23270.84	CID4	<b>−9062.651</b>	<b>18141.36</b>
<b>polymorphism (<i>n</i> = 2010) full tree</b>			<b>polymorphism (<i>n</i> = 1584) genes only tree</b>		
null	−8308.702	16625.42	null	−6631.889	13271.8
BiSSE	−7836.276	15682.58	BiSSE	−6212.01	12434.06
HiSSE	<b>−7797.93</b>	<b>15615.97</b>	HiSSE	<b>−6095.232</b>	<b>12210.6</b>
CID2	−7998.589	16009.22	CID2	−6347.981	12708.01
CID4	−7866.933	15749.94	CID4	−6220.085	12456.26

with larger latitudinal ranges, are more likely to be polymorphic. To test this hypothesis, we used species' latitudinal ranges, collected from distribution data [27]. Since ranges are smaller in tropical species [28], we used the mean breeding latitude as a co-variable. We used a phylogenetically controlled logistic regression implemented in the R package *phylolm* [29] to investigate the relationship between the presence of polymorphism and the latitudinal range of a species as well as the average breeding latitudes. To test whether the number of samples might influence the detection of polymorphisms we used a phylogenetically controlled logistic regression to test for a correlation between polymorphism and the number of samples.

### (e) Global distribution of dark-skinned species

To illustrate the distribution of dark skin we imported bird distribution data [27] using 'sf' [30] and made a SpatialPolygons-DataFrame of all dark-skinned bird species samples, as well as one containing only polymorphic species. Using 'lets.presab' [31], we then estimated for each dataset which species are found in which grids using distributions from resident and breeding species. This resulted in two maps: one showing the distribution of all black skinned species and another showing the distribution of all polymorphic species. Colour intensity corresponds to the number of species.

## 3. Results

Of the 3033 species investigated, we found dark skin in 660 species (compared to the 141 previously reported) from 21 novel families (86 in total), of which 229 species were polymorphic (electronic supplementary material, file S1–S3; figure S1). We found that polymorphism was influenced by the number of samples per species ( $p$ -value < 0.05) suggesting that the number of polymorphic (and dark skinned birds) might be an underestimation. Evolutionary models showed that the ARD model best explains the evolution of dark skin (electronic supplementary material, table S1). Furthermore, most of the changes occur between dark and polymorphic, suggesting that polymorphism is not necessarily a required evolutionary intermediate (electronic supplementary material, table S2). Our SSE-models showed that both dark skin and

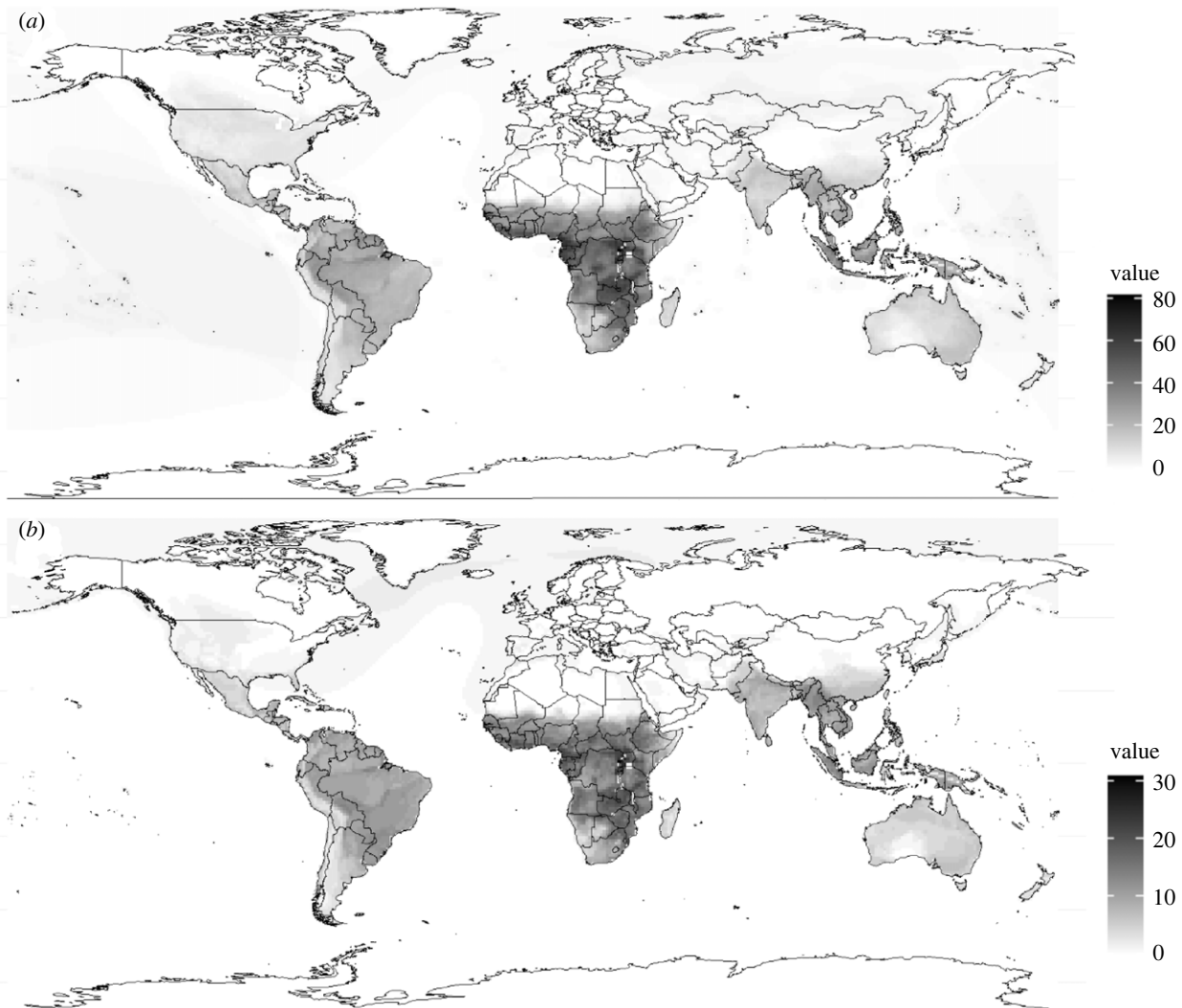
the polymorphisms promotes net diversification. However, for dark skin this was only true for the full tree and not the genes-only tree. As such, these results have to be interpreted with care if not ignored. Furthermore, given that the best model is the HiSSE model, other factors are involved as well (table 1). This is expected, as the evolution of diverse clades, such as birds, are affected by multiple factors (e.g. nest type [2]).

Furthermore, polymorphism in skin colour seems to largely track the distribution of dark skin in general (figure 1 *a,b*), although larger proportions of species are polymorphic in oceanic and/or marine-adjacent regions. Nonetheless, colour polymorphism and distribution range (table 2) are significantly negatively related, i.e. polymorphic species tend to have small distribution ranges.

## 4. Discussion

Of the 660 black skinned species, some families have only one dark skinned specimen (e.g. Strigopidae, generally not having dark skin), one dark skinned species (Pelecanidae, *Pelecanus rufescens*), many new families have multiple dark skinned species (Cacatuidae, Psittacidae, Psittaculidae but also Meropidae and Zosteropidae). Other families have steep increases in the number of dark skinned species (e.g. Icteridae, from 1 to 44 dark skinned species), likely the result of re-sampling species-rich but genus-poor families. These results show that at least 7% (*sensu* [9]), but potentially up to 22% (this study), of bird species have dark skin.

We found that dark skin, together with an unknown trait, increases net diversification but only when using the full tree and not the genes-only tree. When the genes-only tree was used, HiSSE produced the second-best model, with CID-4 being the best model. This might be because the sample size reduction influences the diversification analyses, or because the full tree introduces false signals because it introduces unrealistic tips and branch lengths. It is unclear whether this is a true signal since the sample size reduction between the two trees used was not proportional between dark-skinned and light-dark skinned species, as all species



**Figure 1.** (a) The distribution of the number of species with dark skin across the globe. (b) The distribution of the number of species with skin polymorphism across the globe.

**Table 2.** The results of the phylogenetically controlled logistic regression between skin polymorphism and range size + average breeding latitude. Results are shown for an MCC tree, as well as run on 100 random trees.

estimates over (100 simulations)	range size	average breeding latitude
mean estimate	-0.0182	-0.0172
range estimate	-0.026, $-9 \times 10^{-04}$	-0.0355, 0.0239
estimate MCC	-0.0194197	0.263901
mean <i>p</i> -value	0.0189	0.0199
range <i>p</i> -value	0, 0.7213	0, 0.2057
<i>p</i> -value MCC	0	0
median <i>p</i> -value	0.0003	0.0047
number of	6	10
<i>p</i> -values > 0.05		

removed from the tree were light-skinned. Furthermore, HiSSE still produces the second-best model. Future trees that have an even higher number of species with more genetic information could solve this outstanding question. In the case that the

observed pattern observed in the full tree is true, then this might occur through increased speciation (e.g. when white feathers are involved in sexual selection, or in camouflage), or decreased extinction (e.g. through the protective abilities of melanin). More than 65% of white-crowned birds investigated have dark skin, suggesting that dark skin co-evolves with the white feathers that are often used in sexual display (electronic supplementary material, file S1) [9]. Allocating resources toward elaboration of sexual ornamentation might compromise an organism's ability to track environmental changes [32]. While unexposed and therefore not usually visible, dark skin may influence diversification through the relaxation of other selective pressures allowing the evolution of ornamentation while also tracking environmental changes. Indeed, the evolution of dark skin allows birds to evolve novel plumage that normally would render them vulnerable to UV damage. However, this explanation relies on dark skin evolving prior to, or (on an evolutionary timescale) almost simultaneously, the evolution of white feathers, a prediction that can be tested in future studies.

In addition to dark skin, the presence of both dark and light skin within a species (i.e. polymorphism) promotes net diversification, although other traits are likely involved as well. How does polymorphism influence net diversification? In a few cases (e.g. *Xanthocephalus xanthocephalus*), polymorphism

is explained by sexual dichromatism of head feathers, where females have dark and males have lighter feathers resulting in light and dark skin colour, respectively. This is unlikely the result of sexual selection on skin colour as the skin is not visible (except in for example tragopans), but rather follows the general pattern of lighter feathers resulting in darker skin. In others (e.g. *Threskiornis molucca*) specimens with feathers have non-dark skin, while naked specimens have dark skin. Similarly, in other cases polymorphisms are linked to distinct subspecies that differ in plumage and/or occurrence (e.g. *Columbia livia targia*, which has a lighter head and occurs in the Central Sahara) although this is not generally the case. Furthermore, polymorphism itself might be a result of the ability of a species to change skin colour (i.e. labile skin colour) as a function of time and place and across distributions that might be heterogeneous in UV radiation. Indeed, the benefits of melanin in UV rich regions are clear, but in regions with little UV radiation melanin might come at a (metabolic) cost [33]. These differences in time and space might be sufficient to cause speciation. Furthermore, variation promotes net diversification, and species with skin colour polymorphism are more variable than monomorphic species.

Polymorphism is (significantly) more common in species with small breeding ranges (table 2). We speculate that increased net diversification rates and smaller range sizes of polymorphic species are because these species recently diverged. In this case, they might differ in feather, and thus skin colour, but because of their recent divergence may not have yet fixed one skin colour. Dark-skinned birds are generally found at lower latitudes and polymorphism seems to follow this pattern, although this effect was not consistent throughout the analyses (table 2). Proportionally, there are many polymorphic species at higher latitudes, a pattern with two potential explanations. First, these species are generally oceanic species that migrate long distances and thus experience fluctuating UV conditions. Similarly, higher latitudes experience a wide range of environmental conditions throughout the year, potentially promoting polymorphism.

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A potential caveat is that the probability of finding polymorphisms is related to the number of specimens sampled. Since dark skin is also temporarily present in multiple species during moult (e.g. jays [9]) it is possible that the polymorphisms observed are caused by sampling of birds during different stages of moult (although we did not see any indication that any of the specimens were moulting crown feathers). Future research could focus on whether specific moulting strategies are related to polymorphism. In addition, the presence of dark skin in juveniles, while known, has not been studied thoroughly and remains an interesting avenue for future research [9]. Regardless, the evolution of differences in concealed skin colour remains intriguing, as they show that even hidden traits can influence large scale evolutionary events such as diversification in birds. This effect is likely indirect through the relaxation of constraints placed by natural selection on sexual selection, allowing the evolution of ornamentation while also tracking environmental changes.

**Ethics.** No ethic statement is required. No live animals were used.

**Data accessibility.** Scripts can be found at <https://doi.org/10.5061/dryad.8pk0p2ntc> [34].

Supplementary material is available online [35].

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors' contributions.** M.P.J.N.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; R.V.: conceptualization, data curation, investigation, writing—review and editing; M.D.S.: conceptualization, funding acquisition, methodology, writing—original draft, writing—review and editing; L.D.: conceptualization, data curation, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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