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Habitat-driven diversification, hybridization and cryptic diversity in the Fork-tailed Drongo (Passeriformes: Dicruridae: *Dicrurus adsimilis*)

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Species complexes of widespread African vertebrates that include taxa distributed across different habitats are poorly understood in terms of their phylogenetic relationships, levels of genetic differentiation and diversification dynamics. The Fork-tailed Drongo (*Dicrurus adsimilis*) species complex includes seven Afrotropical taxa with parapatric distributions, each inhabiting a particular bioregion. Various taxonomic hypotheses concerning the species limits of the Fork-tailed Drongo have been suggested, based largely on mantle and upperpart coloration, but our understanding of diversity and diversification patterns remains incomplete. Especially given our lack of knowledge about how well these characters reflect taxonomy in a morphologically conservative group. Using a thorough sampling across Afrotropical bioregions, we suggest that the number of recognized species within the *D. adsimilis* superspecies complex has likely been underestimated and that mantle and upperpart coloration reflects local adaptation to different habitat structure, rather than phylogenetic relationships. Our results are consistent with recent phylogeographic studies of sub-Saharan African vertebrates, indicating that widespread and often morphologically uniform species comprise several paraphyletic lineages, often with one or more of the lineages being closely related to phenotypically distinct forms inhabiting a different, yet geographically close, biome.

1 | INTRODUCTION

Diversification patterns of widespread African vertebrates remain poorly understood. A growing body of literature has focused either on the patterns of genetic variation within species that are restricted to a particular region or habitat (e.g., lowland Forest: Bell et al., 2017; Fuchs & Bowie, 2015; Huntley & Voelker, 2016; Marks, 2010; Portik et al., 2017;

TABLE 1 Taxonomic history within the *Dicrurus adsimilis* superspecies among primary classification schemes. We listed species and their subspecies (between parentheses). The number of subspecies within *D. macrocercus* has been constant through time and their range (Indo-Malaya) is not part of the present study. *[1] Vaurie considered the subspecies *fugax* to be a synonym of *adsimilis* sensu stricto. *[2] the subspecies *apivorus* was described by Clancey in 1976 (Vaurie, 1949, could not distinguish it from *adsimilis* sensu stricto and *fugax*)

Vaurie (1949)	Pearson (2000)	Rocamora and Yeatman-Berthelot (2009)	Dickinson and Christidis (2014), Gill and Donsker (2016)
macrocercus (seven subspecies)	(not treated)	*macrocercus* (seven subspecies)	*macrocercus* (seven subspecies)
waldenii	*waldenii*	*waldenii*	*waldenii*
fuscipennis	*fuscipennis*	*fuscipennis*	*fuscipennis*
forficatus (*forficatus*, *potior*)	*forficatus* (*forficatus*, *potior*)	*forficatus* (*forficatus*, *potior*)	*forficatus* (*forficatus*, *potior*)
aldabranus	*aldabranus*	*aldabranus*	*aldabranus*
adsimilis (*divaricatus*, *coracinus*, *modestus*, *adsimilis**[1], *atactus*)	*adsimilis* (*divaricatus*, *fugax*, *apivorus**[2], *adsimilis*)	*adsimilis* (*divaricatus*, *fugax*, *apivorus**[2], *adsimilis*)	*adsimilis* (*divaricatus*, *fugax*, *apivorus**[2], *adsimilis*)
	modestus (*atactus*, *coracinus*, *modestus*)	*modestus* (*atactus*, *coracinus*, *modestus*)	*modestus* (*atactus*, *coracinus*, *modestus*)

Voelker et al., 2013; Eastern Arc Mountains: Bowie, Fjeldså, Hackett, & Crowe, 2004b; Bowie, Fjeldså, Hackett, Bates, & Crowe, 2006; Bowie, Pasquet, McEntee, Njilima, & Fjeldså, 2018; Ceccarelli et al., 2014; Fuchs, Fjeldså, & Bowie, 2011; Southern Africa: Oatley, Voelker, Crowe, & Bowie, 2012; Ribeiro, Lloyd, & Bowie, 2011; Ribeiro, Lloyd, Dean, Brown, & Bowie, 2014; Sithaldeen, Ackermann, & Bishop, 2015; da Silva & Tolley, 2017) or on species-level phylogenies that have employed limited intraspecific species sampling (e.g., *Cercomela*: Outlaw, Voelker, & Bowie, 2009; *Mymecocichla* Voelker, Bowie, Wilson, & Anderson, 2012). In contrast, the phylogenetic relationships, levels of genetic differentiation and diversification dynamics of superspecies complexes that are distributed across different life zones have been less well-studied (Barlow et al., 2013; Fuchs, Crowe, & Bowie, 2011; Fuchs, Fjeldså, & Bowie, 2017; Fuchs, Pons, & Bowie, 2017; Furman et al., 2015; Moodley & Bruford, 2007).

Recent studies on African passerine birds have repeatedly demonstrated that traditional taxonomy is misleading with respect to the evolutionary history of many taxa, especially those distributed across the savannah belt (Fuchs, Crowe, et al., 2011; Fuchs, Fjeldså, et al., 2017). For example, the Southern Fiscal *Lanius collaris* (arid zone of southern Africa) is more closely related to Souza's Shrike *L. souzae* (Miombo woodlands) than to the Northern Fiscal *L. humeralis* (arid zones of central, eastern and western Africa), with which it was traditionally considered conspecific (Fuchs, Crowe, et al., 2011). Similarly, the West African populations of Square-tailed Drongo *Dicrurus ludwigii* (dense secondary and gallery forests) are more closely related to the Shiny Drongo *D. atripennis* (lowland rainforest) than to the eastern and southern populations of *D. ludwigii* (Fuchs, Fjeldså, et al., 2017). Although these studies mostly agree that the species biogeography is more complex than previously thought, several uncertainties remain regarding the exact location of

genetic breaks in many taxa (e.g., S Tanzania; *Lanius;* N Tanzania, *D. ludwigii*). Furthermore, the two studies identified above reached very different conclusions with respect to the differentiation of populations in the northern Savannah belt, with one finding very limited genetic differentiation (*Lanius*, Fuchs, Crowe, et al., 2011) and the other finding substantial differentiation across the Niger River (*D. ludwigii*, Fuchs, Fjeldså, et al., 2017), a barrier also recovered for lowland evergreen forest species (*Campethera caroli* and *C. nivosa* Fuchs & Bowie, 2015).

The drongos (Dicruridae) are a family of corvoid birds distributed across Africa, southern Asia, the Indian Ocean islands and Australasia, as well as numerous oceanic islands throughout this region (Rocamora & Yeatman-Berthelot, 2009). Approximately 25 species are recognized (Gill & Donsker, 2016), and overall, the group is notable for their limited variation in plumage coloration, although tail shapes are quite variable. The *Dicrurus adsimilis* superspecies sensu Vaurie (1949) consists of six species: (i) *D. macrocercus* with seven subspecies distributed across Indo-Malaya, (ii) *D. adsimilis* with five subspecies distributed across the Afrotropics as well as four taxa distributed across the Indian Ocean Islands constituted by the Comoros archipelago, (iii) *D. waldenii* on Mayotte, (iv) *D. fuscipennis* on Grande Comore, (v) *D. aldabranus* on Aldabra Atoll, and (vi) *D. forficatus forficatus* on Madagascar and *D. f. potior* on Anjouan. The species limits of the Indo-Malayan and Indian Ocean taxa are well established, and the colonization history and phylogeography of the Indian Ocean taxa have already been described (Fuchs et al., 2013; Pasquet, Pons, Fuchs, Cruaud, & Bretagnolle, 2007). In contrast, the relationships and taxonomic status of the Afrotropical subspecies have remained problematic for nearly 70 years.

Vaurie (1949) recognized five subspecies within *D. adsimilis*, merging all Afrotropical taxa into a single species. In contrast, most subsequent authors have recognized a

species-level distinction between taxa distributed in the tropical lowland forests (*D. modestus atactus* in the Upper Guinea Forest Block extending to western Nigeria, *D. m. coracinus* in the Lower Guinea Forest Block and *D. m. modestus* on Príncipe Island) from those taxa distributed across more open habitats spanning the savannah belt (*D. adsimilis adsimilis* in Southern/Eastern Africa, and *D. a. divaricatus* distributed from Senegal in the west extending to Somalia in the east, Dickinson & Christidis, 2014; Gill & Donsker, 2016; Pearson, 2000; Table 1). Furthermore, most authors since Vaurie (1949) have recognized the validity of the subspecies *D. a. fugax* (coastal Eastern Africa extending from Mozambique to southern Somalia). Finally, the distinctiveness of the drongo populations distributed in Angola, southern DR Congo, Zambia, Namibia, Botswana and northern South Africa was recognized in 1976 with the description of *D. a. apivorus* (Clancey, 1976).

The first molecular phylogeny of the Dicruridae confirmed the monophyly of the *Dicrurus adsimilis* superspecies as well as the close phylogenetic relationships between all taxa distributed across Indian Ocean islands with the exception of *D. fuscipennis*, which was more divergent (Pasquet et al., 2007). Pasquet et al. (2007) sampled two taxa from the Afrotropics, *D. a. fugax* (Tanzania) and *D. m. modestus* (Príncipe Island), and found the two taxa to not be sister species, with "*D. macrocercus*" found as sister to *D. a. fugax*. This would suggest that the two Afrotropical taxa may warrant species status. However, during the course of the present study, we discovered that a sample mix up occurred during tissue subsampling of "*D. macrocercus*" (FMNH 347969), which was determined to actually be *D. leucophaeus* (J. Fuchs, unpubl. data); the individual included in Pasquet et al. (2007) is actually *D. a. adsimilis* (FMNH 390192) (D. Willard, FMNH, in litt). This has two primary consequences: (i) *Dicrurus macrocercus* was not sampled by Pasquet et al. (2007); and (ii) the monophyly of *D. adsimilis–D. modestus* complex could not be rejected, despite the lack of strong support for this relationship.

More recently, Fuchs, Fjeldså, et al. (2017) reconstructed the biogeographic history of the Square-tailed (*D. ludwigii*) and Shiny (*D. atripennis*) Drongos and sampled several Afrotropical taxa of the *D. adsimilis* superspecies. Neither *D. adsimilis* nor *D. modestus* were recovered as monophyletic; *D. a. divaricatus* was recovered as the sister group of *D. modestus atactus* in both the mitochondrial topology and multilocus species tree, whereas *D. a. fugax* and *D. a. adsimilis* were sister taxa. The relationships of *D. macrocercus*, *D. forficatus* and *D. m. modestus* with respect to the *D. a. divaricatus/D. m. atactus* and *D. a. fugax/D. a. adsimilis* clades were unresolved (Fuchs, Fjeldså, et al., 2017). At first glance, this would suggest a similar pattern to the *D. ludwigii–D. atripennis* clade with a major biogeographic break between Central/West and East/South Africa and a shift in

habitat preference in the Central/West clade. However, further conclusions were not possible because several crucial Afrotropical taxa from the *D. adsimilis* superspecies complex (e.g., *D. a. apivorus*, *D. m. coracinus*) were not sampled.

Here, using a thorough sampling of the Afrotropical taxa from the *D. adsimilis* superspecies complex, we sought to resolve the biogeography and taxonomy of the African taxa and to understand in greater detail the species limits and evolution of habitat preferences among the different African lineages. Based on our results, we propose a new classification for the *D. adsimilis* superspecies complex.
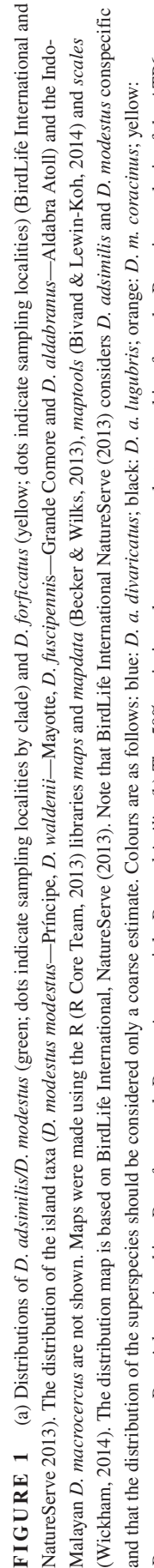
2 | MATERIAL AND METHODS

2.1 | Sampling

We included representative sampling of species level diversity in the Dicruridae (Pasquet et al., 2007) in order to test the monophyly of the *Dicrurus adsimilis* superspecies and to compare the degree of genetic divergence among lineages within this superspecies to that of traditionally recognized species. We included individuals from all recognized African subspecies comprising the *Dicrurus adsimilis* superspecies, and our sampling encompassed most of their African distributional ranges ($n = 103$: Figure 1a and Table S1). We included 31 individuals of the Crested Drongo (*Dicrurus forficatus*), endemic to Madagascar, and for which a previous study (Fuchs et al., 2013) recovered considerable within species allelic and nucleotide diversity at some nuclear loci (e.g., Myoglobin intron-2). These diverse alleles may be present in other members of the *D. adsimilis* superspecies and, if so, could provide useful insight about the diversification processes on the African continent. Phylogenetic trees were rooted with representatives of the Corvidae (*Corvus corone*) and Laniidae (*Lanius collaris*).

2.2 | Laboratory protocols

We extracted DNA from tissue, toe pads or blood using the Qiagen extraction kit (Qiagen, Valencia, CA) following the manufacturer's protocol, and sequenced one mitochondrial protein-coding gene (ATP synthase subunit 6, ATP6), three nuclear introns (myoglobin intron-2, MB; beta fibrinogen intron-5, FGB; transforming growth factor beta-2 intron-5, TGFb2) and one Z-linked intron (Brahma protein intron-15, BRM). Primers and PCR protocols for the fresh samples were identical to those reported in Fuchs, Fjeldså, et al. (2017). We obtained mitochondrial sequences from historical specimens (toe-pad samples) by performing several overlapping PCR amplifications (size 200–350 bp) using specific primers designed in this study (available from author upon request). The PCR-amplification protocol included an initial denaturation at 94°C for 3 min, followed by 35 cycles at 94°C for 30 s,

FIGURE 1 (a) Distributions of *D. adsimilis/D. modestus* (green; dots indicate sampling localities by clade) (yellow; dots indicate sampling localities) (BirdLife International and NatureServe 2013). The distribution of the island taxa (*D. modestus modestus*—Príncipe, *D. waldenii*—Mayotte, *D. fuscipennis*—Grande Comore and *D. aldabranus*—Aldabra Atoll) and the Indo-Malayan *D. macrocercus* are not shown. Maps were made using the **R** (R Core Team, 2013) libraries *maps* and *mapdata* (Becker & Wilks, 2013), *maptools* (Bivand & Lewin-Koh, 2014) and *scales* (Wickham, 2014). The distribution map is based on BirdLife International, NatureServe (2013). Note that BirdLife International NatureServe (2013) considers *D. adsimilis* and *D. modestus* conspecific and that the distribution of the superspecies should be considered only a coarse estimate. Colours are as follows: blue: *D. a. divaricatus*; black: *D. a. lugubris*; orange: *D. m. coracinus*; yellow: *D. m. atactus*; green: *D. a. jubaensis*; white: *D. a. fugax*; red: *D. a. apivorus*; pink: *D. a. adsimilis*. (b) The 50% majority rule consensus rule tree resulting from the Bayesian analysis of the ATP6 gene (only unique haplotypes are included). Numbers close to nodes refer to posterior probabilities >.95

54–60°C for 30 s, and 72°C for 30 s, and was terminated by a final elongation step at 72°C for 15 min.

Individuals were sexed by PCR using the primer pair 2550F and 2718R under standard PCR-amplification conditions (Fridolfsson & Ellegren, 1999). Newly generated sequences have been deposited in Genbank (Accession Number MG762217-MG762565).

2.3 | Phasing of nuclear alleles and testing for selection and recombination

We used PHASE v2.1.1 (Stephens, Smith, & Donnelly, 2001), as implemented in DNASP 5.0 (Librado & Rozas, 2009), to infer the alleles for each nuclear locus. Three runs were performed, and results were compared across runs. Using the recombination model, we ran the iterations of the final run 10 times longer than for the initial runs. We considered the output of the long final PHASE run as the best estimate of haplotypes. The McDonald–Kreitman test (MK; McDonald & Kreitman, 1991) in DNASP 5.0 (Librado & Rozas, 2009) was used to test for evidence of selection acting on ATP6. Significance was assessed using Fischer's exact test and a threshold of 0.05. We performed four MK tests on the *D. adsimilis* superspecies clade using sequences from four different proximate outgroups (*D. leucophaeus*, *D. bracteatus*, *D. ludwigii ludwigii* and *D. aeneus*). We tested for selection acting on the nuclear loci using the Hudson–Kreitman–Aguadé test (HKA; Hudson, Kreitman, & Aguadé, 1987), as implemented in the software HKA (https://bio.cst.temple.edu/~hey/software/software.htm). Sequences from *D. leucophaeus* were used as the outgroup.

We tested for evidence of recombination within each nuclear locus using the GARD (genetic algorithm for recombination detection) and SBP (single breakpoint) algorithms (Kosakovsky Pond, Frost, & Muse, 2005; Kosakovsky Pond, Posada, Gravenor, Woelk, & Frost, 2006) as implemented on the DATAMONKEY webserver (www.datamonkey.org; Delport, Poon, Frost, & Kosakovsky-Pond, 2010).

2.4 | Phylogenetic reconstruction

Gene tree reconstructions of unique haplotypes and alleles were performed using Bayesian inference (BI), as implemented in MRBAYES 3.2 (Ronquist et al., 2012). We used the *nst=mixed* and *rates=invgamma* options such that model uncertainty is taken into account during the phylogenetic reconstruction. Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 5×10^6 iterations, with trees sampled every 10^3 iterations.

Species trees were reconstructed using the coalescent-based model implemented in *BEAST (Heled & Drummond, 2010) on four data sets: mitochondrial, autosomal, nuclear (autosomal and Z-linked) and mitochondrial/nuclear. The species tree algorithm in *BEAST requires at least one

sequence per "species" per locus be present in the data set; nuclear data were not obtained from lineages where DNA was extracted from museum toe-pad tissues: *D. fuscipennis*, *D. modestus coracinus* (see Results about the level of differentiation from *D. modestus modestus*) and the eastern portion of the range of *D. adsimilis divaricatus* (see Results), or FGB for *D. aldabranus*; hence, these taxa could not be included in analyses involving nuclear data. We selected the substitution model for each locus using TOPALI (Milne et al., 2009) under the Bayesian information criterion. Each locus had its own substitution rate matrix and clock model (all assigned to a strict clock model). We used a Yule process for the tree prior with a normal prior distribution for the ATP6 (0.026 substitutions/site/lineage/million year -s/s/l/myr-; 95% HPD: 0.021–0.031 s/s/l/myr) and TGFb2 (0.0017 s/s/l/myr; 95% HPD: 0.0013–0.0022 s/s/l/myr) rates, corresponding to those obtained by Lerner, Meyer, James, Hofreiter, and Fleischer (2011). Substitution rates for the other nuclear loci were estimated in relation to the Lerner et al. (2011) rates for ATP6 and TGFb2. We conducted two runs for 5×10^8 iterations, with trees and parameters sampled every 5×10^3 iterations, discarded the first 25×10^6 iterations as the burn-in period. We used the CIPRES 3.1 gateway server (www.cipres.org; Miller, Pfeiffer, & Schwartz, 2010) to run MRBAYES 3.2 (Ronquist et al., 2012) and the *BEAST analyses.

TRACER v1.6 (Rambaut & Drummond, 2009) was used to ensure that our effective sample size for all Bayesian analyses of the underlying posterior distribution was large enough (>200) for meaningful estimation of parameters.

2.5 | Network analyses

Multilocus networks were reconstructed using POFAD v1.03 (Joly & Bruneau, 2006) and SPLITSTREE v4.0 (Huson & Bryant, 2006). We included only individuals from the *D. adsimilis* superspecies for which sequences from all five loci were available ($n = 93$), along with *D. leucophaeus*, the closest relative of the *D. adsimilis* superspecies. We used uncorrected *p*-distances as input for POFAD and made use of the standardized matrix for network reconstruction.

2.6 | Estimating divergence times

We estimated divergence times using BEAST 1.8 (Drummond, Suchard, Xie, & Rambaut, 2012). We performed analyses using the HKY + G model with either the strict or uncorrelated lognormal molecular clock models enforced with a Yule tree prior. MCMC chains were run for 25 to 50×10^6 steps and were sampled every 10^3 steps. We used two substitution rates and their associated uncertainties to calibrate the trees. The first one corresponds to the ATP6 substitution rate (0.026 s/s/l/myr; 95% HPD: 0.021–0.031 s/s/l/myr), that is derived from complete mtDNA genomes of the

honeycreepers (Passeriformes, Drepanididae) and calibration points based on the age of volcanic islands in the Hawaiian archipelago (Lerner et al., 2011). The second substitution rate was obtained by Subramanian et al. (2009) based on fourfold degenerated sites from complete mtDNA sequences of Adelie Penguins (*Pygoscelis adeliae*) to be 0.073 (95% HPD: 0.025–0.123 s/s/l/myr); this is a mutation rate and hence theoretically independent of variation in body size or other life history traits.

We also used a body mass-corrected mitochondrial clock recently proposed by Nabholz, Lanfear, and Fuchs (2016). We employed the equation $10^{(-0.145 \times \log_{10} (\text{body\_mass}) + 0.459)}/100$, corresponding to their calibration set 2, to calculate the body mass-corrected substitution rate for the ATP6 third codon position. We assumed an average body mass across drongos of 40 g. We used the mitochondrial topology (Figure 1b) to estimate the third codon position branch lengths using PAML v4.9 (Yang, 2007). The branch lengths were then converted to divergence times in R using scripts from Nabholz et al. (2016).

We used TRACER v1.6 (Rambaut & Drummond, 2009) to help ensure that the effective sample size of the underlying posterior distribution was large enough (>200) for meaningful estimation of parameters.

2.7 | Molecular species delimitation methods

To delimit putative species, we used a Bayesian implementation of the general mixed Yule-coalescent model (bGMYC 1.0; Reid & Carstens, 2012) with our molecular data. This implementation is an extension of the generalized mixed Yule-coalescent (GMYC) model (Pons et al., 2006) that incorporates gene tree uncertainty by sampling over trees randomly selected from the posterior distribution We obtained a posterior distribution of ultrametric gene trees of the unique *D. atripennis*–*D. ludwigii* mitochondrial haplotypes using BEAST v1.8 (Drummond et al., 2012) under a strict clock model (0.026 s/s/l/myr, $SD = 0.0025$). We ran MCMC for 10^7 iterations, sampling parameters and trees every 10^3 iterations, and we removed the first 10% of the samples as the burn-in period. We analysed 100 trees sampled randomly from the posterior distribution and used the default setting in bGMYC. We ran the MCMC chains for 5×10^4 iterations, with a burn-in of 4×10^4 iterations, and sampled parameters every one-hundred iterations.

For an alternative approach to the bGMYC species delimitation method, we also used the newly developed multirate Poisson tree processes as implemented in mPTP (Kapli et al., 2017) using both the maximum-likelihood and Markov chain Monte Carlo algorithms (number of iterations: 50×10^4; burn-in: 10×10^4). We performed the analyses using both the single and multiple rates options with the minimum branch length being detected from the data

set. As an input topology, we used a maximum-likelihood tree of the unique ATP6 haplotypes rooted with *Corvus corone* and reconstructed using RAXML (RAxML black box, http://embnet.vital-it.ch/raxml-bb/, Stamatakis, Hoover, & Rougemont, 2008) and a GTR + G model.

Finally, we also used the software BPPv3.1 (Rannala & Yang, 2003; Yang, 2015; Yang & Rannala, 2010) to estimate the joint probability of the species tree and the speciation probability (model A11, Yang & Rannala, 2014). A speciation probability of 1.0 on a node indicates that every species delimitation model visited by the rjMCMC algorithm supports the hypothesis that the two lineages descending from a particular node represent distinct populations (putative species); speciation probability values >.95 were considered to indicate a putative speciation event. We used a gamma prior on the population size parameters (θ) and the age of the root in the species tree (τ_0), and we parameterized other divergence time parameters using a Dirichlet prior (Yang & Rannala, 2010). We used the same data set as for the *BEAST analyses of the mitochondrial/ nuclear analyses (i.e., we did not include *D. aldabranus*, *D. fuscipennis* or *D. a. divaricatus* East of Lake Chad due to the lack of nuclear DNA data). We restricted the analyses to eleven taxa—the nine lineages within the *D. adsimilis* superspecies, and two outgroup species (*D. aeneus* and *D. leucophaeus*). We evaluated the influence of the priors on the posterior probability distribution by changing the priors for θ and τ_0, assuming either small or large ancestral population sizes with G set to (2, 2000) and (1, 10), respectively, and shallow or deep divergence with G set to (2, 2000) and (1, 10), respectively. We allowed the loci to have different rates (locus rate = 1, Dirichlet distribution) and took into account the differences in heredity scalar (heredity = 2). We ran the rjMCMC analyses for 4×10^5 generations with a burn-in period of 4×10^4 and different starting seeds. Each analysis was run twice.

3 | RESULTS

3.1 | Mitochondrial DNA

We analysed the complete ATP6 sequence (684 bp) for 154 *Dicrurus* individuals representing all described African taxa; partial sequences were obtained for two further individuals. Among the 142 individuals from the *D. adsimilis* superspecies complex, 104 haplotypes were detected with very limited sharing of haplotypes among taxa, except for the subspecies *adsimilis* and *fugax*. The McDonald–Kreitman test did not detect any evidence of selection (Fisher's exact test; *D. aeneus* $p = .39$, *D. bracteatus* $p = 1.0$, *D. leucophaeus*: $p = .22$, *D. ludwigii ludwigii* $p = .23$). The Bayesian 50% majority rule consensus tree recovered the monophyly of the *D. adsimilis* superspecies complex (PP: 1.0), with the Ashy

Drongo (*D. leucophaeus*) being the most closely related taxon (PP: .95; Figure 1b). Six primary lineages emerged within the *D. adsimilis* superspecies: (i) the Indo-Malayan *D. macrocercus*; (ii) the clade West of Lake Chad comprising *D. m. atactus* and *D. a. divaricatus* (PP: 1.0); (iii) the clade East of Lake Chad consisting of *D. a. divaricatus* (PP: 1.0); (iv) the *D. m. modestus–D. m. coracinus* clade (PP: 1.0); (v) the clade consisting of the four Indian Ocean taxa (*D. fuscipennis*, *D. aldabranus*, *D. forficatus*, *D waldenii*: PP: 0.57); and (vi) a clade consisting of the subspecies *D. a. apivorus–D. a. adsimilis–D. a. fugax* (PP: 1.0; Figure 1b).

The mitochondrial topology suggests that geographic proximity is a better predictor of lineage relationships within the *D. adsimilis* superspecies complex than current taxonomy, especially given that two species (*D. adsimilis* and *D. modestus*) were not recovered as monophyletic in our topology (Figure 1b). The lineages were sorted geographically with the exception of three individuals. UWBM 53209 and UWBM 70422, both collected in Melmoth (Kwazulu-Natal, South Africa), nested within the *fugax* and the *adsimilis* clades, respectively. The third individual (MNHN CG 1968-365), collected in Katanga (DR Congo), was related to three individuals collected in Ethiopia and Somalia. The average number of nucleotide substitutions per site between populations (Dxy) was as follows: *D. m. atactus–D. a. divaricatus* W Lake Chad: 0.02595; *D. a. apivorus/(a. adsimilis–a. fugax)*: 0.03820; *D. a. adsimilis/a. fugax*: 0.01948; and *D. m. modestus/m. coracinus*: 0.01243.

3.2 | Nuclear DNA

We did not detect any evidence of recombination in the four nuclear introns using the GARD and SBP algorithms or any indication of selection using the HKA test ($p = .65$). Five individuals (*D. aldabranus*, *D. paradiseus* and *D. adsimilis fugax* MOM 2007.2.345, FMNH 447943, ZMUC 140641) could not be sexed and were considered as females in the analyses.

Nuclear data were obtained from the 110 individuals where DNA was extracted from buffered or frozen tissues; the only exception was *D. aldabranus*, for which we could not obtain the FGB sequence. The 50% majority rule consensus trees resulting from the analyses of individual introns (FGB: 93 alleles, 563 bp; MB: 94 alleles, 817 bp; TGFb2: 92 alleles, 584 bp; BRM: 41 alleles, 363 bp) were very similar in that (i) alleles were widely shared among taxa from the *D. adsimilis* superspecies complex, and (ii) the relationships among the Dicruridae alleles formed a large polytomy (Figures S1–S4).

3.3 | Species tree analyses and multilocus network

With the exception of one lineage (see below), the species tree analyses were congruent with the mitochondrial results, although relationships among members of the *Dicrurus adsimilis* superspecies were poorly supported.

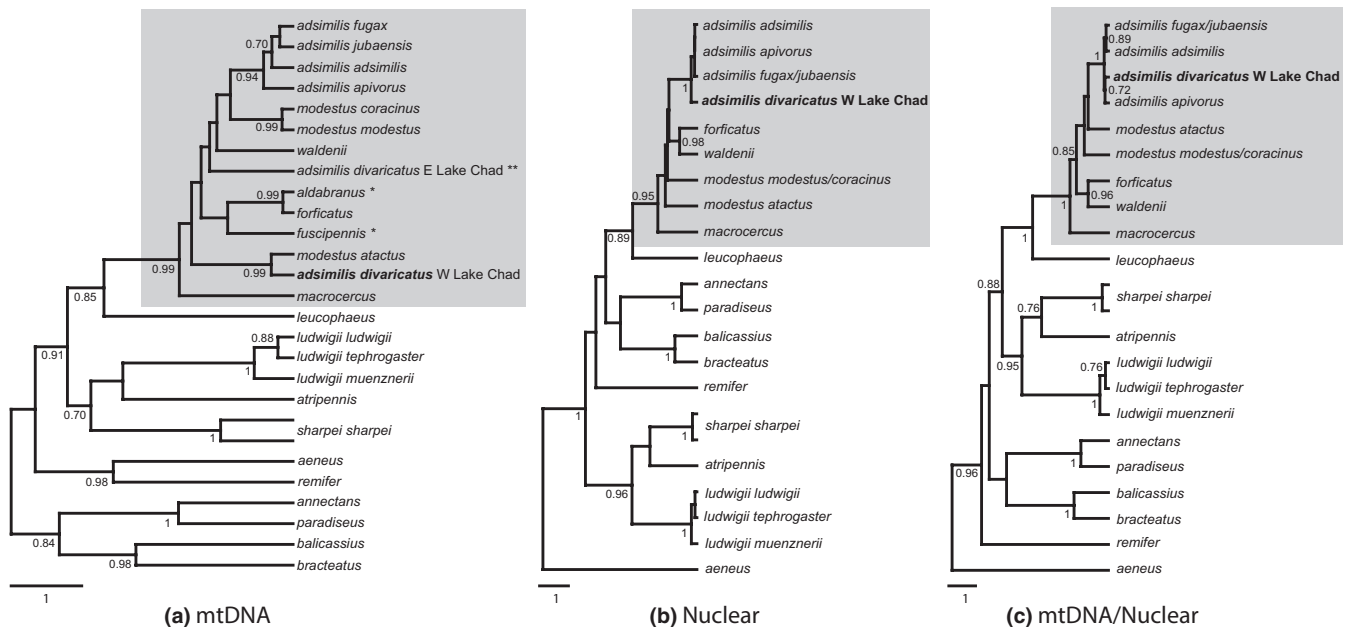As expected, the recovered topology using a coalescent framework to analyse the mitochondrial locus (Figure 2a) was

FIGURE 2 Species trees obtained using the algorithm implemented in *BEAST (Heled & Drummond, 2010) with sequences from (a) the mitochondrial locus, (b) nuclear loci, and (c) mitochondrial and nuclear loci combined. Some lineages (*D. fuscipennis, D. aldabranus* and *D. a. divaricatus* East of Lake Chad) could not be included in all analyses as nuclear sequences were not available. For analyses using nuclear DNA data, *D. a. jubaensis* and *D. m. coracinus* were merged with *D. fugax* and *D. m. modestus*, respectively. Numbers close to nodes refer to posterior probabilities >.70
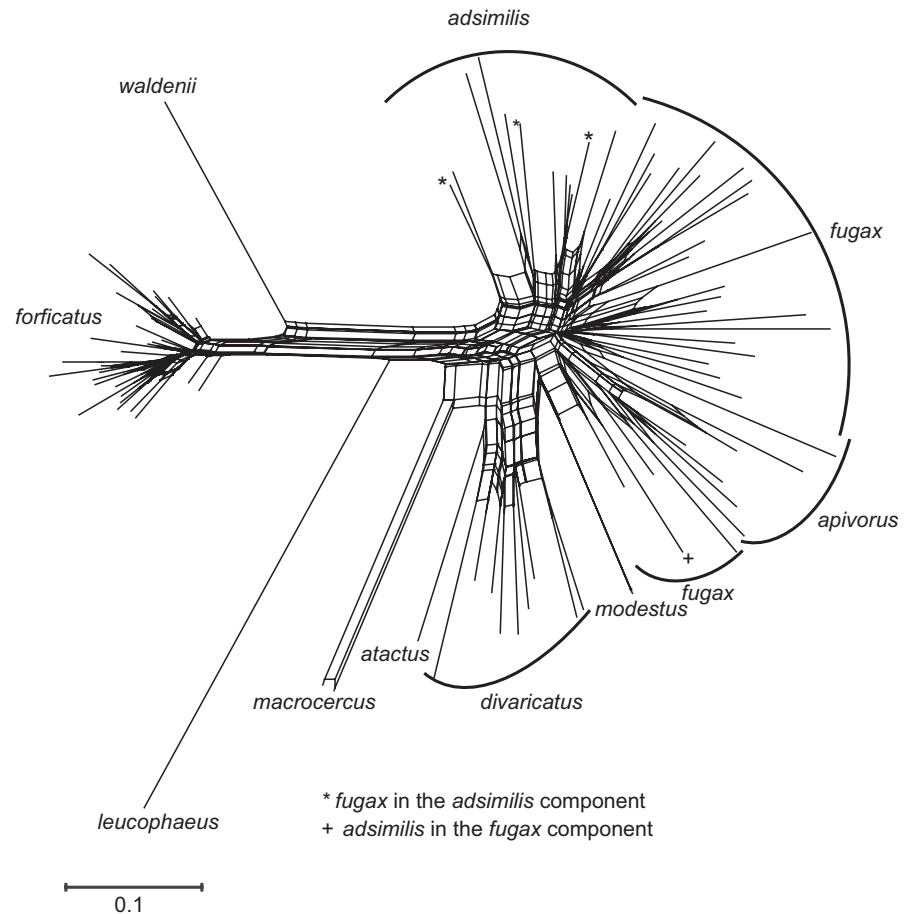
FIGURE 3 Multilocus network obtained using standardized genetic distances from the five loci for all individuals from the *D. adsimilis* superspecies complex for which all loci were available (*n* = 94)

very similar to the haplotype tree, with the only differences being nodes that did not receive high posterior probability support. Very few nodes were supported with posterior probabilities >.95; these were *D. aldabranus/forficatus* (PP: .99) and *D. m. atactus/a. divaricatus* W Lake Chad (PP: .99). The monophyly of the clade consisting of the eastern and southern subspecies of *D. m. modestus/m. coracinus* and *adsimilis* (*jubaensis*, *fugax*, *adsimilis*, *apivorus*), although recovered, was not quite statistically supported (PP: .94).

The monophyly of the *Dicrurus adsimilis* superspecies complex was also recovered in the nuclear species topology (PP: .95), but very few relationships were supported, with the exception of the sister–species relationship between *D. forficatus* and *D. waldenii* (PP: .98) and the monophyly of a clade consisting of *D. a. adsimilis*, *D. a. fugax*, *D. a. apivorus* and *D. a. divaricatus* W Lake Chad.

The species tree topologies were markedly different concerning the relationships of *D. a. divaricatus* W Lake Chad; the mitochondrial topology supported a relationship with the parapatric *D. m atactus* (PP: .99) whereas the nuclear DNA suggested affinities with the eastern and southern populations of *D. adsimilis* (PP: 1.0). This conflict is also highlighted in the multilocus network (Figure 3), where a substantial degree of reticulation was present for *D. m. modestus* and *D. a. divaricatus*, and within *adsimilis* and *fugax*.

The species tree topology resulting from the analyses of the combined mitochondrial and nuclear data was similar to the nuclear DNA topology regarding the relationships of *D. waldenii* and *D. a. divaricatus* W Lake Chad. The Black Drongo *D. macrocercus* was the sister species of all remaining species of the *D. adsimilis* superspecies (PP: .85), a relationship that was also recovered in the mitochondrial and nuclear topologies, although with no support.

3.4 | Divergence times

Our divergence time estimates were strongly dependent on calibration and methodological assumptions (Table 2). Assuming the body mass-corrected mitochondrial rate from Nabholz et al. (2016), the *D. adsimilis* superspecies diverged from its sister species, the Ashy Drongo, about 16.7 mya (13.3–20.3 mya) before further diversifying about 6.7 mya (5.2–8.1 mya) with the split of the Indo-Malayan *D. macrocercus*. The African and Indian Ocean lineages of the *D. adsimilis* superspecies complex radiated in two pulses around 5 mya and 1.4–2 mya. The mitochondrial estimates using the Lerner et al. (2011) and Subramanian et al. (2009) rates were approximately three to four times more recent, irrespective of methodological assumption (species tree vs. haplotype tree), with the diversification of the *D. adsimilis* superspecies

TABLE 2 Estimates of divergence times within the *Dicrurus adsimilis* superspecies

Clade	Mitochondrial data only				Nuclear data only	Nuclear and mitochondrial data
	ATP6 Body mass-corrected rate (clock, third codon position, Rate 2)	ATP6 clock Lerner et al. (2011) rate	ATP6 fourfold (mtDNA only)	ATP6 clock Species tree, Lerner et al. (2011)	TGFb2 clock (species tree Nuclear—*BEAST)	ATP6 and TGFb2 clock, Lerner et al. (2011) (species tree nuclear and mtDNA—*BEAST)
D. leucophaeus/D. adsimilis superspecies	16.7 (13.2–20.3)	3.4 (2.5–4.4)	3.0 (1.3–5.3)	2.7 (1.8–3.6)	2.3 (1.3–3.5)	2.9 (1.9–3.2)
D. adsimilis superspecies	6.7 (5.2–8.1)	1.8 (1.3–2.3)	2.3 (1.0–4.0)	1.6 (1.2–2.1)	1.4 (0.75–2.2)	1.5 (1.0–1.9)
D. a. divaricatus W Lake Chad/*D. m. atactus*	1.8 (1.5–2.2)	0.6 (0.4–0.9)	0.8 (0.2–1.5)	0.4 (0.05–0.8)	NA	NA
D. a. divaricatus E Lake Chad/sister group	5.4 (4.2–6.6)	1.5 (1.1–1.9)	1.7 (0.8–3.1)	1.2 (0.9–1.6)	NA	NA
D. m. modestus-D. m. coracinus/sister group	4.8 (3.8–5.9)	1.5 (1.0–2.0)	1.4 (0.6–2.5)	0.8 (0.4–1.3)	1.0 (0.6–1.5)	0.9 (0.5–1.3)
D. m. modestus/D. m. coracinus	0.5 (0.4–0.7)	NA	0.5 (0.2–1.0)	0.2 (0.05–0.3)	NA	NA
D. apivorus/D. a. adsimilis–D. a. fugax	2.0 (1.6–2.4)	0.7 (0.5–0.9)	0.7 (0.3–1.3)	0.4 (0.2–0.7)	0.09 (0.03–0.16)	0.16 (0.10–0.24)
D. a. adsimilis/D. a. fugax	1.4 (1.0–1.7)	0.5 (0.3–0.36)	0.7 (0.3–1.2)	0.3 (0.15–0.45)	0.08 (0.025–0.15	0.09 (0.06–0.13)
D. aldabranus/D. forficatus	0.35 (0.3–0.4)	0.3	NA	0.15 (0.04–0.3)	NA	NA
D. waldenii/D. aldabranus–D. forficatus	4.6 (3.5–5.4)	1.3 (0.9–1.6)	1.2 (0.4–2.1)	1.1 (0.7–1.4)	0.6 (0.3–1.0)	0.8 (0.4–1.2)
D. fuscipennis/sister group	5.1 (4.0–6.2)	1.5 (1.1–1.9)	1.2 (0.6–2.3)	0.9 (0.4–1.4)	NA	NA
D. macrocercus–sister taxa	6.7 (5.2–8.1)	1.8 (1.3–2.3)	2.0 (0.8–3.5)	1.6 (1.2–2.1)	1.4 (0.75–2.2)	1.5 (1.0–1.9)

NA means 'Non Applicable' and refers either to clade that could not be evaluated due to one lineage missing (e.g., no nuclear data available) or due to one lineage nested in the other (e.g., *D. aldabranus* in *D. forficatus* in the ATP6 fourfold analyses).

occurring during the Pleistocene (1.6–2.3 mya). The species trees analyses based on the nuclear data and combined nuclear and mitochondrial data also supported a Pleistocene diversification for the *D. adsimilis* superspecies complex (1.4–1.5 mya). The estimates from the species tree analyses were always more recent than those based on the gene tree sensu stricto—an expected pattern, as gene divergence precedes population divergence.

3.5 | Molecular species delimitation methods

The results from the different molecular species delimitation methods are summarized in Table 3.

The analyses performed using the bGMYC method indicated that the species-level diversity within the *D. adsimilis* superspecies complex is likely underestimated. Several lineages were recovered as specifically distinct at the 0.05 level (Figure S5): (i) *D. a. apivorus*; (ii) *D. a. adsimilis/D. a. fugax/D. a. jubaensis*; (iii) western *D. a. divaricatus/D. m. atactus*; (iv) *D. m. modestus/D. m. coracinus*; and (v) eastern *D. a. divaricatus*, as well as the three Indian Ocean taxa; (vi) *D. fuscipennis*; (vii) *D. waldenii*; (viii) *D. forficatus* (including *D. aldabranus*) and the Indo-Malayan species; (ix) *D. macrocercus*. Hence, instead of two African species, the bGMYC analyses suggest the occurrence of five putative species in Africa.

TABLE 3 Summary of the molecular species delimitation results within the *D. adsimilis* superspecies. For clarity, only Afrotropical taxa are shown. Note that for BPP, *D. m. modestus* and *D. m. coracinus*, and *D. a. fugax* and *D. a. jubaensis* were considered conspecific (no nuclear data were available for *D. m. coracinus* and *D. a. jubaensis*)

	bGMYC	mPTP (single rate)	mPTP (multirate)	BPP Θ G(1, 10) τ_0, G(1, 10) Θ G(1, 10) τ_0, G(2, 2000) Θ G(2, 2000) τ_0, G(1, 10)	BPP Θ G(2, 2000) τ_0, G(2, 2000)
Data type	Mitochondrial	Mitochondrial	Mitochondrial	Mitochondrial/nuclear	Mitochondrial/nuclear
Number of species recognized	5	6	5	6 (*a. divaricatus* E Lake Chad could not be included)	5 (*a. divaricatus* E Lake Chad could not be included)
	(1) *a. apivorus* (2) *a. adsimilis/a. fugax/a. jubaensis* (3) *a. divaricatus* (E Lake Chad) (4) *m. atactus/a. divaricatus* (W Lake Chad) (5) *m. coracinus/m. modestus*	(1) *a. apivorus* (2) *a. adsimilis/a. fugax/a. jubaensis* (3) *a. divaricatus* (E Lake Chad) (4) *a. divaricatus* (W Lake Chad) (5) *m. atactus* (6) *m. coracinus/m. modestus*	(1) *a. apivorus/a. adsimilis/a. fugax/a. jubaensis* (2) *a. divaricatus* (E Lake Chad) (3) *a. divaricatus* (W Lake Chad) (4) *m. atactus* (5) *m. coracinus/m. modestus*	(1) *a. apivorus* (2) *a. adsimilis* (3) *a. fugax/a. jubaensis* (4) *a. divaricatus* (5) *m. atactus* (6) *m. coracinus/m. modestus*	(1) *a. apivorus/a. divaricatus* (2) *a. adsimilis* (3) *a. fugax/a. jubaensis* (4) *m. atactus* (5) *m. coracinus/m. modestus*

The mPTP analyses recovered strikingly different results, as assuming either a single or multirate Poisson process had a strong impact on the number of putative species, ranging from 16 to 24; there was no difference between the maximum-likelihood and Markov chain Monte Carlo algorithm results, and the only significant parameter was single versus multiple rates. Unrealistic results were recovered under the multirate model for non-members of the *D. adsimilis* superspecies; for example, *D. remifer* and *D. aeneus* were considered conspecific under this scheme. We attributed these results among *Dicrurus* "outgroups" to the differences in sampling schemes between *Dicrurus* outgroups (one individual per species) and members of the *D. adsimilis* superspecies (denser subspecies/ populations sampling). Within the *D. adsimilis* superspecies, the single rate mode favoured ten species (*D. a. apivorus*, *D. a. adsimilis/D. a. fugax/D. a. jubaensis*, western *D. a. divaricatus*, *D. m. atactus*, *D. m. modestus/D. m. coracinus*, eastern *D. a. divaricatus*, *D. fuscipennis*, *D. waldenii*, *D. forficatus/D. aldabranus*, *D. macrocercus*) where the multirate mode recognized only nine; in the latter model, *D. a. apivorus* and *D. a. adsimilis/D. a. fugax/D. a. jubaensis* were considered conspecific. In both cases, support for nine or ten species was marginal.

The analyses performed with BPPv3.1 (Rannala & Yang, 2003; Yang, 2015; Yang & Rannala, 2010) using the mitochondrial and nuclear data suggest that the nine primary lineages within the *D. adsimilis* superspecies complex had a speciation probability of one (note that *D. aldabranus*, *D. fuscipennis* and *D. a. divaricatus* E Lake Chad were not included in the BPP analyses) in all but one prior combination. Only in the analyses assuming small population size and small divergence times were eight species recognized, with *D. a. apivorus* and *D. a. divaricatus* emerging as conspecific ($p = 1.0$). We performed further analyses using unrealistic priors with respect to population size where the gamma distribution was set to G (5, 10) and coupled with deep (G (1, 10) or shallow (G (2, 2000) divergence; the resulting analyses recovered varied support for the distinction of different putative lineages, demonstrating that the algorithm was not stuck on a local optimum, thus increasing our confidence in our initial BPP results.

4 | DISCUSSION

Our analyses revealed unexpected biogeographic patterns, phylogenetic relationships and levels of divergence among the primary lineages of the sub-Saharan African members of the *Dicrurus adsimilis* superspecies complex. Although distinct lineages/clades could be defined with confidence, the relationships among these lineages and their Indian Ocean and Indo-Malayan relatives (the *D. adsimilis* superspecies complex sensu lato) were poorly resolved in the species tree

analyses using five loci. Pasquet et al. (2007), in their concatenated analyses using a slightly different gene sampling strategy, recovered the same general pattern with a lack of support among lineages within the *D. adsimilis* superspecies complex. This lack of resolution is likely attributable to several cladogenetic events occurring over a short period of time, thereby making the order of divergence events a challenging problem to resolve. Our present results suggest (Figure 2) that the *D. adsimilis* superspecies complex diversified into seven to nine primary lineages between 1.5 and 2.3 mya, with one lineage occurring in the Indo-Malayan region (*D. macrocercus*), three in the Indian Ocean (*D. waldenii*, *D. fuscipennis* and *D. aldabranus*/*D. forficatus*) and three to five in Africa (*D. m. atactus*, *D. m. coracinus*/*D. m. modestus, D. a. divaricatus* E and W of Lake Chad, and *D. a. adsimilis*/*D. a. apivorus*/*D. a. jubaensis*). This uncertainty in the number of lineages is due to the non-monophyly and complex relationships of the *D. a. divaricatus* populations sampled E and W of Lake Chad. As in Pasquet et al. (2007), our analyses did not recover any consistent support for the monophyly of the Indian Ocean taxa, implying multiple colonization events from the continent or recolonization of the mainland, a pattern found in several other songbird lineages from this region (e.g., Bristol et al., 2013; Fabre et al., 2012; Fuchs et al., 2008; Warren, Bermingham, Bowie, Prys-Jones, & Thébaud, 2003; Warren, Bermingham, Prys-Jones, & Thébaud, 2006).

Within the *D. adsimilis* superspecies complex, neither of the two currently recognized species (*D. modestus* and *D. adsimilis*) are monophyletic. This result is similar to that recovered among members of the *D. ludwigii* superspecies complex (Fuchs, Fjeldså, et al., 2017). Within the *D. adsimilis* superspecies complex, we recovered four primary sub-Saharan mitochondrial lineages that strongly reflect geography.

The first lineage (*D. a. divaricatus*/*D. m. atactus*) is restricted to western Africa, extending from Nigeria to Senegal. This lineage is itself divided into two primary clades distinguished by habitat preference (*D. adsimilis divaricatus* in savannah and *D. m. atactus* in forest). The second lineage comprises all individuals sampled in the savannah east of Lake Chad (part of *D. a. divaricatus*). The third lineage comprises all individuals sampled in the forests of the Lower Congo Forest Block (*D. m. coracinus*; Uganda, Cameroon, Republic of Central Africa, Gabon, DR Congo) and on Príncipe Island (*D. m. modestus*) in the Gulf of Guinea. Finally, the fourth lineage comprises all individuals sampled in the savannah and woodlands of eastern (Kenya, Tanzania, Somalia, southern Ethiopia), central (Malawi, southern DR Congo) and southern (Zimbabwe, South Africa, Namibia, Botswana) Africa. The latter clade consists of three to four subclades that also have a strong taxonomic and geographic component: *D. a. jubaensis* (southern Ethiopia and Somalia),

D. a. apivorus (central and southern Africa), *D. a. adsimilis* (coastal southern Africa) and *D. a. fugax* (Kenya to South Africa extending through Malawi, southern DR Congo and Zimbabwe). One individual (MNHN CG 1968-355, Kolwezi, DR Congo) clustered with the *D. a. jubaensis* clade, although with little support.

4.1 | Divergence in the Lower Guinea Forest Block

Our analyses revealed that the populations from Príncipe Island (*D. m. modestus*) and its sister lineage from the Lower Guinea Forest Block (*D. m. coracinus*) are only weakly differentiated in mitochondrial DNA (no nuclear DNA was available for the continental lineage). At first glance, this result is surprising as the two taxa differ markedly in biometric measurements (especially in bill and tail characteristics; de Naurois, 1987; J. Fuchs, unpubl. data), suggesting that morphological changes occurred very quickly on the island due to character release or that there is strong selection and canalization of development due to interspecies competition on the mainland. Such a pattern of rapid morphological differentiation coupled with low genetic differentiation has also been highlighted in other lineages of birds (Heron Island silvereyes; Clegg, Frentiu, Kikkawa, Tavecchia, & Owens, 2008).

Interestingly, and counter to several other forest-associated lowland African species (e.g., Fuchs & Bowie, 2015; Fuchs, Fjeldså, et al., 2017; Fuchs, Pons, et al., 2017; Huntley & Voelker, 2016), the Príncipe/Lower Guinea forest block lineage (*D. m. coracinus*/*D. m. modestus*) was not recovered as sister to the Upper Guinea Forest block lineage (*D. m. atactus*). In all classification schemes, *D. m. atactus* has been considered conspecific with the Lower Guinea Forest Block populations (e.g., Gill & Donsker, 2016; Vaurie, 1949). However, Vaurie (1949) did notice that *D. m. atactus* showed divergent plumage characters from *D. a. coracinus* (primaries never as sombre, immature plumage being more barred below), and in some characters, the taxon resembles *D. a. divaricatus* or "*D. a. adsimilis*" (Vaurie, 1949 did not distinguish *adsimilis* from *fugax*, and *apivorus* was not described). Vaurie (1949) considered *atactus* to be intermediate between *adsimilis*/*divaricatus* and *coracinus*. Our analyses revealed that *D. m. atactus* is distinct from all other taxa in the *D. adsimilis* superspecies complex.

No discrete mitochondrial genetic structure was detected among sampled individuals of *D. m. coracinus*, despite sampling the range boundaries of its distribution. This lack of mitochondrial structure among populations is sometimes recovered for various lineages of flying vertebrates (birds: Bowie, Fjeldså, Hackett, & Crowe, 2004a; Fuchs & Bowie, 2015; Fuchs, Fjeldså, et al., 2017; Fuchs, Pons, et al., 2017; bats: Nesi et al., 2013). However, despite

the above examples—the absence of genetic divergence across the Lower Guinea Forest Block—is uncommon in comparison with most vertebrates including several bird species (e.g., Antony et al., 2007; Bell et al., 2015; Gonder et al., 2011; Hassanin et al., 2015; Leaché, Fujita, Minin, & Bouckaert, 2014; Marks, 2010; Nicolas et al., 2008; Schmidt, Foster, Angehr, Durrant, & Fleischer, 2008; Voelker et al., 2013) and plants (Duminil et al., 2015). These studies typically reveal at least two primary lineages across the Lower Guinea Forest Block. We suggest that these differences in the levels of genetic structure among different vertebrates reflect differential dispersal capacities among lineages, where birds of the mid-storey or canopy (e.g., drongos) are less sensitive to habitat fragmentation than are understorey birds or terrestrial mammals, reptiles or amphibians (see Burney & Brumfield, 2009 for an example of Neotropical birds).

4.2 | Divergence across the Northern Savannah

In *D. a. divaricatus,* a deep divergence was recovered across the Northern Savannah, with two mitochondrial lineages delimited by Lake Chad and which are only distantly related in the mitochondrial topology; populations sampled west of Lake Chad are sister to *D. m. atactus*, whereas individuals east of Lake Chad and extending to southern Sudan are more closely related to the eastern/southern African and Indian Ocean lineages (Figure 2a). This result is at odds with traditional taxonomy, as individuals collected east and west of Lake Chad have been considered morphologically homogeneous (Vaurie, 1949), a hypothesis that would have been more consistent with that recovered for the Fiscal Shrike species complex, where there is limited mitochondrial differentiation from eastern Sudan to Guinea (Fuchs, Crowe, et al., 2011). In contrast, studies of mammals (Brouat et al., 2009; Dobigny et al., 2013) and other bird species (Fuchs & Bowie, 2015; Fuchs, Fjeldså et al., 2016) have recovered deep genetic breaks around the Lake Chad/Niger River system. The variation in avian diversity across Africa shows a distinct drop in species diversity east of the Lake Chad basin (Rahbek, Hansen, & Fjeldså, 2012). This region mainly reflects range disjunctions where widespread savannah species (and notably those associated with wetlands and mesic habitats) are absent or very locally distributed, between the western Niger–Kano–Chad drainage and the drainage system of the Nile and East Africa. Western Chad is also a zone of west–east replacement for numerous avian sister taxa (e.g., *Peliperdix albogularis* and *P. coqui* versus *P. schlegeli*, *Lybius dubius* versus *L. rolleti*, *Poicephalus senegalus* versus *P. meyeri*, *Crinifer piscator* versus *C. zonurus*, *Laniarius barbarus* versus *L. erythogaster*, *Batis senegalensis* versus *B. orientalis*, and

Cisticola rufus versus *C. troglodytes*). In addition, substantial genetic differentiation of populations was recently highlighted for the woodpeckers *Campethera punctuligera* and *Dendropicos obsoletus* (Fuchs, Pons, et al., 2017). All this suggests a significant frequency of historical connectivity breaks between populations distributed west and east of the Lake Chad basin.

Yet, the pattern recovered for *D. a. divaricatus* appears much more complex. The nuclear and species tree analyses recovered *D. a. divaricatus* individuals sampled west of Lake Chad as sister to the eastern and southern African subspecies (*D. a. apivorus/adsimilis/fugax;* Fig 2B, C), suggesting the monophyly of *D adsimilis* as currently defined. In contrast, mitochondrial data suggested that they are related to the Upper Guinean Forest-endemic *D. m. atactus*. Hence, the mitochondrial and nuclear results strongly conflict with one another. Two processes could explain this result: (i) incomplete lineage sorting of ancestral polymorphism or (ii) hybridization. Incomplete lineage sorting of ancestral polymorphism could have occurred during the initial radiation of the *D. adsimilis* superspecies in which all primary lineages appeared. If lineage sorting were the main cause, we would expect similar or almost identical divergence times among the nuclear and mitochondrial data. This is not the observed pattern. Instead, we recovered much more recent mitochondrial divergence times. We suggest that this discrepancy is due to hybridization between members of *D. m. atactus* and the western population of *D. a. divaricatus*, with capture of the *D. m. atactus* mitochondria by *D. a. divaricatus* west of Lake Chad, and further that this hybridization lasted until approximately 0.5 mya (corresponding to the divergence between the two mitochondria lineages). Examples of hybridization and gene flow between taxa at the forest–savannah interface in Africa have been described for elephants (e.g., Mondol et al., 2015), and for birds there is also evidence for such processes in other savannah systems (Shipham, Schmidt, Joseph, & Hughes, 2016). It is striking that during the past 0.5 myrs the two primary *D. a. divaricatus* haplotype lineages remained strongly geographically segregated and that this segregation corresponds to a previously described biogeographic barrier (Lake Chad), which suggests that the two *D. a. divaricatus* populations distributed on either side of the Lake Chad basin might have achieved reproductive isolation. This putative reproductive isolation could either have resulted from classic allopatric divergence where the two lineages accumulated sufficient genetic differentiation leading to incompatibility upon secondary contact, or alternatively due to cytoplasmic incompatibility. In this instance, the populations west of Lake Chad might carry an incompatible mitochondrion from *D. m. atactus* in combination with the nuclear genomic background of populations east of Lake Chad. Whether this is the case, however, remains to be tested (Hill, 2017).

4.3 | Diversification across Eastern and Southern sub-Saharan Africa

All analyses revealed a strongly supported clade consisting of all lineages found in eastern and southern Africa. Depending on the type of loci analysed (mitochondrial or nuclear), this group may also be closely associated with *D. a. divaricatus* of the northern Savannah zone. Our data revealed three (*D. a. apivorus, D. a. adsimilis, D. a. fugax*) or four (*D. a. jubaensis*) clades within the eastern/southern lineage. The putative fourth clade (*D. a. jubaensis*) included four individuals (three collected in Ethiopia/Somalia in July/August and one in southern DR Congo in January) that were differentiated from the three other primary lineages. The range of this latter clade corresponds to the range of the taxon *jubaensis* van Someren, 1931 in southern Ethiopia and Somalia. The latter taxon, not recognized by Vaurie (1949), was thought to be more closely related to the populations of the Sudanian savannah belt (*D. a. divaricatus*). Our results suggest that the Ethiopian/ Somalian populations could be more closely related to the populations of the eastern and southern savannahs, a pattern consistent with genetic structure in Bushbuck (*Tragelaphus scriptus*; Moodley & Bruford, 2007) but not Giraffe (*Giraffa* sp., Fennessy et al., 2016), suggesting that lineages distributed in the north-eastern African savannahs have mixed phylogeographic histories. The sister-group relationship of one individual (MNHN CG 1968-365) from southern DR Congo to the three Ethiopian/Somalian specimens was more surprising, but consistent with phylogeographic pattern recovered for the Bushbuck, where individuals from Kenya/Somalia cluster with those from Zambia (Moodley & Bruford, 2007).

There is also a suggestion that the range of *D. a. fugax* haplotypes overlap with the range of *D. a. adsimilis* and *D. a. apivorus*, potentially indicative of the merging of the different lineages. We recovered widespread haplotype sharing among distant localities (e.g., Kenya/Bostwana or Kenya/ South Africa). Although this result could be due to high levels of gene flow and homogenization in *D. a. fugax*, it could also be explained by seasonal migratory movements of some populations. Interestingly, specimens that shared the mixed haplotypes were all collected at different times of the year: February–March for Kenya, and October–November for South Africa/Botswana, and June for intervening countries (e.g., Malawi).

4.4 | Africa as a model for speciation driven by divergent ecology

The large-scale biogeographic pattern (western, central, southern/eastern) recovered for the *D. a. adsimilis* superspecies complex has similarities to that recovered for the Square-tailed/Shiny Drongo species complex (*D. ludwigii*; Fuchs, Fjeldså, et al., 2017), as well as that of the Fiscal Shrike species complex (*Lanius collaris*; Fuchs, Crowe, et al., 2011). Indeed, most of the divergence time analyses indicated that widespread sub-Saharan bird lineages diversified across habitat boundaries (forest, dense woodland/ Miombo and open savannah) slightly after the beginning of the Pleistocene (2.3–1.5 mya; e.g., this study, Fuchs, Crowe, et al., 2011; Fuchs, Fjeldså, et al., 2017). These divergence time estimates are similar to those recovered for other vertebrates (e.g., Moodley & Bruford, 2007), although some analogous instances of divergence could have happened earlier (e.g., forest and savannah elephants 2.6–5.6 mya; Roca et al., 2015; crombecs 2.8–5.8 mya; Huntley & Voelker, 2017). Hence, it appears that divergence across habitat gradients (i.e., a model of speciation by diversification across broad continental ecotones) has occurred several times over Africa's history and has likely played an important role in generating the rich, contemporary bird diversity on the continent.

4.5 | Plumage evolution and the importance of habitat in diversification

Common findings of most African phylogeographic studies of widespread bird species complexes are the discrepancies between traditional taxonomy and evolutionary relationships as uncovered using molecular data, and the concordance of molecularly defined clades/lineages with geographic barriers. Further, a consistent surprise has been the recovery of readily diagnosable species with distinct plumage characters that occupy distinct habitats being nested within more broadly distributed species: *Lanius souzae* or *L. mackinnoni* for *Lanius collaris*, *D. atripennis* for *D. ludwigii*, mutual paraphyly of *D. adsimilis* and *D. modestus*; Fuchs, Crowe, et al., 2011; Fuchs, Fjeldså, et al., 2017, this study).

In the *Dicrurus adsimilis* superspecies complex, species are primarily discriminated by mantle and upperpart coloration in the context of the habitat the species occupies (forest: velvet blue, open habitat: steel greenish blue; Vaurie, 1949). Recent phylogeographic studies of sub-Saharan African vertebrates have indicated that widespread and often morphologically uniform species are typically paraphyletic, with one of the lineages being closely related to a species with a drastically different phenotype and inhabiting a different, yet geographically proximal biome (Fuchs, Crowe, et al., 2011; Moodley & Bruford, 2007; Oatley et al., 2012).

The pattern we highlight may have two implications for our understanding of the evolution of African birds. First, habitat appears to exert a strong selective pressure on plumage; unrelated bird species or highly differentiated lineages that occur in the same habitat type are more morphologically similar to each other than to phylogenetically closer lineages occurring in different habitats. This

reinforces the view that plumage traits can be poor indicators of phylogenetic relationships (e.g., Alström et al., 2014; Christidis, Rheindt, Boles, & Norman, 2010; Shultz & Burns, 2013), but reasonable indicators of genetic divergence (Christidis et al., 2010). Secondly, diversification and possibly speciation is potentially tightly linked to specialization to a particular habitat, a process which appears to be a common mechanism underlying the divergence of many sub-Saharan Africa vertebrates (e.g., Moodley & Bruford, 2007; Oatley et al., 2012; Roca et al., 2015; da Silva & Tolley, 2017).

4.6 | Taxonomic recommendations

Our phylogenetic and species delimitation analyses confirmed the validity of all recognized subspecies, but the phylogenetic relationships among taxa depart considerably from traditional taxonomy (Table 1). Based on our results, it is clear that the current species limits within the *D. adsimilis superspecies* complex are still in need of further work. Our data strongly suggest that *D. modestus atactus* and *D. m. coracinus*/*D. m. modestus* are distinct species that are differentiated and not directly related in the mitochondrial and nuclear data sets. Both the bGMYC and mPTP species delimitation methods suggest that *D. m. modestus* and *D. m. coracinus* should be considered conspecific, at least from a genetic perspective. Determining the taxonomic status of several taxa distributed across the African savannah belt will require more data, particularly for the *D. a. divaricatus* populations east and west of Lake Chad for which our analyses suggest that the individuals sampled from northern Cameroon and extending to southern Sudan may warrant recognition at the species level. The type locality of *D. a. divaricatus* is in Senegambia; thus, this name should apply to the clade formed by all individuals collected in the western savannas, from Senegal to Nigeria. The subspecies *lugubris* (type locality: Ambukol, Dongola, Sudan; Hemprich and Ehrenberg 1828) has been considered synonymous with *divaricatus* by all taxonomists since Vaurie (1949). Here, we propose to resurrect this name for the populations distributed in the savannah zone from Lake Chad to Ethiopia but suggest that it is better recognized as a subspecies of *D. divaricatus* until further data are available. Similarly, most molecular species delimitation methods we used suggested that the last taxon described in the superspecies complex, *D. a. apivorus*, may also be distinct at the species level from the other eastern and southern subspecies (*D. a. adsimilis*, *D. a. fugax* and *D. a. jubaensis*), although support for this split depends on the methods and prior assumptions used. The *D. apivorus* species would be parapatric with at least two or three taxa distributed across biomes

boundaries, a result similar to that recovered for southern African white eyes (*Zosterops* sp., Oatley, Bowie, & Crowe, 2011; Oatley et al., 2012; Oatley, De Swardt, Nuttall, Crowe, & Bowie, 2017). The determination of the extent of hybridization between *D. a. adsimilis* and *D. a. fugax* will also be decisive in ascertaining their taxonomic status.

Based on our phylogenetic results, we propose a new classification and taxonomy for the *D. adsimilis* taxa distributed in sub-saharan Africa.

Dicrurus atactus Oberholser, 1899. Distribution: Sierra Leone to SW Nigeria

Dicrurus modestus Hartlaub, 1849

  D. modestus modestus Hartlaub, 1849. Distribution: Príncipe I. (Gulf of Guinea)

  D. modestus coracinus J Verreaux and É. Verreaux, 1851. Distribution: SE Nigeria to Kenya, C DR Congo and NW Angola

Dicrurus divaricatus M. H. C. Lichtenstein, 1823

  D. divaricatus divaricatus M. H. C. Lichtenstein, 1823. Distribution: Mauritania to Guinea E to Lake Chad

  D. divaricatus lugubris (Hemprich & Ehrenberg, 1828). Distribution: Lake Chad east to Somalia and N Kenya

Dicrurus apivorus Clancey, 1976. Distribution: se Gabon and Congo to n South Africa

Dicrurus adsimilis Bechstein, 1794.

  D. adsimilis adsimilis Bechstein, 1794. Distribution: W Swaziland and E and S South Africa

  D. adsimilis fugax W. K. H. Peters, 1868. Distribution: Uganda and Kenya S to NE South Africa and Swaziland

  D. adsimilis jubaensis van Someren, 1931. Distribution: Somalia, Ethiopia, S DR Congo

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