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Genomic footprints of adaptation in a cooperatively breeding tropical bird across a vegetation gradient

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Abstract

Identifying the genetic basis of phenotypic variation and its relationship with the environment is key to understanding how local adaptations evolve. Such patterns are especially interesting among populations distributed across habitat gradients, where genetic structure can be driven by isolation by distance (IBD) and/or isolation by environment (IBE). Here, we used variation in ~1,600 high-quality SNPs derived from paired-end sequencing of double-digest restriction site-associated DNA (ddRAD-Seq) to test hypotheses related to IBD and IBE in the Yucatan jay (*Cyanocorax yucatanicus*), a tropical bird endemic to the Yucatán Peninsula. This peninsula is characterized by a precipitation and vegetation gradient—from dry to evergreen tropical forests—that is associated with morphological variation in this species. We found a moderate level of nucleotide diversity (π = .008) and little evidence for genetic differentiation among vegetation types. Analyses of neutral and putatively adaptive SNPs (identified by complementary genome-scan approaches) indicate that IBD is the most reliable explanation to account for frequency distribution of the former, while IBE has to be invoked to explain those of the later. These results suggest that selective factors acting along a vegetation gradient can promote local adaptation in the presence of gene flow in a vagile, nonmigratory and geographically restricted species. The putative candidate SNPs identified here are located within or linked to a variety of genes that represent ideal targets for future genomic surveys.

KEYWORDS

adaptive genetic variation, genotype–environment–phenotype associations, isolation by distance, isolation by environment, Yucatan jay

1 | INTRODUCTION

Unravelling the genetic basis and evolutionary drivers of phenotypic variation is one of the core objectives of evolutionary biology. It is commonplace to believe that selection operates on phenotypes and that morphological variants have an associated adaptive value that makes them evolve through ecologically driven forces (reviewed in Kingsolver, Hoekstra, & Hoekstra, 2001; Newton, 2003). However, many examples suggest that significant phenotypic differentiation can also arise by genetic drift, patterns of relatedness (Campagna, Gronau, Silveira, Siepel, & Lovette, 2015; Gray et al., 2015; Zink & Remsen, 1986) or as a result of phenotypic plasticity across groups of individuals (Mason & Taylor, 2015). Furthermore, when populations are not effectively isolated from each other or are arranged across environmental gradients that may influence phenotypic variation, they may conform to patterns of isolation by distance (IBD) or isolation by environment (IBE), two outcomes that are sometimes difficult to distinguish from each other (reviewed in Forester, Jones, Joost, Landguth, & Lasky, 2016).

Heterogeneous landscapes can increase genetic differentiation by affecting gene flow between populations, regardless of geographic distance (Foll & Gaggiotti, 2006; Nosil, Vines, & Funk, 2005; Thorpe, Surget-Groba, & Johansson, 2008; Wang & Bradburd, 2014). This IBE pattern is thought to be generated by local adaptation (Bradburd, Ralph, & Coop, 2013; Wang & Bradburd, 2014; Wang & Summers, 2010), especially under strong selective regimes that constrain dispersal and affect mating synchrony along an environmental gradient (Dennenmoser, Rogers, & Vamosi, 2014; Mendez, Rosenbaum, Subramaniam, Yackulic, & Bordino, 2010; Nielsen et al., 2009; Saint-Laurent, Legault, & Bernatchez, 2003; Schweizer et al., 2016; Sexton, Hangartner, & Hoffmann, 2014). This effect is, however, controversial because gene flow is thought to stall local adaptation (Bridle, Polechová, Kawata, & Butlin, 2010; Haldane, 1930; Wright, 1943), implying that IBD patterns may be more common in nature (Meirmans, 2012; Slatkin, 1993; Wang, Glor, & Losos, 2013). However, IBE has become a likely explanation for population genetic differences in many taxa and environmental frameworks, including some orchids (Mallet, Martos, Blambert, Pailler, & Humeau, 2014), fish (Dennenmoser et al., 2014), birds (Manthey & Moyle, 2015) and mammals (Lonsinger, Schweizer, Pollinger, Wayne, & Roemer, 2015; Mendez et al., 2010), which suggests that IBE is also frequently found in nature. Disentangling the relative effects of IBD and IBE is thus essential to understanding the ecology of local adaptation and phenotypic evolution (Bradburd et al., 2013; Sexton et al., 2014; Wang & Bradburd, 2014; Wang et al., 2013).

Birds are good models for testing hypotheses related to IBD/IBE, mostly because they tend to be highly vagile and form large populations that exhibit significant phenotypic variability (Husby et al., 2015), which may suggest that local adaptation is taking place (Manthey & Moyle, 2015). Recent studies have further shown that avian genomes are highly conserved at the nucleotide sequence and syntenic at the chromosomal structure level (Ellegren, 2013; Gossmann et al., 2014 Jarvis et al., 2014; Zhang, Li, et al., 2014), hence facilitating the assembly of databases in non-model taxa (e.g., Lemmon, Emme, & Lemmon, 2012; DaCosta & Sorenson, 2014). Furthermore, the availability of bird specimens in collections makes the assessment of morphometric variation easier. When correctly integrated into genotype–environment associations, this variation can greatly improve the identification of candidate genes and connect genomics to fitness-related traits (e.g., Haasl & Payseur, 2016; Hancock et al., 2011; Talbot et al., 2016).

The Yucatan jay is a cooperatively breeding bird endemic to and continuously distributed in the Yucatán Peninsula (comprising southeastern Mexico, northern Guatemala and northern Belize), where it forms large populations across the environmental gradient that characterizes this region (Brown, 1987; Raitt & Hardy, 1976). This gradient is mainly driven by northwest to southeast changes in precipitation and humidity (Howell & Webb, 1995), which generate floristic changes. For instance, tropical dry forests dominate the drier northwest of the peninsula, and tropical evergreen forests, the more humid southeast (Rzedowski, 1990; Figure 1). Significant morphometric variation, putatively associated with this gradient, has been reported in Yucatan jay populations (Chablé-Santos, 1999; Figure 1). Because the Yucatán Peninsula has no significant

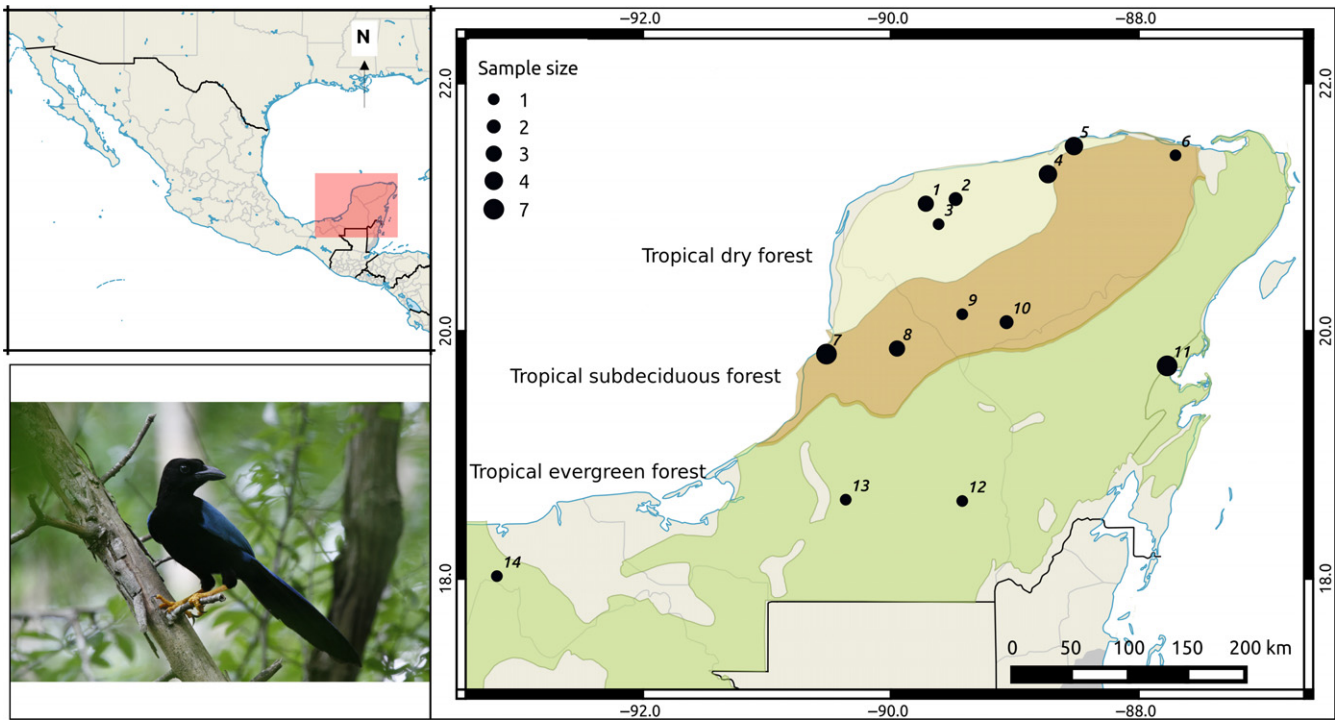

FIGURE 1 Sampling locations of the Yucatan jay (*Cyanocorax yucatanicus*) specimens selected for this study, along vegetation types in the Yucatán Peninsula (Rzedowski, 1990). Dot size is proportional to sample size at each location. The average distance between specimens from the same location is 9.2 km (min.: 5.4 km and max.: 18.9 km). See Table S1 for full information on the specimens [Colour figure can be viewed at wileyonlinelibrary.com]

geographical barriers that could hamper dispersal in this species—it is mainly a large plain where all rivers are subterranean and hills are not higher than 350 m a.s.l. (Lugo-Hubp & García-Arizaga, 1999; Vázquez-Domínguez & Arita, 2010)—it can be hypothesized that environmental changes promote, at least in part, morphological and genetic variation in this species.

In this study, we used an Illumina next-generation sequencing (NGS) platform with paired-end sequencing of double-digest restriction site-associated DNA (ddRAD) tags (Peterson, Weber, Kay, Fisher, & Hoekstra, 2012) to assess genome-wide variation and explore potential environmental drivers of population genetic structure in the Yucatan jay. Consistent with previous studies of cooperative breeders (Delaney, Zafar, & Wayne, 2008; Edwards, 1993; Mcdonald, Potts, Fitzpatrick, & Woolfenden, 1999; Woxvold, Adcock, & Mulder, 2006), we anticipated geographic variation across localities at the landscape scale, and this despite the small geographic area in which this bird is distributed (over ~135,500 km^2). Cooperative breeding social systems have been shown to be adaptive in environments with high interannual variability in climate, as they facilitate sustained breeding and reproduction in both harsh and favourable years (Koenig & Walters, 2015; Rubenstein & Lovette, 2007). We first identified environmental predictors of phenotypic variation and then associated them with SNP genotypes. Finally, we determined whether putative neutral and candidate markers differentially conformed to patterns of IBD and IBE.

2 | METHODS

2.1 | Sampling and collection of morphological and climate data

Specimens were collected in geo-referenced localities in 1996 (Chablé-Santos, 1999), and tissues were preserved in a deep freezer (−70°C) in the Ornithological National Collection at the Institute of Biology, UNAM (Colección Nacional de Aves (CNAV), Ciudad Universitaria, AP 70-153, CdMx 04510, México). Sixty-eight of these specimens, all adults or subadults (i.e., at stages where growth in body size had stopped; Chablé-Santos, 1999), were selected for this study. There were two to eight individuals per sampling point (Table S1), spanning the entire range of the species (Figure 1). The geographic distance between sampling points (as estimated with the great-circle method) was used in the models and analyses below (Bayesian Estimation of Differentiation in Alleles by Spatial Structure and Local Ecology, BEDASSLE).

All selected specimens were scored for six morphometric traits that had been found to change along the geographic gradient (Chablé-Santos, 1999): tarsus length, wing length, tail length, culmen length, bill width and bill depth. Each measure was taken ten times, and averages were used in the analyses (associated standard errors were always very low; data not shown). Because there is no sexual dimorphism in this species (Hardy, 1973), and sex data were not available for all individuals, analyses were performed without taking sex into account. Climate data were gathered for each sampling point from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; www.worldclim.org) and comprised 19 bioclimatic layers representing mean, maximum and minimum temperature and precipitation, and range values of precipitation (from 10 to 400 mm) and temperature (from 14 to 20°C) across the study region. After removing two layers (Bio1, annual mean temperature and Bio7, temperature annual range = Bio5–Bio6) that showed collinearity with other variables, we evaluated which of the remaining layers best predicted phenotypic variation through a series of generalized linear models (GLMs) with stepwise (backward) logistic regressions. These models were used as guidelines to identify the variants that could be influencing phenotypic evolution in the Yucatan jay, following a similar rationale as in previous studies in humans (Hancock et al., 2011) and pine (Talbot et al., 2016). Each morphometric trait was independently correlated to the remaining 17 bioclimatic variables, and the model that best explained each trait was selected based on the Akaike information criterion. In each model, the significance of each variable was assessed after adjusting the *p*-value (with the p.adjust function in R) using a false discovery rate (FDR) threshold of .1 and a *p*-value of .05 (Benjamini & Hochberg, 1995; Wright, 1992). Bioclimatic variables that fulfilled the above criteria in at least two models for two phenotypic traits or more were retained for the association tests using genotypic data (see below).

2.2 | DNA isolation and preparation of genomic libraries

Total DNA was extracted from each bird specimen with a QIAGEN DNeasy Blood & Tissue Kit according to the manufacturer's instructions. Libraries were prepared using the ddRAD-Seq protocol (Peterson et al., 2012) standardized for birds with genome sizes similar to those of the zebra finch (*Taeniopygia guttata*) and the American crow (*Corvus brachyrhynchos*; ~1.23 Gb; Peterson, Stack, Healy, Donohoe, & Anderson, 1994; Andrews, Mackenzie, & Gregory, 2009). DNA samples were digested with *Eco*RI-HF and *Sph*I restriction enzymes (New England Biolabs), and custom adapters with attached individual barcodes were ligated to each digested sample with T4 DNA ligase (New England Biolabs). Fragments 345–407 bp long and cut by both enzymes (one enzyme per end) were selected with a Pippin Prep electrophoresis cassette (Sage Science), and libraries were pooled on equal concentrations. A short PCR was performed in quadruplicate on this pool using the KAPA HiFi *Taq* (Kapa Biosystems), as follows: initial denaturation at 94°C for 2 min; followed by 12 cycles at 94°C for 15 s, 57°C for 30 s and 72°C for 1.2 min; and final extension at 72°C for 1 min. Pools were tested for DNA quality and quantity with qPCR and flow cytometry in an Agilent 2100 Bioanalyzer and sequenced in a single lane of an Illumina HiSeq2000 sequencer at the Bauer Center for Systems Biology, Harvard University, with paired-end reads (100 bp each). Sequence reads were obtained in two runs (Run 1 and Run 2), one run per end, and each one representing the restriction sites of the enzymes used.

2.3 | Bioinformatic pipeline

DNA sequence reads were demultiplexed with the "process-radtag" routine available in STACKS v1.30. Sequences were quality-filtered with the FASTX_toolkit-0.0.12 (http://hannonlab.cshl.edu/fastx_toolkit/index.html, by Hannon Lab), and any read with a Phred score lower than 20 was eliminated. Retained reads were trimmed to 91 and 94 nucleotides for Run 1 and Run 2, respectively, with the NGSQCTOOLKIT_v2.3.3 (Patel & Jain, 2012) to remove possible errors in the sequence tails (Pujolar et al., 2014). Afterwards, PCR clone sequences were eliminated with "clonefilter" in STACKS v1.30 (Catchen et al., 2011).

Filtered paired-end reads were aligned with the Genomic Short-read Nucleotide Alignment Program (GSNAP, version 2014-12-17; Wu & Nacu, 2010), after disabling the terminal alignments option. Because of the high genome synteny of birds (Ellegren, 2013; Gossmann et al., 2014; Jarvis et al., 2014; Zhang, Li, et al., 2014), and specifically of corvids (Roslik & Kryukov, 2001), the American crow genome assembly (NCBI assembly: ASM69197v1, Accession no: GCA_000691975.1) was used as pseudo-reference (PRG) for alignment. This allowed for additional positioning information, and facilitated detecting rare allele variants (Peterson et al., 2012) that are often removed from de novo assemblies, as they can be confounded with sequencing errors.

For comparison purposes, reads were also assembled de novo without alignment to a PRG (using STACKS), and mapped to the zebra finch as a secondary PRG (using GSNAP). This last alignment yielded fewer loci than the two others and resulted in different estimates of population diversity and major allele frequencies. Assemblies using no PRG or the American crow as PRG yielded similar basic population parameters, although they differed in the number of final RAD loci (Figs S1–S6). After following recommendations by Davey et al. (2013) and Nevado, Ramos-Onsins, and Perez-Enciso (2014), we selected the American crow PRG alignment as the most robust framework to recover SNPs. Parameters for this alignment included a terminal threshold of 500, a maximum number of mismatches allowed (*m*) of 5, and an indel penalty (*-i*) of 2, as recommended by Catchen et al. (2011). DNA sequences were sorted out by coordinates in the reference genome, and optical duplicates (sequencing artefacts) were removed using picard-tools-1.119 (Wysoker, Tibbetts, & Fennell, 2013). Sequences with low mapping quality (i.e., below 20) were also eliminated with SAMTOOLS 0.1.18 (Li et al., 2009).

SNP discovery and genotype calling were performed with the STACKS pipeline v1.30 (Catchen et al., 2011) using the correction module "rxstacks", which makes a population-based correction to genotype calling on individuals. This module facilitates removing putative sequencing errors, paralogs and low-coverage loci from the final data set. The reference-aligned sequences were processed with the ref_map.pl pipeline by allowing a maximum of three mismatches (*n*) between loci, and three loci per stack (max_locus_stacks); a SNP call model error upperbound (epsilon) of .05 was also used, while a maximum likelihood (*ln*ls) value of 8 was employed for the correction module.

2.4 | Population analyses

Relatedness is always a major concern in association studies, as it can lead to spurious associations (Wang, Barratt, Clayton, & Todd, 2005). To control for this factor is particularly important when studying cooperative-breeders, like the Yucatan jay, in which yearlings can delay migration and breeding for two or more years (Brown, 1987; Raitt & Hardy, 1976), and thus increase consanguinity within flocks. Although we minimized the number of birds sampled from the same social group to reduce relatedness (i.e., only selected two to eight birds per sampling point), we further assessed this parameter by estimating pairwise kinship coefficients between individuals. We used the algorithm developed by Manichaikul et al. (2010) and implemented in the software VCFTOOLS (Danecek et al., 2011; –relatedness2 flag) on the final SNP data set. All individual pairs showed coefficients below .04, suggesting that they were unrelated at the 3rd degree or lower (Manichaikul et al., 2010; see Fig. S7 for the distribution of kinship coefficients in the final data set).

Basic estimates of population and nucleotide diversity were inferred with the populations programme in STACKS v1.30 (Catchen et al., 2011). Nucleotide diversity (π), heterozygosity (H_o and H_e) and fixation index (F_{IS}) were determined from a filtered set of SNPs that included only those in Hardy–Weinberg equilibrium and with minor allele frequencies (MAF) above 0.05 (n = 1,649 SNPs). Population structure was tested at the individual level using STRUCTURE v.2.3 (Pritchard, Stephens, & Donnelly, 2000). Ten runs were performed with the admixture model and assuming uncorrelated allele frequencies for k values ranging from 2 to 14. Each run consisted of 100,000 MCMC iterations after a burn-in period of 10,000 steps. The most likely value of k was determined with the criteria of Evanno, Regnaut, and Goudet (2005) available in structureHarvester.py (Earl & VonHoldt, 2012). The final plot was produced with CLUMPP 1.2.1 (Jakobsson & Rosenberg, 2007) and DISTRUCT 1.1 (Rosenberg, 2004). However, given the limitations that Bayesian clustering methods may have under IBD frameworks, we corroborated our results using the discriminant analysis of principal components (DAPC) available in the ADEGENET 2.0 package (Jombart, 2008) for R 3.2.0 (R Development Core Team, 2015). First, we assessed the overall population structure (gstat.randtest function) with the Nei's estimator (Nei, 1973) of pairwise F_{st} (HIERFSTAT 0.04.22 package; Goudet & Jombart, 2015) on 999 Monte Carlo simulations, and then performed two DAPCs, one without predefined clusters (find.cluster and dapc function), and a second one assuming three groups (i.e., the number of Operative Geographic Units suggested for the Yucatan jay from morphometric data; Chablé-Santos, 1999). Only the clustering that best accommodated the data was retained to avoid overfitting.

2.5 | Outlier detection and genotype–phenotype–environment associations

Putative candidate SNPs were identified by scanning the data with two complementary models; we avoided using outlier-based

algorithms (e.g., Bayescan; Foll & Gaggiotti, 2008) as they have been shown to perform poorly when selection acts on environmental gradients, when allele frequencies are correlated within or between localities, and/or when samples consist of a few individuals per locality, for many localities on a landscape (e.g., De Mita et al., 2013; Lotterhos & Whitlock, 2015; de Villemereuil, Frichot, Bazin, François, & Gaggiotti, 2014). We first used Latent Factor Mixed Models (LFMM 1.3; Frichot, Schoville, Bouchard, & Francois, 2013) to detect genotype–environment (and indirectly phenotype) correlations with the climatic variables retained above. Each analysis consisted of 10 repetitions of the Gibbs Sampling algorithm with 10,000 iterations each, which were performed after discarding the initial 5,000 steps as burn-in. The number of latent factors was set from one to three, and only those loci systematically recovered across analyses with different latent factors were kept. *p*-Values were re-adjusted in R using the Stouffer method on the combined *z*-scores from all runs, as recommended in the LFMM manual. Significance was assessed after correcting with a FDR threshold of .1 and a median *z*-score larger than 3 and *p*-value < .01, as advised for these kinds of analyses (de Villemereuil et al., 2014).

Second, we explored associations with the Bayesian method available in BAYPASS V1.01 (Gautier, 2015) under the AUX covariate mode (-covmcmc and -auxmode flags), after scaling the variables with the -scalecov flag, as suggested in the manual. We preferred this method over Bayenv (Coop, Witonsky, Rienzo, & Pritchard, 2010; Günther & Coop, 2013) because it is more precise and efficient when estimating the covariance structure matrix (Ω) and more sensitive for identifying SNPs displaying weak association signals resulting from soft adaptive sweeps or involved in polygenic characters (Gautier, 2015), such as morphological or climate-related variation. As for LFMM, analyses were independently performed for each climatic variable. Parameters were adjusted through twenty pilot runs of 1,000 iterations each, and then a final run of 25,000 steps was carried out for each association analysis; samples were taken every 250 iterations after an initial burn-in of 5,000 steps. Significance was assessed based on the Bayes Factor (BF) between models and according to Jeffrey's rule (1961); that is, markers with moderate ($3 < BF < 10$) to decisive evidence ($BF > 20$) were retained.

To disentangle the stochastic and putatively adaptive processes affecting population structure (and thus to confirm that the spatial distribution of alleles at candidate loci was not driven by IBD), the relative contribution of environmental (αE) and geographic (αD) distances (Euclidean) to genetic differentiation (i.e., allele frequency covariation) was finally explored with the software BEDASSLE (Bradburd et al., 2013). This was performed for both alleles of a randomly chosen SNP in each candidate RAD-loci detected above. As a control, analyses were also carried out for subsets of unlinked markers (both alleles) not retained as candidates and which matched both the number and MAF of the candidates. Unlinked noncandidate markers were pinpointed in PLINK with the –r flag (Purcell et al., 2007), using the squared correlation coefficient (r^2) between all genotypes (coded 0, 1, 2) as a proxy of linkage disequilibrium (LD; see Fig. S8).

The distance matrices implemented in BEDASSLE consisted of Euclidean "climatic" distances, estimated with VEGAN 2.4.2 (vegdist function in R: R Development Core Team 2015; Oksanen et al., 2017) from the variables retained from the GLMs, and the Great Circle distances determined above (see sampling subsection). The beta-binomial model of BEDASSLE was run for 5 million generations, and samples were taken every 100 iterations after discarding the first two million runs as burn-in for each data set. Performance and convergence of the models were evaluated by comparing the acceptance rates and parameter trace plots of two replicated runs per data set according to Bradburd et al. (2013). Significant differences between the distribution of $\alpha E/\alpha D$ values across data sets ware evaluated with a *t*-test (means) and a wilcoxon test (medians).

Although limitations exist for pinpointing specific candidate genes from de novo assemblies or from those constructed based on genomes from other taxa (given that decay of linkage disequilibrium or synteny may vary among species and that scaffolds are not yet arranged into chromosomes), the coding regions located the closest to the putative candidate RAD-loci were inferred through a MegaBlast analysis (Zhang, Schwartz, Wagner, & Webb, 2000) against the most recent bird genome assemblies (Jarvis et al., 2014), for discussion purposes only. A match was considered positive when at least 80% of sequence identity and an *e*-value below 1e-4 were obtained. Molecular and biological functions of these genes were obtained from Uniprot (The UniProt Consortium, 2015), QuickGO (Binns et al., 2009), and EMBL-EBI (Kanz et al., 2005) databases.

3 | RESULTS

3.1 | DNA sequence data and species diversity

As the ddRAD-Seq protocol is sensitive to tissue degradation and prone to sequencing errors, an issue also recently pointed out by Shultz, Baker, Hill, Nolan, and Edwards (2016), we preferred having few samples with high-quality data over a greater number of individuals with many missing and/or potentially erroneous genotypes. Following this rationale, and after applying highly conservative filters (see Methods), the best quality reads were aligned to the American crow assembly, covering ~0.02% of this species' genome. We had to remove 26 individuals because of poor DNA quality (likely due to age and storage conditions (i.e., in EDTA at −70°C), and four more because of low Phred score (<20) in most sequence reads. This resulted in a final data set of 1,780,046 paired-end reads for 38 individuals (an average of 26,567 reads per individual).

The final alignment and "ref_map" Stacks assembly generated 4,040 unique RAD-loci, 124 of which were polymorphic and contained 1,649 SNPs per individual. These RAD-loci were aligned to 110 scaffolds of the *C. brachyrhynchos* genome. A mean of six SNPs per polymorphic RAD locus was found. A nonsignificant relationship was observed between the number of SNPs and the length (in bp) of *C. brachyrhynchos* scaffolds (adjusted $R^2 = 0.020$; $p = .072$), suggesting an uneven distribution of markers across the reference genome, likely as a result of low coverage (Fig. S9).

Overall estimates showed a relatively high nucleotide diversity (π = .008; *SE* = .0004), observed heterozygosity (H_o = .0069; *SE* = .0003) and expected heterozygosity (H_e = .0075; *SE* = .0004) for a bird. The average fixation index (F_{IS}) was slightly positive and nonsignificant (0.0036; *SE* = .0005; Figs S3 and S4). Population structure was low for the Yucatan jay. The distribution of (AMOVA-derived) F_{ST} per SNP is shown in Figure 2. Markers with F_{ST} values between 0.003 and 0.0077 were the most abundant, and the highest estimate was 0.21. The admixture analyses indicated that the most likely number of genetic populations (*k*) was 1 (Fig. S10). The DAPC (Jombart, 2008) further confirmed this result (p = .186; Fig. S11A), showing that clusters could not be clearly differentiated without overfitting the data (Fig. S11B).

3.2 | Climatic predictors of morphology and associations with genotype

After eliminating two collinear variables and estimating a GLM for each quantitative trait, nine climatic variables (Bio4, Bio5, Bio8, Bio9, Bio12, Bio13, Bio16, Bio17 and Bio19) that were significantly and recurrently associated with at least two of these traits were retained for the associations with genotypic data (Tables 1 and S2). These climatic variables should thus be viewed as proxies for selective pressures acting on phenotypic variation (sensu Hancock et al., 2011) and provide additional support for the identification of putative candidate genes. Associations performed with these variables allowed 96 SNPs distributed over 11 RAD loci to be identified as putative candidates, with 27 of the significant associations supported by both methods used (LFMM and BAYPASS; Table 1). Some examples are illustrated in Figure 3. Bio4 (temperature seasonality) was the variable that had the greatest number of significant associations, both in total and supported by both methods. Other variables exhibiting a large number of significant associations included Bio12 (annual precipitation), Bio13 (precipitation of wettest month), Bio16 (precipitation of wettest quarter) and Bio19 (precipitation of coldest quarter).

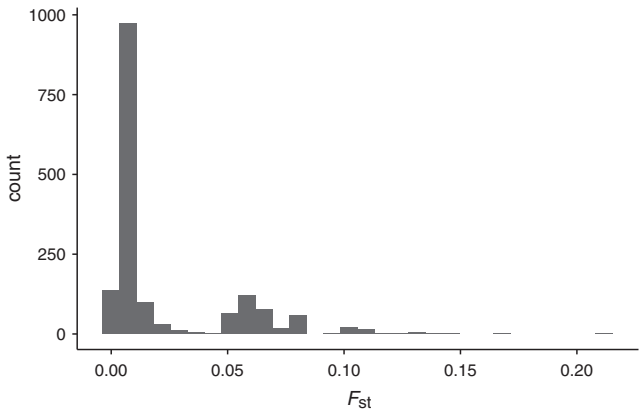

FIGURE 2 Distribution of corrected AMOVA F_{ST} values per locus, estimated with 1,649 high-quality SNPs, among Yucatan jay (*Cyanocorax yucatanicus*) individuals

Of the 11 candidate RAD loci, four were located in introns of known coding genes (Tables 1 and 2) according to the American crow genome annotation: locus 2,144 in a *CCDC8* (coiled-coil domain) gene, locus 7,557 in a *MALDR* (MAM-LDL receptor) gene, locus 29,878 in a *RANGAP1* (Ran GTPase-activating protein) gene and locus 7,746 in a *RGS6* (Regulator of G-protein signalling 6) gene. Although located far away from the nearest gene (i.e., between 56 and 108 kb in the zebra finch genome), five of the remaining RAD loci are worth mentioning (given the identity of their closest genes): RAD loci 4,972, 6,116, 6,238, 1,041 and 733. The closest gene to the first locus (4,972) is an integrin/ubiquitin gene, the closest one to the second locus (6,116) is a zinc-finger protein gene, while the third one mapped near genes encoding for a sal-like protein and a dyslexia-associated protein (which have been annotated in over 50 bird genomes so far). RAD locus 733, which showed significant associations with all climatic variables (e.g., Table 1, Figure 3), was located on Scaffold 89 of the American crow genome and mapped to chromosome 2 of the zebra finch. Its closest known gene is an *ARC* (activity-regulated cytoskeleton-associated) gene. Finally, locus 1,041 was mapped close to a metallophosphoesterase domain containing 2 (*MPPED2*) gene, and a *Hsp40* homologue gene.

These candidate loci, and their corresponding SNPs, showed significantly higher mean and median $\alpha E/\alpha D$ ratios ($p < .001$) than random subsets of unlinked and putatively neutral SNPs matching both their number and MAF (Table 3). For the candidate loci, $\alpha E/\alpha D$ ratios were consistently higher than 1.0 across runs (mean = 3.4), whereas for the noncandidate loci, they were rarely above 1.0 (mean = 0.63), consistent with the hypothesis that factors other than IBD explain the spatial distribution of alleles in particular regions of the Yucatan jay genome.

4 | DISCUSSION

This study represents one of the first attempts to use next-generation sequencing to identify patterns of genomic variation possibly related to IBE in an endemic tropical bird. We took advantage of the high synteny recently found across bird genomes (Ellegren, 2013; Gossmann et al., 2014; Jarvis et al., 2014; Zhang, Jarvis, & Gilbert, 2014) and used the available draft genome of a related corvid (*Corvus brachyrhynchos*), together with stringent bioinformatic filters, to obtain ~1,600 high-quality SNPs for the Yucatan jay. We believe that our framework associating genotypes to environmental variables that covary with phenotypic traits helped us not only to differentiate between patterns of IBD and IBE, but also to pinpoint interesting genomic regions that may be associated with fitness-related traits.

We expected the Yucatan jay, an endemic tropical bird with a cooperative breeding system, to have low genome-wide nucleotide diversity, as such taxa usually have low effective population sizes and significant levels of consanguinity. However, the nucleotide diversity estimates obtained herein (π = .008) were in the same range as those reported for much more widespread temperate birds, like the zebra finch (*Taeniopygia guttata;* π = .01; Balakrishnan &

TABLE 1 Outlier RAD loci (including, in parentheses, the number of significantly associated SNPs per locus) identified by LFMM (–log10[*p*-value]) and BayPass (Bayes factor [BF]) association analyses with nine environmental variables that explain morphometric variation in the Yucatan jay (*Cyanocorax yucatanicus*). The morphometric variables associated to each climatic variable are also indicated (see Table S2 for more details). Values in italic are significant associations in both analyses. The loci in bold are located in introns of known coding genes

	Bioclimatic and morphometric variables LFMM -log10 [*p*-value]/BayPass BF								
	BIO4	**BIO5**	**BIO8**	**BIO9**	**BIO12**	**BIO13**	**BIO16**	**BIO17**	**BIO19**
Locus (number of SNPs)	**WIL CUL**	**TRL TAL BIW**	**TRL TAL BIW**	**TAL BIW**	**TRL WIL TAL CUL BIW BID**	**WIL TAL**	**TAL CUL BIW**	**TAL CUL**	**TAL BIW BID**
2,144 (10)	*3.5/12.9*		na/6		na/3	na/5.4	na/13		na/14.3
4,972 (17)	*8.5/20.6*	*5.3/16.6*		na/12.3	na/18.5	na/5.5	na/12.8	na/52.9	na/21.6
6,116 (9)	*4.8/11.3*				na/5.5				
6,757 (3)	3/na		na/52.9			na/8.9	na/16.4		na/5.8
6,525 (16)	3/na		na/14		na/5	na/15.7	na/18.6	na/9.8	na/5
7,557 (2)	*3.2/22.8*	na/14		na/3.4	na/14.3	na/53.9	na/13.6	na/6.2	na/4.2
1,041 (20)	3.5/na	*5.5/27*			na/12.6	na/16	na/8.3	na/12	na/14.3
29,878 (2)			na/4.8		na/8.9	na/5.8	na/6.4	na/5.6	na/6.7
733 (14)	5/na	5/na	*5/5.9*	*5/5.4*	*5/52.9*	*4.8/8.7*	*5/7.7*	*5/20.9*	*5/3.4*
6,238 (1)	*3/4*				*3/6.5*	*5/13.8*	*3/9.2*	*3/6.8*	3/na
7,746 (2)	3.3/na		3.3/na	*3.3/4*	3.3/na	*3.3/8.1*	3.3/na		*3.3/8.3*

Bio4, temperature seasonality (standard deviation*100); Bio5, maximal temperature of warmest month; Bio8, mean temperature of wettest quarter; Bio9, mean temperature of driest quarter; Bio12, annual precipitation; Bio13, precipitation of wettest month; Bio16, precipitation of wettest quarter; Bio17, precipitation of driest quarter; Bio19, precipitation of coldest quarter; TRL, tarsus length, WIL, wing length; TAL,tail length; CUL, culmen length; BIW, bill width; BID, bill depth.

Edwards, 2009; Backström et al., 2010), the willow grouse (*Lagopus lagopus*; π = .008; Quintela, Berlin, Wang, & Oglund, 2010) and the white-throated sparrow (*Zonotrichia albicollis*; π = .0076; Huynh, Maney, & Thomas, 2010). However, because genome-wide diversity values are not currently available for other tropical endemics and/or cooperative breeders, interspecies comparisons are difficult to make and interpret. It was thus not possible, at the time of this study, to assert whether these diversity estimates are representative or not of tropical endemics and cooperative breeders.

On the other hand, and contrary to our expectations and previous observations in other cooperative breeders, Yucatan jay genetic diversity was not spatially structured, either among locations or across vegetation types (k = 1). Other jays exhibiting similar cooperative reproductive and social behaviours, like the western scrub jay (*Aphelocoma californica*; Mcdonald et al., 1999; Delaney et al., 2008) and the apostlebird (*Struthidea cinerea*), do display significant genetic differentiation, especially among breeding flocks distributed in small geographic areas (Woxvold et al., 2006). Although our findings may suggest that the seasonal fusion–fission dynamics characteristic of the Yucatan jay (Raitt & Hardy, 1976) promotes gene flow through interflock movement, they should be interpreted cautiously, as both our sampling strategy and the filters chosen to produce the final data set were intended to reduce relatedness among individuals. This implies that our sample was inadequate to capture fine-scale genetic structure. This possibility thus remains a hypothesis to be tested in a future study.

Some ecological features of the Yucatan jay, however, are consistent with the lack of population structure observed herein. For instance, this bird is continuously distributed across a region that is mostly covered by forests and has no obvious geographical barriers to gene flow—there are no mountain ranges, and all rivers are subterranean. Yucatan jay flocks are also highly mobile, being able to cover 1 or 2 km in less than an hour, and philopatry decreases at the end of the breeding season (Raitt & Hardy, 1976; F. Termignoni-García, personal observations). Experiments performed with banded individuals (Raitt & Hardy, 1976), indeed, showed that some birds switched groups at particular times of the year, which should promote gene flow. According to the population genetics theory, these characteristics are thus more consistent with a geographical gradient in allele frequencies, such as that arising from isolation by IBD and/or IBE and as suggested by our results (see Table 3), than with an island model in which clear genetic clusters are generated.

For several technical reasons, we ended up with a relatively small sample size (n = 38), which normally affects statistical power when pinpointing candidate adaptive genes (Korte & Farlow, 2013; Long & Langley, 1999). However, preferred data quality over quantity—that is, few individuals with high-quality data instead of a greater number of individuals with many missing genotypes—and using a design in

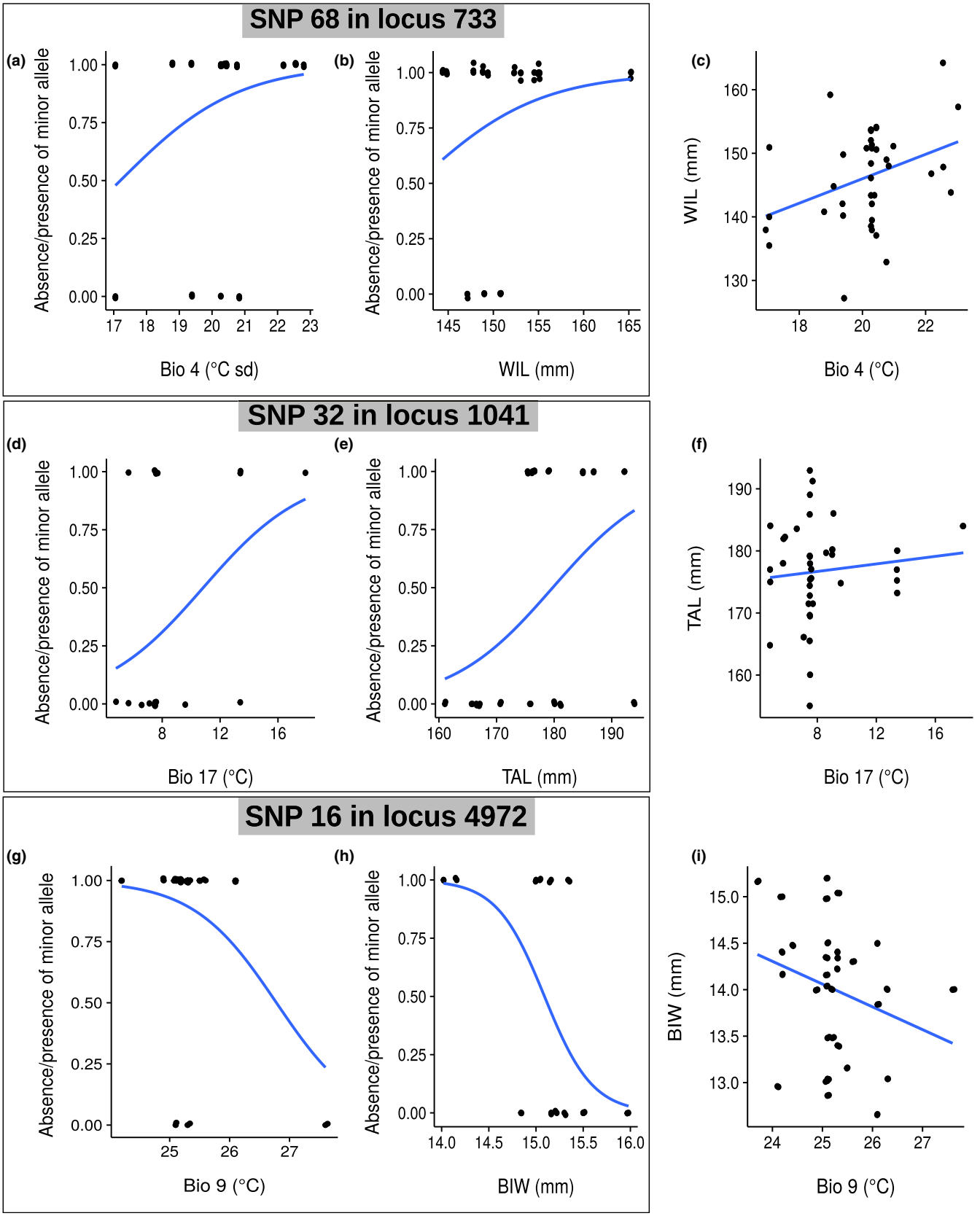

FIGURE 3 Examples (a-b, d-e, g-h) of significant logistic regressions between the absence/presence of the minor allele of candidate SNPs and selected bioclimatic variables related to morphometric variation in the Yucatan jay (*Cyanocorax yucatanicus*). Regressions between climatic and morphometric measures are shown to the right (c, f, i). See Table 1 for all significant associations and Table S2 for the regressions of all climatic predictors on morphometry. Bio4, temperature seasonality; Bio9, mean temperature of driest quarter; Bio17, precipitation of driest quarter; WIL, wing length; TAL, tail length; BIW, bill width [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Name, identity, location on the two reference genomes and putative molecular/biological function of the genes closest to the outlier loci identified by LFMM and BAYPASS in the Yucatan jay (*Cyanocorax yucatanicus*; see Table 1 for more details). The loci in bold are located in introns of known coding genes

Locus	BLAST genes[a]	BLASTed on birds sp.[b]	Scaffold/ Chr[c]	Product	Molecular and biological function[d]
2144	CCDC85C	7	1/5	Coiled-coil domain containing 85C	Cerebral cortex development
4972	ITGA4 ′5/UBE2E3 ′3	2	255/7	Integrin, alpha 4 (antigen CD49D, alpha 4 subunit of VLA-4 receptor)/Ubiquitin-conjugating enzyme E2 E3	Protein involved in the adherence of cells to other cells or to a matrix/Ubiquitin-like modifier conjugation pathway
6116	ZNF521 ′5/SS18 ′3	3	106/2	Zinc finger protein 521, transcript variant X2/Synovial sarcoma translocation, transcript variant X3	Ligand-dependent nuclear receptor transcription coactivator activity/Metal ion and nucleic acid binding. Neuronal stem cell population maintenance
6757	MMS22 5′/POU3F2 3′	38	14/3	Methyl Methanesulfonate-Sensitivity Protein 22-Like/POU domain, class 3, transcription factor 2	Double-strand break repair via homologous recombination and replication fork processing/DNA binding, astrocyte epidermis development
6525	INO80C 5′/TMEM245 3′	2	7/2	INO80 complex subunit C/ Transmembrane protein 245	Chromatin remodelling and regulation of transcription, DNA-template/Integral component of membrane
7557	MALRD1	3	167/2	MAM LDL-receptor class A domain-containing protein 1	Cholesterol homeostasis, biosynthetic process
1041	MPPED2 5′/DNAJC24 3′	14	281/5	Metallophosphoesterase domain containing 2/Hsp40 homolog, subfamily C, member 24	Hydrolase activity. Metabolic process/ DNAJ-Hsp40 proteins are highly conserved and play crucial roles in protein translation, folding, unfolding, translocation and degradation
29878	RANGAP1	3	54/1A	Ran GTPase activation protein	Trafficking protein with interaction with ubiquitin-conjugating
733	PSCA ′5/ ARC ′3	3	89/2	Prostate stem cell antigen-like/ activity-regulated cytoskeleton-associated	Involved in the regulation of cell proliferation/actin binding, associated with the cell cortex of neural soma and dendrites
6238	SALL 5′/KIAA0319 3′	50	146/2	Sal-like protein 3/dyslexia-associated protein	DNA binding transcription factor activity, involved in negative regulation of transcription-pituitary gland development, outer ear morphogenesis and gonad development/neuronal migration and negative regulation of dendrite development
7746	RGS6	5	115/5	Regulator of G-protein signaling 6	GTPase activator activity and intracellular signal transduction

[a]Genes flanking this part of subject sequence on 5′ and 3′ on the American crow genome.
[b]Sequence BLASTed on bird species with 80%–100% identity and e-value 1e-4 or below. The first two always are American crow and Hooded crow.
[c]Scaffold number of the American crow/chromosome number of the zebra finch.
[d]Molecular and biological function known on zebra finch or chicken, obtained on Uniprot, QuickGO EMBL-EBI and NCBI gene.

which samples were fairly evenly distributed across the study site and that included only a few individuals per flock—which reduced relatedness and the autocorrelation of allele frequencies—resulted in relatively good performance of the genotype–environment association methods (see also De Mita et al., 2013; Manthey & Moyle, 2015; Munshi-South, Zolnik, & Harris, 2016; Derkarabetian, Burns, Starrett, & Hedin, 2016 for more examples and a detailed discussion). Indeed, we were able to identify interesting coding gene regions that helped us to differentiate between two competing landscape genetics hypotheses, which suggests that it is unlikely that all putative candidate RAD loci are false positives. The annotation of these loci can actually be taken as further evidence: four of them were located in introns of genes that have been highlighted, both in similar surveys and in functional studies of model bird taxa (see below).

In addition, the BEDASSLE analyses showed that the spatial distribution of alleles of the putative candidates could not be explained by geographic distance alone — that is, it was more likely caused by

TABLE 3 Mean and confidence intervals of the relative contribution of environmental distance (αE) and geographic distance (αD) to the spatial distribution of candidate and noncandidate SNPs detected in the Yucatan jay (*Cyanocorax yucatanicus*). The results of two independent BEDASSLE runs are shown for each allele

Runs	Mean ratio αE/αD	95% Confidence interval
Outlier SNPs		
Allele 1	3.45	0.0002–4.87
Allele 1 rep	1.7	0.0016–10.25
Allele 2	3.90	0.0006–19.40
Allele 2 rep	2.16	0.001–6.90
Non outlier SNPs		
Allele 1	0.63	0.0002–2.22
Allele 1 rep	0.52	0.0005–1.84
Allele 2	0.56	0.0004–1.96
Allele 2 rep	0.64	0.0003–2.21

IBE than by IBD—, while the nonretained markers fitted an IBD framework. Such patterns can be produced by either reduced dispersal across habitats, strong local selective forces or a combination of both. Given the absence of obvious barriers to gene flow and the lack of overall genetic differentiation across vegetation types, we hypothesize that the climate conditions across the environmental gradient where the Yucatan jay is distributed may exert differential pressures on specific targets throughout its genome.

Our analyses point to temperature seasonality and several precipitation variables as the main drivers of adaptation along this environmental gradient. Several studies on adaptation have shown that selective forces act on phenotypes (Joron et al., 2011; Lamichhaney et al., 2016; Esquerré & Keogh, 2016) and that, according to Allen's rule (Allen, 1877), climate variation is an important driver of phenotypic variation in birds, especially in wing and bill morphology (McCollin, Hodgson, & Crockett, 2015; Symonds & Tattersall, 2010). It is thus likely that the candidate regions identified herein affect morphometric variation in the Yucatan jay and that climatic factors exert selective pressures on that variation. This, however, remains a hypothesis to be tested through further association analyses involving more developed (and mapped) genomic tools and the survey of related individuals with a known pedigree (e.g., Fariello et al., 2014; Vaysse et al., 2011).

The Yucatan jay has been described as an omnivorous, opportunistic bird that takes advantage of temporary and localized food sources like caterpillars, berries and slugs (Raitt & Hardy, 1976). However, food supply varies greatly from year to year and among local habitats in the Yucatán Peninsula. For instance, in seasonal forests like the tropical dry forest, fruit availability is usually limited to the rainy season, while some invertebrates are accessible throughout the year. In contrast, in the less seasonal tropical evergreen forest, both fruits and invertebrates can easily be obtained throughout the year (Arita & Rodríguez, 2002; Islebe, Calmé, León-Cortés, & Schmook, 2015; Ramírez-Barahona, Torres-Miranda, Palacios-Ríos, & Luna-Vega, 2009; Vázquez-Domínguez & Arita, 2010). This might translate into contrasting dietary pressures between forest types and be reflected at the morphological and genomic levels, particularly in bill shape and size and underlying genes. Indeed, bills are among the most plastic morphological structures in birds, and bill variation has provided some classic examples of local adaptation for more than a century (e.g., Baldassarre, Thomassen, Karubian, & Webster, 2013; Darwin, 1845; Luther & Greenberg, 2014).

Our short list of candidate genomic regions (Table 2) provides some promising avenues for future studies, especially if the markers detected here are linked to the actual targets of selection. However, such linkage remains to be confirmed in some cases, as the genes located the closest to the matching regions of five of our candidates were actually located at large distances (between 56 and 108 kb) on the zebra finch and American crow genomes, according to our BLAST searches. However, as the recombinational landscape of the Yucatan jay genome is still unknown, it is far too early to completely discard these genes. Moreover, the noncoding regions regulating the expression of these genes might still represent good candidates for further studies (Edwards, Shultz, & Campbell-Staton, 2015).

Temperature, including seasonality, is an important limiting factor for the distribution of birds. Even if it does not vary as much on the Yucatán Peninsula—between 14 and 36.3°C throughout the year—as it does in more temperate regions that most corvids inhabit, the limitations that temperature can impose on the physiology of a species could be strong enough to generate adaptive patterns, even in tropical taxa. The candidate SNPs associated with climate/morphology (Tables 1 and 2) were located in four RAD loci matching introns of known coding genes of the American crow genome. These included the coiled-coil domain containing 85C (*CCDC8*) gene, which is important for epithelial proliferation in several organs (Tanaka, Izawa, Takenaka, Yamate, & Kuwamura, 2015) and cortical development (Mori et al., 2012); the Ran GTPase-activating protein (*RANGAP1*) gene, a trafficking protein with cellular response to vasopressin (Hori et al., 2012); the MAM-LDL receptor (*MALDR*) gene, which is involved in regulating bile acid biosynthetic process in cholesterol homeostasis (Mouzeyan et al., 2000; Phan, Pesaran, Davis, & Reue, 2002; Vergnes, Lee, Chin, Auwerx, & Reue, 2013); and the Regulator of G-protein signalling 6 (*RGS6*) gene, which regulates the G protein-coupled receptor signalling cascades (Posner, Gilman, & Harris, 1999). These genes should thus be worth exploring in future studies, as some of them (e.g., *MALDR* and *CCDC8*) may affect basal metabolic rate and body mass, which in turn are affected by temperature (Root, 1988).

This study allowed us to identify footprints of IBE in the presence of gene flow. Despite the controversies about IBE, recent studies suggest that it is rather common in nature (Dennenmoser et al., 2014; Lonsinger et al., 2015; Mallet et al., 2014; Manthey & Moyle, 2015; Mendez et al., 2010) and that selection can be detected in the presence of (and even promoted by) high gene flow (Nielsen et al., 2009; Saint-Laurent et al., 2003; Schweizer et al., 2016). Such conditions may well apply to the Yucatan jay, as the dynamics of the cooperative breeding social system can be altered by environmental

gradients. This social strategy has been shown to be flexible and vary across this species' range, following a similar spatial pattern as morphometric and candidate SNP variation (F. Termignoni-Garcia & P. Escalante Pliego, unpublished data). These observations support the hypothesis that cooperative breeding is adaptive in environments characterized by high interannual variability, as it facilitates breeding and reproduction in both harsh and advantageous years (Koenig & Walters, 2015; Rubenstein & Lovette, 2007). However, additional genomic studies, both on the Yucatan jay and other cooperative breeding species, are needed to further document these patterns of diversification.

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DATA ACCESSIBILITY

Data and processing files are available via Dryad Digital Repository, https://doi.org/10.5061/dryad.2t6t8, including FASTQ sequence files, info database with IDs, geographic coordinates, morphometric and bioclimatic data, output from STACKS ref_map.pl pipeline and populations program (SNPs, consensus sequences, summary statistics, STRUCTURE and PLINK inputs), BLAST and input/output files for LFMM, BAYPASS and BEDASSLE.

AUTHOR CONTRIBUTION

The study was planned, the genomic libraries were made, the analyses are performed, the results are analysed and the manuscript was written by F.T.-G. Data analyses were planned, the results were interpreted and writing the manuscript was helped by J.P.J.-C. The field work was done and samples were provided by J.C.S. Standardizing the ddRAD-Seq bench protocol was helped by A.J.S. Making the genomic libraries was helped by M.L. Funding for sequencing and laboratory work was provided and writing the manuscript was helped by S.V.E. The study was planned and extra funding was provided by P.E.-P.

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