EVOLUTIONARY ASPECTS OF THE FAMILY CORVIDAE (AVES): A SYNTHESIS OF PHYLOGENETICS, BIOGEOGRAPHY AND NICHE EVOLUTION

BY

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Abstract

Despite intensive research attention over the decades, many aspects of the evolutionary history of the bird family Corvidae remain to be assessed. This dissertation focuses on several such details, such as the (a) phylogenetic relationships, (b) biogeography, and (c) evolutionary ecology of this passerine radiation, using diverse analytical approaches. Here, I focus on three subfamilies of the family Corvidae: the Cyanocoracinae (New World jays), distributed across most of the New World, and the Crypsirininae (treepies) and Cissinae (blue/green magpies), both distributed in tropical South and Southeast Asia. In chapter one, I reconstruct the geographic origin of the New World jays. In chapter two, I investigate the molecular phylogenetics and biogeography of the Crypsirininae and Cissinae, using genome-wide sampling of molecular characters. Finally, in the third and fourth chapters I reconstruct the climatic niches of the NWJs and treepies and blue/green magpies, respectively, and attempt to understand the dynamics of climatic niches through evolutionary time. Additionally, from the phylogenetic, biogeographic, and niche reconstruction outcomes of these focal clades, I attempt to understand how the combined effects of different evolutionary phenomena have paved the way to the current diversity and distributions in the family Corvidae as a whole.

Acknowledgments

Words cannot express my deepest gratitude to my mentor, Dr. A. Townsend Peterson, for accepting me into his lab, and for his immense guidance, knowledge, encouragement and care given throughout this long learning experience. I admire the kindness and patience with which he tolerated my certain flaws; being the silent person I am with minimal communication skills, yet he continued to have faith in me. I am extremely grateful for the motivational uplift he gave me every single time, in a calm and lovable way. I cannot thank him and Rosa enough for everything they both did for my husband and me during our stay here in Lawrence.

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Introduction

The avian family Corvidae is a monophyletic group of songbirds (order Passeriformes), which includes crows, jays, magpies, and allies. The family consist of 24 genera and ~132 species (Jønsson et al. 2016; Ericson et al. 2005; Bonaccorso and Peterson 2007), often grouped in six subfamilies (i.e., Corvinae, Cissinae, Crypsirininae, Cyanocoracinae, Perisoreinae, Pyrrhocoracinae), with a worldwide distribution. The group is represented in almost all habitats, with its members living under a broad variety of conditions. These birds' unusual intelligence, repertoire of vocalizations, and fascinating behavioral adaptations of the family, have all intrigued biologists for decades, drawing much research attention.

Quite a number of studies has focused on phylogenetic relationships among major corvid lineages (Bonaccorso and Peterson 2007; Ericson et al. 2005; Monteros and Cracraft 1997; Rice et al. 2003). Other studies have focused on particular genera or sublineages (McCormack et al. 2008; McCormack et al. 2010). However, many aspects of corvid evolution remain unanswered, including neglected lineages and unanswered questions. Hence, this dissertation focuses on several such unknown details of the phylogenetic relationships, biogeography, and evolutionary ecology of this family, using numerous novel methods and approaches.

In Chapter 1, I investigated the geographic origin of New World jays, which was an equivocal concept at the time of publishing. I conducted a biogeographic analysis along with divergence time estimation, based on a dense phylogenetic hypothesis for the early branches of corvids; the goal was to explore how the New World jays (NWJ) originated when some early corvid lineage colonized the Americas in the historical past. Biogeographic reconstructions indicated that NWJs originated from an ancestor in the Eastern Palearctic or Eastern + Western Palearctic, diversified in Mesoamerica, and spread subsequently to North and South America.

Furthermore, the group has been diversifying in the New World since the late Miocene. This chapter was published in *Neotropical Biodiversity*.

In Chapter 2, I explored the molecular phylogenetics and biogeography of two non-sister clades of the family Corvidae, the treepies and blue/green magpies (i.e., subfamilies Crypsiririnae and Cissinae). The two clades include some of the more threatened and most colorful taxa of the family, and yet these subfamilies are also among the least-well-known corvids in terms of systematics and ecology. In this chapter, I produced species-level phylogenies for treepies and blue/green magpies, inferred from thousands of ultra-conserved element sequences (UCEs) and up to 6 Sanger-sequenced gene regions followed by biogeographic analyses for the two clades. Treepies and blue/green magpies originated in East Asia, and East Asia and Sundaland, respectively, during the late Miocene and dispersed out of the Asian mainland later on. This chapter has been submitted for publication to *Journal of Avian Biology*.

In Chapter 3, I examined climate niche evolution in the New World Jays (NWJs) by mapping temperature and humidity niches on to a comprehensive and well-resolved phylogenetic framework, using a novel methodology that explicitly incorporates the uncertainty associated with species' climate niches. This method was employed to avoid overinterpretation of niche evolution that commonly results from other ancestral niche reconstruction analyses. My results revealed that, in NWJs, humidity niches tend to be more dynamic compared to temperature niches, and that different clades display different degrees of niche conservatism (*versus* niche dynamism). In this chapter, I provide a synthetic view of ecological niche in the NWJs, and its evolution over time by relating observed evolutionary changes to species' distributional patterns, ecological aspects, and Earth's geological history.

In Chapter 4, I investigated climatic niche stability *versus* dynamism, and geographic range evolution in treepies and blue/green magpies. In general, my climate niche reconstructions indicated that temperature niches in treepies and magpies are more dynamic than humidity niches, perhaps suggesting that temperature acts as a more significant driver in shaping species' distributions and diversification, in the tropics. In this chapter, I also attempted to relate environmentally driven evolutionary patterns to biogeographic processes with a goal toward understanding species' distributions across spatial and temporal scales.

CHAPTER 1*

Reconstructing the geographic origin of the New World jays (family Corvidae)

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*Fernando, S. W., A. T. Peterson, and S.-H. Li (2017). Reconstructing the geographic origin of the New World jays. Neotropical Biodiversity 3:80–92.

Abstract

We conducted a biogeographic analysis based on a dense phylogenetic hypothesis for the early branches of corvids, to assess geographic origin of the New World jay (NWJ) clade. We produced a multilocus phylogeny from sequences of three nuclear introns and three mitochondrial genes, and included at least one species from each NWJ genus and 29 species representing the rest of the five corvid subfamilies in the analysis. We used the S-DIVA, S-DEC, and BBM analyses implemented in RASP to create biogeographic reconstructions, and BEAST to estimate timing of NWJ diversification. Biogeographic reconstructions indicated that NWJs originated from an ancestor in the Eastern Palearctic or Eastern + Western Palearctic, diversified in Mesoamerica, and spread subsequently to North and South America; the group has been diversifying in the New World since the late Miocene.

Introduction

The New World jays (NWJs) are a monophyletic group of corvids (Monteros and Cracraft 1997) presently considered to comprise 7 genera (*Aphelocoma*, *Calocitta*, *Cyanocitta*, *Cyanocorax*, *Cyanolyca*, *Gymnorhinus*, and *Psilorhinus*); the ~36 species (Madge and Burn 1994; Goodwin 1976) represent the product of a radiation across much of the Americas . The group has long been a focus of research in behavioral ecology, in light of complex behavioral repertoires, particularly as regards social behavior (Brown 1974, 1963; Peterson 1992).

The origins of corvids can be traced to Australia, from where the ancestor of the family dispersed to Asia, followed by radiations in Asia, Europe, and elsewhere (Sibley and Ahlquist 1985). Ericson and colleagues (Ericson et al. 2002; Ericson and Johansson 2003; Ericson et al. 2005) provided evidence that the origin of the oscine passerines, to which the Corvidae belongs, dates to the split of the Australo-Papuan tectonic plate from Antarctica in the early Tertiary, ~53M years ago. Thus, the replacement of the early Tertiary rainforests in Australia by drier vegetation may have placed presumably forest-adapted early corvids in more open habitats, resulting in a new radiation that led to the present global distribution of the family. However, a recent study (Jønsson et al. 2016) estimated the age of the family at ~20M years. Colonization of the New World by corvids occurred more recently, apparently via a trans-Beringian route (Sibley and Ahlquist 1985). The ancestor of NWJs, thought to be jay-like lineages related to *Cissa* and *Urocissa*, reached North America 10−8M years ago, in the Miocene (del Hoyo et al. 2009). Once in the Americas, a rapid radiation in South America by the early Pliocene, was apparently followed by a secondary radiation in North America (Monteros and Cracraft 1997). This hypothesis was not supported by the later analyses of Bonaccorso and Peterson (2007), who offered support for a hypothesis that the NWJ ancestor was in Mesoamerica or North America +

Mesoamerica, and then radiated into North and South America independently. The origins of this diverse clade are of considerable interest in light of questions about the biogeography of Asian and American tropical groups (Benz et al. 2006), morphological innovation (Zusi 1987), and the evolutionary origins of social behavior (Zusi 1987).

Several previous studies have examined the evolutionary history, phylogeny, and biogeography of the NWJs, but invariably based on sparse representation of NWJ genera and limited outgroup sampling. Monteros and Cracraft (1997) proposed a first hypothesis of intergeneric relationships in the group based on cytochrome *b* sequences. Ericson et al. (2005) added markers, but included only single species per genus. Saunders and Edwards (2000) examined mitochondrial DNA control region (CR) variation among representatives of all NWJ genera. Finally, Bonaccorso and Peterson (2007) derived a multilocus phylogeny with much-improved NWJ species representation, and included a historical biogeographic analysis that concluded that NWJ origins were in Mesoamerica or Mesoamerica + North America.

These previous studies, however, did not provide sufficient detail in terms of representation of taxa of NWJs and other corvids to permit thorough understanding the geographic origin of NWJs, or to identify their closest corvid relatives. The key deficiency has been in terms of representation of taxa from the deepest branches of the corvid phylogeny; thus, we here derive a denser phylogenetic hypothesis by deriving DNA sequences for these early lineages, placing several species of treepies, blue magpies, and green magpies in a molecular phylogeny for the first time, to permit more robust biogeographic analyses. In light of this new dataset, we discuss geographic origins of NWJs, and offer a new hypothesis.

Methods

Taxon and gene sampling

Taxon sampling included at least one species from each NWJ genus, 29 species representing the rest of the five corvid subfamilies, and *Lanius* as a definitive outgroup (Table 1.1). Frozen tissue samples (muscle tissue) were obtained from the American Museum of Natural History, Louisiana State University Museum of Natural Science, National Taiwan Normal University, and the University of Kansas Natural History Museum. We also added DNA sequences from GenBank from previous studies (Andersen et al. 2015a; Bonaccorso 2009; Bonaccorso et al. 2010; Bonaccorso and Peterson 2007; Cibois and Pasquet 1999; Cicero and Johnson 2001; Cracraft and Feinstein 2000; Ericson et al. 2005; Feldman and Omland 2005; Fuchs et al. 2011; Gonzalez et al. 2008; Helm-Bychowski and Cracraft 1993; Jønsson et al. 2012; Kennedy et al. 2012; Kryukov et al. 2004; Kryukov et al. 2012; Morinha et al. 2016; Price et al. 2014; Slager et al. 2014; Zhang et al. 2012; Monteros and Cracraft 1997) that overlapped our sequenced gene regions.

DNA sequences were obtained for three mitochondrial genes (cytochrome *b*, or Cyt*b*; nicotinamide adenine dinucleotide dehydrogenase subunit 2, or ND2; and nicotinamide adenine dinucleotide dehydrogenase subunit 3, or ND3), and three nuclear introns (the seventh intron of the beta-fibrinogen gene, or βfib7; the second intron of the myoglobin gene, or Myo2; and the fifth intron of the transforming growth factor β2, or TGFβ2). Genes were amplified using the following primers: Cytb, L14851 (Primmer et al. 2002) and L428 and H494 (Reddy 2008); ND2, L5215 and H6313 (Sorenson et al. 1999); ND3, L10755 and H11151 (Chesser 1999); βfib7, FIB-B17U and FIB-B17L (Prychitko and Moore 1997); Myo2, Myo2 (Fjeldså et al. 2003) and Myo3f (Slade et al. 1993); and TGFβ2, TGF5 and TGF6 (Primmer et al. 2002).

DNA extraction, PCR amplification, sequencing, alignment, and model selection

DNA was extracted from frozen tissues using proteinase K digestion under manufacturer's protocols (Qiagen DNeasy tissue kit). PCR amplifications were performed using Promega GoTaq Flexi DNA polymerase. We employed a touchdown protocol for amplification of ND2 and ND3, with annealing temperatures of 55°C and 50°C, respectively. Constant annealing temperatures of 58°C, 50°C, 59°C, and 56°C were used for Cyt*b*, βfib7, Myo2, and TGFβ2, respectively. PCR products were sent to Beckman Coulter Genomics (Danvers, MA) for purification and final sequencing.

Sequences were cleaned, assembled, and aligned in Geneious 8.1.6 (Biomatters, Auckland, New Zealand), and checked against an automated alignment in MUSCLE (Edgar 2004). Sequence data were partitioned by codon position for mitochondrial DNA and by gene for nuclear introns. We used MrModelTest 2.3 (Nylander 2004) to identify appropriate substitutional models for each partition under the Akaike Information Criterion (AIC).

Phylogenetic analysis

Single-gene matrices were concatenated using Geneious 8.1.6 to produce an overall mitochondrial dataset, a nuclear intron dataset, and a total combined matrix. Phylogenies were estimated with Bayesian analysis (BA) and maximum-likelihood (ML) inference methods. GARLI v2.01 (Zwickl 2006) was used for the maximum-likelihood analysis. We performed 100 independent analyses, and chose the tree with the best likelihood score. Nodal support values for topologies were evaluated via 500 non-parametric bootstrap replicates (Felsenstein 1985). The 50% majority-rule consensus tree was acquired in PAUP* 4.0 (Swofford 2003); 70% bootstrap support was considered as indicative of solid nodal support (Hillis and Bull 1993; Wilcox et al. 2002).

Bayesian phylogenetic estimates were obtained in MrBayes 3.2.2. (Altekar et al. 2004; Ronquist et al. 2012; Ronquist and Huelsenbeck 2003) Two independent Markov chain Monte Carlo (MCMC) runs of 2 × 107 generations using four chains (temp = 0.1) per run were conducted. We sampled trees every 2000 generations, and discarded the first 25% of the trees as burn-in. We used TRACER 1.6 (Rambaut et al. 2014) to assess convergence of parameter estimates and posterior probabilities. The remaining trees were summarized to obtain a 50% majority-rule consensus tree.

Ancestral area reconstructions

We employed S-DIVA (Statistical Dispersal-Vicariance Analysis), “Bayes−Lagrange” or Statistical Dispersal-Extinction-Cladogenesis (S-DEC, (Ree et al. 2005; Ree and Smith 2008)), and Bayesian Binary Method (BBM) analysis implemented in RASP 3.2 (Yu et al. 2010; Yu et al. 2015) to reconstruct ancestral areas of corvid lineages. DIVA is an event-based method in which vicariance is assumed, and includes potential contributions for dispersal and extinction by assigning a cost (Ronquist 1997). S-DIVA is an expansion of Bayes-DIVA implemented by Nylander et al. (Nylander et al. 2008) that incorporates the entire posterior distribution of tree topologies, thus accounting for both phylogenetic and ancestral state uncertainty (Yu et al. 2015; Yu et al. 2010). S-DEC model has been implemented using the source code for the C++ version of Lagrange (Smith 2010). This model gives the likelihood of all possible biogeographic scenarios estimated at a given node, and it summarizes biogeographic reconstructions across all user-supplied trees (Yu et al. 2015). BBM is a statistical procedure in which a full hierarchical Bayesian approach is used to reconstruct ancestral distributions at ancestral nodes (Ronquist 2004); it is implemented in RASP, wherein the source code of MrBayes 3.1.2 is used to create the MCMC analysis.

We defined eight geographic areas (A = North America, B = Mesoamerica, C = South America, D = Western Palearctic, E = Eastern Palearctic, F = Afrotropics, G = Indo-Malaya, H = Australia). We assigned each species included in the phylogenetic analysis to a region or regions, based on published range maps (eBird 2015). S-DIVA, S-DEC, and BBM analyses were conducted using 10,000 post burn-in trees derived from the overall combined data matrix from the Bayesian MCMC procedure implemented in BEAST 1.8.2. (Drummond et al. 2012). For the S-DEC analysis, we considered the probability of dispersal between areas as equal, and all values in the dispersal constraint matrix were set to 1. BBM analysis used the maximum clade probability tree (condensed tree) from the BEAST analysis, and included two independent runs of 10 chains (temp = 0.1) that ran for 1M generations, sampling every 100 generations, but discarding the initial 25% as burn-in. We used the F81+G evolutionary model for the analysis, based on the results of the model testing described above. In all analyses, the maximum number of areas included in ancestral distributions was set to 2. We excluded the broadly distributed outgroup *Lanius* from these analyses.

Timing of diversification

The fossil record for passerine birds is scarce and many described fossils lack information necessary for use as informative calibration points (Parham et al. 2012). Thus, we estimated the time of diversification of NWJs using previously published ND2 substitution rate priors using BEAST 1.8.2 under a relaxed clock model. We unlinked nucleotide substitution models, and used MrModelTest 2.3 (Nylander 2004) to obtain best-fitting substitutional models. We linked clock and tree models, used a birth-death speciation process, and ran them for 5 ×108 generations, sampling every 50,000th generation. Convergence was examined in TRACER (Rambaut et al. 2014); all effective sample size (ESS) values were >200. We discarded the initial 25% of samples as burn-in. Calibrating a phylogeny based on empirically-determined mitochondrial DNA substitution rates offers only a rough estimate of actual time, though lacking fossils within the clade, such an external rate calibration offers the only option for linking to actual dates (Hosner et al. 2013). ND2 is widely studied in ornithology (Andersen et al. 2015b); we used two empirically estimated substitution rate priors derived from ND2 substitution rates (2.4 and 3.3% / lineage / million years) for Hawaiian honeycreepers (Lerner et al. 2011) that were derived based on three recently obtained geologic calibration points, to estimate divergence times for various corvid lineages.

Results

Topologies inferred via ML and BA analysis were highly congruent for the concatenated mitochondrial and nuclear sequence datasets (Figure 1.1). Results from the BEAST analysis were similar to the ML and BA topologies, except that *Pyrrhocorax* was placed as sister to clade A in the BEAST analysis (posterior probability 0.84); ML and BA could not resolve the placement of this genus. In general, these mostly-congruent phylogenetic hypotheses all agreed in identifying five clades within the corvids: A, including *Dendrocitta*, *Crypsirina*, *Platysmurus* and *Temnurus*; B, including *Cissa* and *Urocissa*; C, including *Cyanopica* and *Perisoreus*; D,

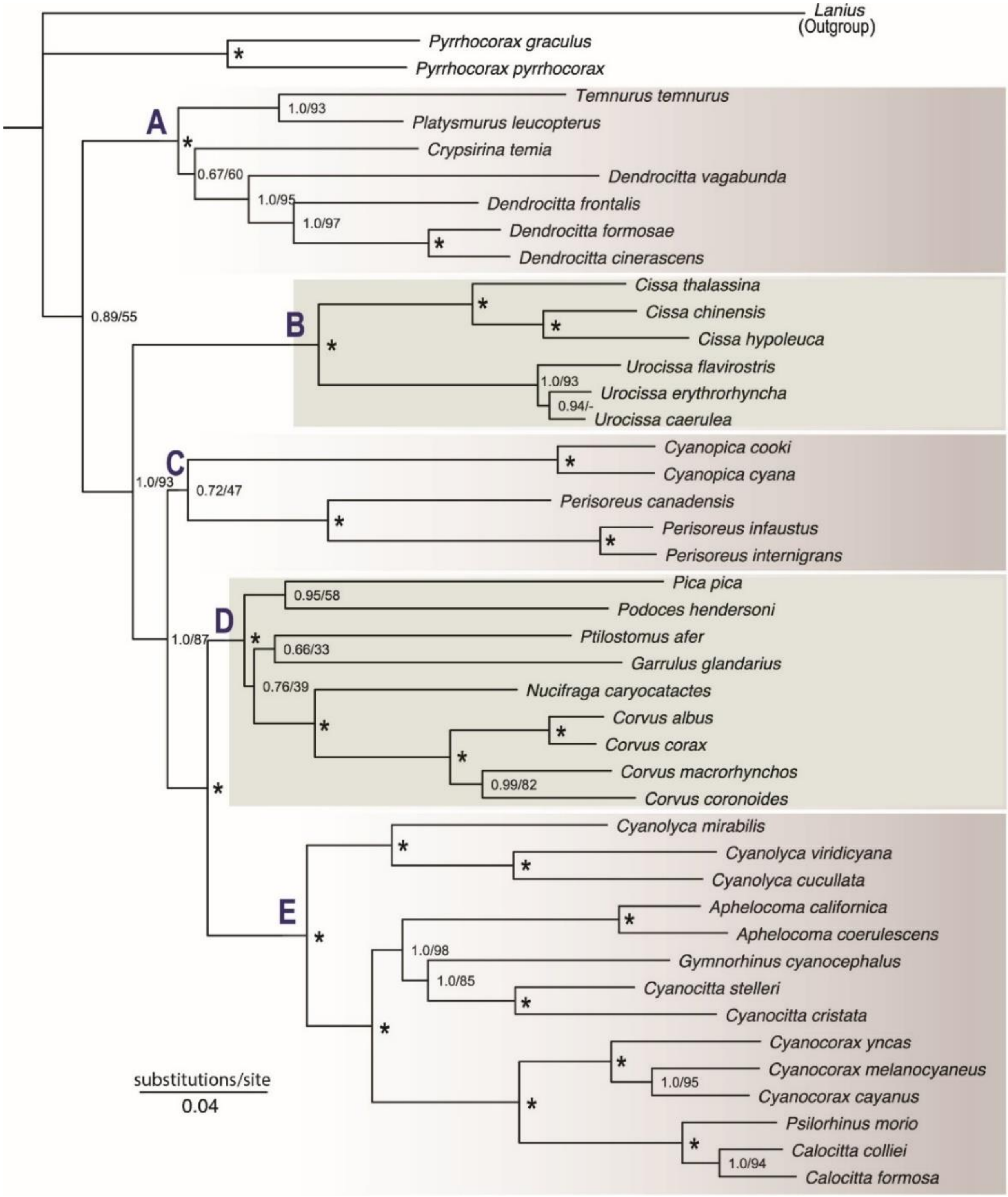

Figure 1.1. Phylogeny of Corvidae based on Bayesian and Maximum Likelihood analyses of the combined data-set. Numbers at the nodes refer to Bayesian posterior probability/ML bootstrap support. Asterisks indicate 1.0 posterior probability and 100% bootstrap support. Letters at nodes indicate five major clades of the family.

including *Corvus*, *Garrulus*, *Nucifraga*, *Pica*, *Podoces*, and *Ptilostomu*; and E, including, *Aphelocoma*, *Calocitta*, *Cyanocitta*, *Cyanocorax*, *Cyanolyca*, *Gymnorhinus*, and *Psilorhinus*. The NWJ clade (clade E) was placed as sister to clade D with strong support (posterior probability 1.0, 100% ML bootstraps). Monophyly of the clades C, D, and E was highly supported (1.0, 87%), although the sister relationship of *Perisoreus* and *Cyanopica* was ambiguous (0.72, 47%). Placement of *Podoces* as sister to *Ptilostomus* (Ericson et al. 2005) was not well-supported; in contrast, a sister relationship between *Podoces* and *Pica* was better-supported, with a posterior probability of 0.95 and 58% bootstrap support.

S-DIVA, S-DEC, and BBM ancestral area reconstructions for NWJs produced congruent results, estimating Mesoamerica as the most-probable ancestral area for the common ancestor of clade E (Figure 1.2). According to S-DIVA analysis, Mesoamerica + Eastern Palearctic was the most probable ancestral area ($p = 1.0$) for the common ancestor of clades D and E. S-DEC also showed Mesoamerica + Eastern Palearctic as the most probable ancestral area ($p = 0.63$), and Eastern Palearctic was the other possible area ($p = 0.37$). BBM results were equivocal, with four possible ancestral areas: Eastern Palearctic ($p = 0.40$), Eastern Palearctic + Western Palearctic ($p = 0.31$), Western Palearctic ($p = 0.16$), and ambiguous ($p = 0.13$). Because all NWJ lineages were connected to American areas, uncertainty in phylogenetic arrangements within clade C had no effect on our reconstructions of areas of lineages ancestral to the NWJs.

BEAST relaxed-clock analysis based on the two substitution rate priors indicated that the time to the most recent common ancestor for NWJs was 5.8−4.3M years. The split of the NWJ clade (clade E) from its sister clade (clade D) was estimated at 6.7−5.0M years (Figure 1.3). Our analysis estimated that the Corvidae likely originated in the late Miocene, 8.0−5.9M years ago.

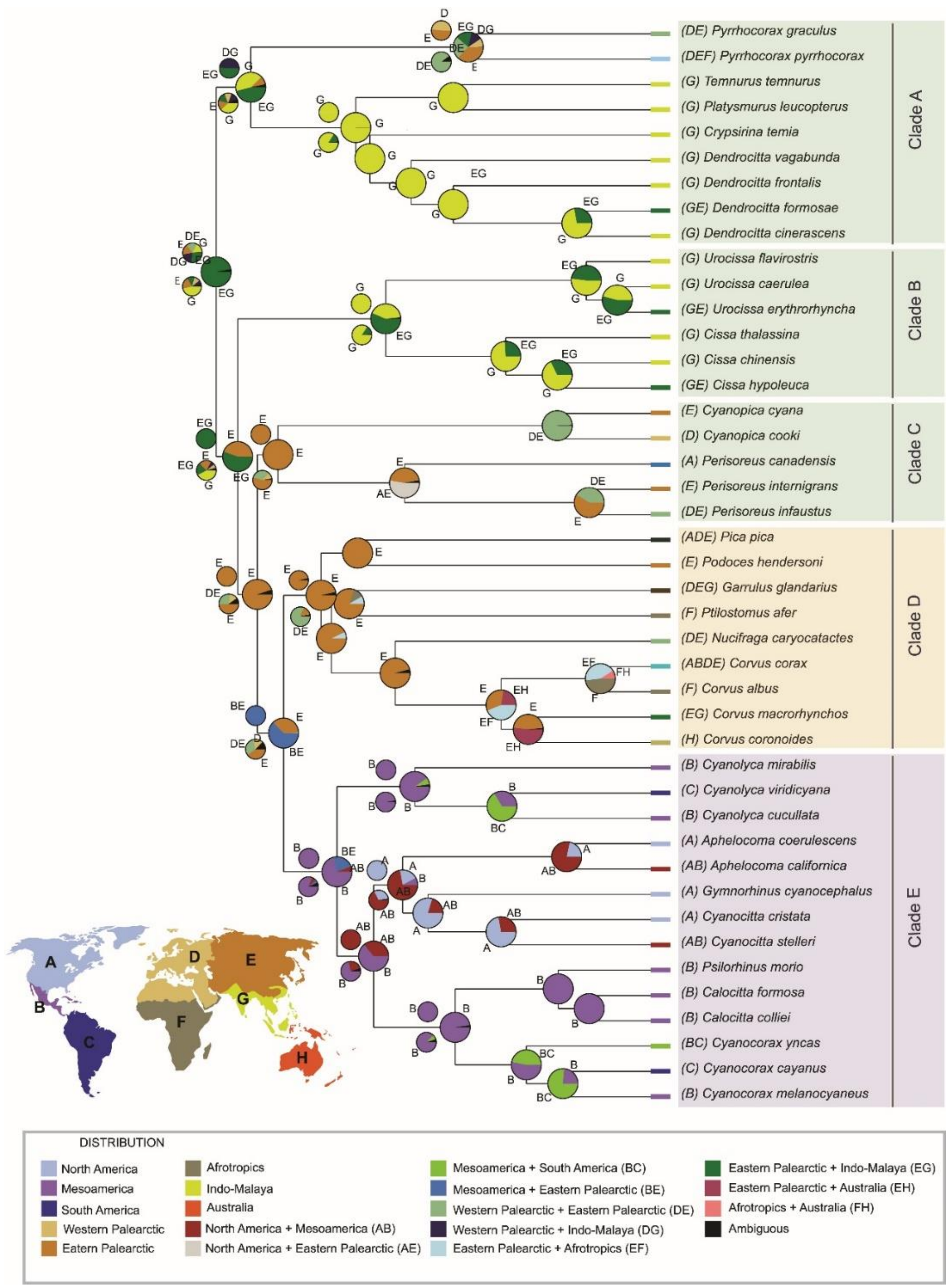

Figure 1.2. Reconstruction of the ancestral area of lineages of Corvidae. Pie charts indicate probability of various ancestral area combinations. Pie charts at nodes were derived from S-DEC analysis; the smaller charts above and below at the nodes obtained from S-DIVA and BBM analyses, respectively. Ancestral areas are shown only for basal nodes. The New World jay clade (clade E), its sister clade (clade D) and all other basal clades (C, B and A) of corvids, are outlined in light blue, orange and green boxes, respectively.

Table 1.1. List of samples used in the study. GenBank sequences from previous studies are denoted by “G”. Institutional abbreviations: AMNH, American Museum of Natural History; KUNHM, University of Kansas Natural History Museum; LSUMNS, Louisiana State University Museum of Natural Science; NTNU, National Taiwan Normal University.

Genus/species	Institution/	Locality	GenBank Accession					
	Sample #		ND2	ND3	Cytb	Myo2	Fib7	TGF
Aphelocoma californica	GenBank		AY030142	AY030162	AY030116	-	DQ912638	-
Aphelocoma coerulescens	GenBank		DQ912601	-	U77335	AY395580	AY395598	-
Calocitta colliei	GenBank		DQ912603	-	DQ912591	-	DQ912640	-
Calocitta formosa	GenBank		DQ912602	-	U77336	AY395581	DQ912639	-
Cissa chinensis	KUNHM 30894	Vietnam: Kon Tum, Ngoc Linh Nature Reserve	KY492676	KY492613	JQ864486^{G}	KY492636	KY495261	-
Cissa hypoleuca	KUNHM 23241	Vietnam: Dong Nai; Vinh Cuu Reserve	KY492677	KY492614	-	KY492637	KY495262	KY492656
Cissa thalassina	LSUMZ 19185	Zoo/Captive	KY492678	KY492615	KY492609	KY492638	KY495263	KY492657
Corvus albus	GenBank		JQ024060	JQ023990	AY527262	-	-	-
Corvus corax	GenBank		JQ864446	-	JQ864490	KP070388	-	KP070515
Corvus coronoides	GenBank		JQ023957	JQ024031	AF197837	-	-	-
Corvus macrorhynchos	KUNHM 10955	Philippines: Cagayan; Calayan Island	KY492679	KY492616	HE805915^{G}	KY492639	KY495264	KY492658
Crypsirina temia	KUNHM 23219		KY495243	KY492617	KY492610	-	-	-
Cyanocitta stelleri	GenBank		KM115187	AY030159	KF208991	-	DQ912642	-
Cyanocitta cristata	KUNHM 2271	USA: Kansas; Shawnee	KY495244	KY492618	X74258^{G}	KY492640	KY495265	KY492659
Cyanocorax cayanus	GenBank		GU144814	-	GU144857	-	DQ912650	-
Cyanocorax yncas	GenBank		KJ455397	-	KJ456245	KJ454784	GU144910	-
Cyanocorax melanocyaneus	KUNHM 9260	El Salvador: La Laguna	KY495245	KY492619	GU144897^{G}	KY492641	KY495266	KY492660
Cyanolyca cucullata	GenBank		FJ598175	-		-	FJ598267	-
Cyanolyca mirabilis	GenBank		DQ912606	-	DQ912592	-	DQ912644	-
Cyanolyca viridicyana	KUNHM 21176	Peru: Puno	KY495246	KY492620	U77333^{G}	KY492642	KY495267	KY492661
Cyanopica cooki	GenBank		-	-	AY701180	-	-	-
Cyanopica cyana	LSUMZ 17007	Japan	KY495247	KY492621	JQ393672^{G}	KY492643	KY495268	KY492662
Dendrocitta cinerascens	KUNHM 17738	Malaysia: Sabah	KY495248	KY492622	KY492611	KY492644	KY495269	KY492663
Dendrocitta formosae	KUNHM 23470	Vietnam: Dien Bien; Muong Nhe Nature Reserve	KY495249	KY492623	JQ864494^{G}	KY492645	KY495270	KY492664
Dendrocitta frontalis	KUNHM 15238	Myanmar: Jed Lwe	KY495250	KY492624	JQ864495^{G}	KY492646	KY495271	KY492665
Dendrocitta vagabunda	GenBank		JQ864453	-	JQ864496	KJ454790	-	-
Garrulus glandarius	KUNHM11120	China: Guizhou; Kuan Kuo Shui Nature Reserve	KY495260	KY492625	AB242559^{G}	KY492647	KY495272	KY492666
Gymnorhinus cyanocephalus	GenBank		AY030141	AY030161	AY030115	AY395589	DQ912651	-
Nucifraga caryocatactes	KUNHM 25176	China: Szechwan	-	KY492626	KJ456365^{G}	KY492648	KY495273	KY492667
Perisoreus canadensis	LSUMZ 51588	USA: Idaho	KY495251	KY492627	PCU77331^{G}	KY492649	KY495274	KY492668
Perisoreus infaustus	GenBank		-	-	PIU86042	AY395591	AY395608	-
Perisoreus internigrans	GenBank		-	-	AY395621	-	-	-
Pica pica	KUNHM 28683	Mongolia: Gobi Altai; Han Taishir Mountain	KY495252	KY492628	KJ456399^{G}	KY492650	KY495275	KY492669
Platysmurus leucopterus	LSUMZ B58660	Malaysia:Sarawak	KY495253	KY492629	KY492612	-	-	-
Podoces hendersoni	KUNHM 20618	Mongolia: Omnogobi; Halzan Mountain	KY495259	KY492630	-	KY492651	KY495276	KY492670
Psilorhinus morio	KUNHM 21842	Mexico: Campeche; Silvituc	KY495254	KY492631	DQ912594^{G}	KY492652	KY495277	KY492671
Ptilostomus afer	GenBank		-	-	PAU86040	AY395594	AY395613	-
Pyrrhocorax graculus	AMNH DOT11085		JQ864479^{G}	NC_025927^{G}	JQ864522^{G}	-	-	-
Pyrrhocorax pyrrhocorax	KUNHM 28865	Mongolia: Bulgan Soum; Baitag Boyd Mountain	KY495255	KY492632	JQ864523^{G}	KY492653	KY495278	KY492672
Temnurus temnurus	GenBank		-	-	AY395626	AY395596	AY395614	-
Urocissa caerulea	NTNU		KY495256	KY492633	-	KY492654	KY495279	KY492673
Urocissa erythrorhyncha	KUNHM 11247	China: Dashahe Nature Preserve	KY495257	KY492634	KJ456508^{G}	KY492655	AY395615^{G}	KY492674
Urocissa flavirostris	KUNHM 15139	Myanmar: Ma Jed	KY495258	KY492635	JQ864528^{G}	-	-	KY492675
Lanius collaris	GenBank		AY529960	JQ239269	EF635018	HQ996796	-	HQ996870
Lanius collurio	GenBank		-	-	-	-	AY395617	-

Discussion

Our biogeographic analysis was based on denser taxonomic sampling of the early branches of the corvid phylogeny than had been available in any previous study. Our results provided solid evidence regarding the geographic origin of NWJs. Mesoamerica + Eastern Palearctic or Eastern Palearctic was consistently identified as the most probable ancestral area for the ancestor of the NWJ and its sister clade; thus, the lineage probably reached the New World from the Eastern Palearctic through a trans-Beringian route. An interesting observation that resulted from the ancestral area reconstruction was the absence of the common ancestor of clades D and E in North America (Figure 1.2). A plausible explanation to this observation can be drawn from studies on other taxa: for example, Fox (2000), based on mammalian fossils, documented aridification of North America during the late Miocene, thus linking it with increased seasonality. Similarly, Kohn and Fremd (2008) documented decreased faunal diversity in western North America in the late Miocene, which they postulated to coincide with increased aridity and seasonality. The ancestor of clades D and E probably largely bypassed North America during the late Miocene, perhaps using western coastal habitats under the climate-stabilizing effects of the Pacific Ocean that may have offered temporary corridors for passage from the Eastern Palearctic to Mesoamerica. Hence, early cladogenesis—at least among extant taxa—of the NWJ lineage probably took place either in Mesoamerica or in the Eastern Palearctic.

Our results indicated that the NWJs are most closely related to a clade comprising *Pica*, *Podoces*, *Garrulus*, and others. Ericson et al. (2005) identified Indo-Malaya as the ancestral area of origin of these taxa. In another study, (Monteros and Cracraft 1997) recovered *Perisoreus* as the sister taxon to the NWJ clade. Additionally, del Hoyo et al. (2009) described a close relationship between the NWJ ancestor and *Cissa* + *Urocissa*. Our results refute these hypotheses, with better taxonomic representation, a more robust multilocus dataset, and better support (Figure 1.1).

All our analyses identified Mesoamerica as the most probable area for the most recent common ancestor of NWJs. This result narrows down the results of Bonaccorso and Peterson (2007), which showed the ancestral distribution of the NWJs as either Mesoamerica or Mesoamerica + North America. The proposed origin of *Calocitta* + *Cyanocorax* + *Psilorhinus* in Mesoamerica, dispersing thence into South America (Bonaccorso and Peterson 2007), was supported in our analysis. However, our results were unclear as to whether the *Aphelocoma* + *Cyanocitta* + *Gymnorhinus* clade originated in North America versus North America + Mesoamerica.

Monteros and Cracraft (1997) proposed the idea that the origin of the NWJs was the result of a single dispersal event into the Americas, which could have taken place around the early Miocene. However, our time calibration estimates indicated a later (Miocene−early Pliocene) origin for the NWJs (Figure 1.3), in which the ancestor probably dispersed to the New World from the Eastern Palearctic, or Eastern + Western Palearctic, around 6.7−5.0 M years ago (Figure 1.3). This event could have taken place when a continuous coniferous belt linked Northern Asia and America across Beringia from mid-to-late Miocene to the late Pliocene (Sanmartin et al. 2001), yet the timing of our reconstructions does not appear to coincide with any specific geological events that might have triggered the dispersal event.

Our time calibration estimated a late Miocene–early Pliocene origin for the most recent common ancestor (MRCA) of NWJs. This timing makes intuitive sense considering the absence of the MRCA in North America given the continent's increased seasonality and aridity by that

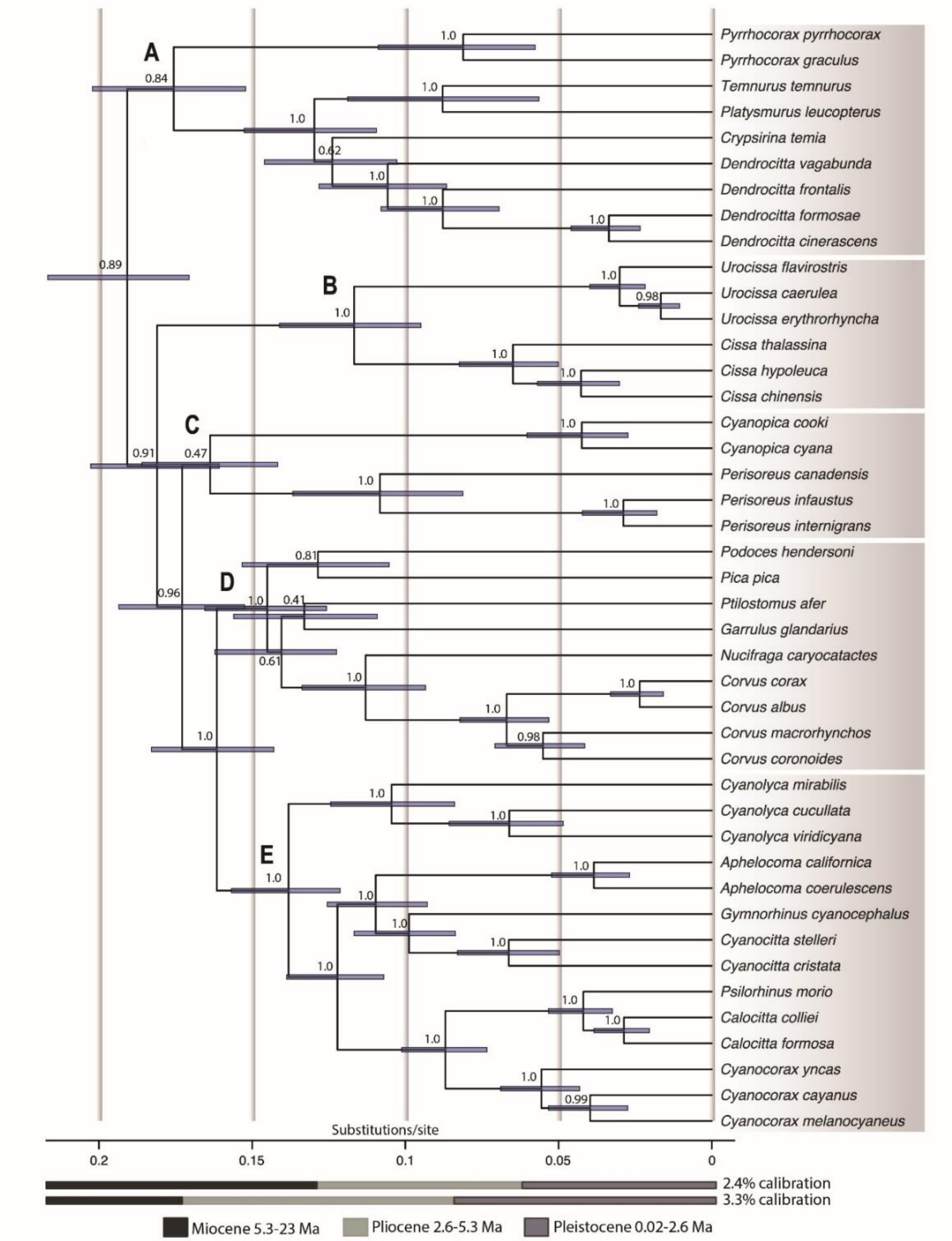

Figure 1.3. Approximate timeframe for the diversification of the Corvidae, with particular focus on New World jays. Time scales are based on ND2 substitution rates of 2.4% and 3.3% per lineage per million years. Bars at nodes indicate the highest posterior density (HPD) interval. Numbers at nodes refer to Bayesian posterior probabilities. Letters at nodes indicate the five major clades of the family.

time period, as stated above (Fox 2000). The time calibration further estimated the age of the family Corvidae at ~8.0−5.9 M years, substantially younger than the recent estimate of ~20M years in the phylogeny of corvoid passerine birds (Jønsson et al. 2016). However, we note that the timing of Corvidae-Laniidae split of the recent phylogeny of songbirds based on ~5000 loci by Moyle et al. (2016) coincides with our estimate for the same node (not shown here). Moreover, our time estimates for the MRCA of the South American genera (2.8−2.0M years for *Cyanolyca*, and 2.3−1.7M years for *Cyanocorax*) make intuitive sense, since dispersal of theses clades from Mesoamerica into South America should post-date the emergence of the Isthmus of Panama, around 2.8 M years ago (O'Dea et al. 2016). However, we emphasize that our time estimates are rough estimates of actual time, and must be considered with caution.

Our results provide novel insights to the biogeographic origin of NWJs, offering a solid hypothesis based on different ancestral area reconstruction methods, backed by strong support from a robust, multilocus phylogeny. However, clearly, more complete taxon representation with genome-level sampling could perhaps improve support for some remaining ambiguous nodes in the phylogenetic hypothesis. Such an improved phylogeny would help to resolve ambiguities associated with some of our phylogenetic and geographic hypotheses, and could allow insight into other important questions, such as tropical-temperate transitions in the family.

CHAPTER 2

Molecular phylogenetics and historical biogeography of treepies and blue/green magpies (family Corvidae)

Abstract

Treepies and blue/green magpies (subfamilies Crypsirininae and Cissinae) are two clades of the family Corvidae, confined to southern and eastern Asia, which include some of the most colorful and threatened bird species, yet they are also among the least understood corvid groups in terms of their ecology and systematics. To date, no robust phylogenetic hypothesis has been proposed; hence, their geographic origin and the history of diversification remain unclear. Here, we present species-level phylogenies of (a) treepies and (b) blue/green magpies, inferred from thousands of ultra-conserved elements (UCEs) and up to six Sanger-sequenced gene regions (nuclear introns and mtDNA). Biogeographic reconstructions indicate that the treepie and blue/green magpie clades originated in East Asia, and in East Asia and Sundaland, respectively, during the late Miocene. Dispersal of treepies out of the Asian mainland and into both the Indian Subcontinent and Sundaland occurred around the Miocene-Pliocene boundary, whereas much of the diversification of the blue/green magpie clade occurred after the mid-Pliocene. Our biogeographic and divergence-time analyses suggest that both treepies and blue/green magpies dispersed into the Indian Subcontinent during the mid-Pliocene, reaching all the way to Western Ghats and Sri Lanka.

Introduction

Distributed across the tropical and subtropical forests of southern and eastern Asia, treepies and blue/green magpies represent two subclades in the family Corvidae (Ericson et al. 2005; Fernando et al. 2017; Goodwin 1976). These lineages, which represent two early splits within the family (non-sister to one another; see Figure 2.1), include some of the most colorful and threatened bird species, yet they are also among the least well-understood groups of the family in terms of their phylogenetics and ecology. Numerous phylogenetic studies have focused on the relationships of major corvid lineages (Bonaccorso and Peterson 2007; Ericson et al. 2005; Monteros and Cracraft 1997), and on key sublineages (Bonaccorso 2009; Bonaccorso et al. 2010; Peterson 1992). However, to date, no detailed phylogenetic or biogeographic hypotheses exist for the treepie and blue/green magpie clades, mainly for lack of molecular data on which to base conclusions about relationships.

The blue/green magpies include five species of blue magpies in the genus *Urocissa* (*U. caerulea*, *U. erythrorhyncha*, *U. flavirostris*, *U. ornata*, and *U. whiteheadi*), and four species of green magpies in the genus *Cissa* (*C. chinensis*, *C. hypoleuca*, *C. jefferyi*, and *C. thalassina*) (Madge and Burn 1994; Van Balen et al. 2013). The blue magpies inhabit the forests of southern and eastern Asia, and are among the most colorful species in the family; Whitehead's Magpie (*U. whiteheadi*) has a shorter tail and no trace of blue in its plumage and, as such, is an exception. *Urocissa erythrorhyncha*, *U. flavirostris*, and *U. whiteheadi* range across tropical South and Southeast Asia, whereas *U. caerulea* and *U. ornata* are restricted to islands (Taiwan and Sri Lanka, respectively). The green magpies differ from the blue magpies mainly in having shorter tails and predominantly green and chestnut or red coloration. They are found in Southeast

Asia and on major islands of the Sunda Shelf; the two groups are phylogenetically each other's closest relatives (Ericson et al. 2005; Goodwin 1976; Jønsson et al. 2016).

The treepies are a group of long-tailed, largely arboreal corvids that inhabit South and Southeast Asia. They do not have bright colors, and have thick bills with strongly curved culmens (del Hoyo et al. 2009). This clade comprises four genera (*Dendrocitta*, *Crypsirina*, *Temnurus*, and *Platysmurus*) and 11 species (Jønsson et al. 2016). *Dendrocitta* includes 7 species (*D. bayleyi*, *D. cinerascens*, *D. formosae*, *D. frontalis*, *D. leucogastra*, *D. occipitalis*, and *D. vagabunda*). Two species of *Crypsirina* (*C. cucullata* and *C. temia*) are distributed in Southeast Asian lowland forests and are some of the smallest-sized members of the family. Finally, *Platysmurus* and *Temnurus* are monotypic genera found in the Malay Peninsula and Sundaland, and Indochina, respectively.

Tropical South and Southeast Asia rank among the most species-rich regions in the world, with high degrees of endemism. Geological and climatic processes have apparently altered the spatial distribution of terrestrial habitats in this region dramatically through time (Bird et al. 2005), promoting speciation and lineage diversification. However, patterns and processes of diversification in regional biotas remain poorly understood, particularly on the Indian Subcontinent where only a few studies have documented speciation patterns and biogeographic histories (Reddy 2014; Tamma and Ramakrishnan 2015). *Dendrocitta* (three species) and *Urocissa* (one species) are the only two corvid genera that have colonized peninsular India, apart from the widespread genus *Corvus*. Hence, analyzing the diversification and colonization of such taxa should also give insights into the general biogeographic patterns of the Indian Subcontinent, during that period of geological history.

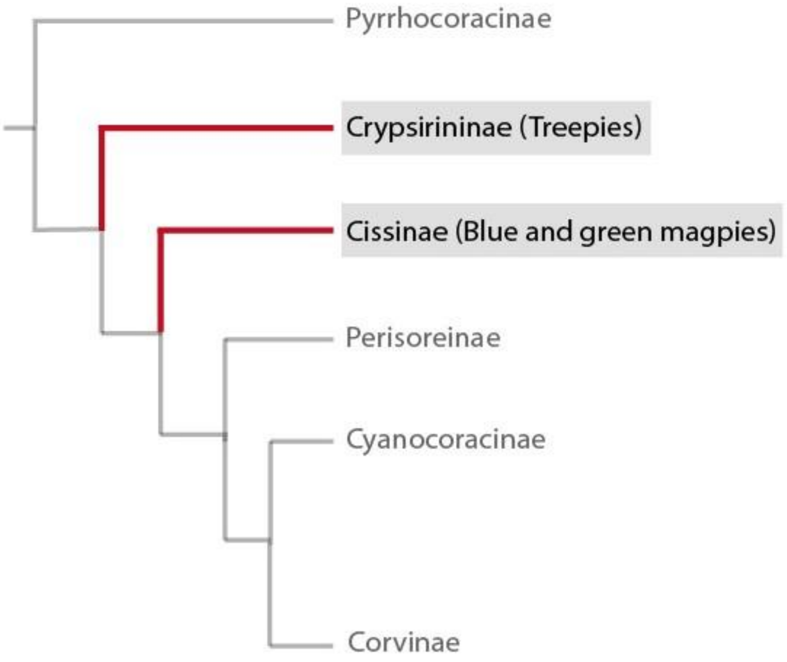

Figure 2.1. Placement of the two focal clades (treepies and blue/green magpies) within the overall corvid phylogenetic framework

In this study, we aim to develop a first robust, species-level phylogenetic hypotheses for the treepie and blue/green magpie clades, using genome-wide, ultra-conserved elements (UCEs), and Sanger-sequenced gene regions. Using these phylogenetic hypotheses, we investigate patterns of biogeography, colonization history, and diversification of the two clades, with reference to climatic and geological history of the region. We specifically explore and test the hypothesis of an East Asian *versus* a South Asian (Indian Subcontinent) origin for each of these two clades; we also explore Pliocene-Pleistocene biogeographic patterns of these two clades on the Indian Subcontinent, based on our phylogenetic and biogeographic inferences.

Materials and methods

Sampling and DNA preparation

In this study, we incorporated eight of the nine recognized magpie species, lacking only *Cissa thalassina*. We also included 10 of the 11 recognized treepie species, lacking only *Crypsirina cucullata*. We extracted and purified DNA from fresh muscle tissues, or from toepads from museum specimens, using Qiagen DNeasy Blood and Tissue Kits following the manufacturer's protocols. To extract DNA from toepads, we used a laboratory space in which no previous corvid work had been conducted, to minimize risk of contamination (Mundy et al. 1997). DNA extracts were quantified using a Qubit 2.0 Fluorometer (Thermo Fisher Scientific).

Library preparation and sequencing of ultra-conserved elements

For fresh tissue samples, we sheared 500 ng DNA of each sample to 400–600 bp in 50 ml volume using a Covaris S220 sonicator. We followed methods detailed in Oliveros et al. (2019a) and Moyle et al. (2016) for library preparation. Kapa Biosystems library prep kits were used to perform ¼ reactions of end-repair, A-tailing, and adapter-ligation. To allow dual indexing, we ligated universal iTru stubs (Glenn et al. 2016). We incorporated iTru dual-indexes (Glenn et al. 2016) in library fragments using a 17-cycle PCR, and quantified libraries using a Qubit 2.0 fluorometer. For enrichment, we combined libraries in pools of 8 equimolar samples of tissues and toepads separately, and performed target enrichment using a commercially synthesized Mycroarray MYbaits kit for tetrapods (UCE 5K version 1), which targets 5060 UCE loci. We amplified the fragments in a 17-cycle PCR amplification step, and quantified and sequenced them in a high-throughput paired-end run of 100 cycles on an Illumina HiSeq 2500 System at OMRF Clinical Genomics Center (Oklahoma City, Oklahoma).

Data assembly

For contig assembly and alignment, we followed the Python package PHYLUCE (Faircloth 2015), which is described in https://github.com/faircloth-lab/phyluce. Low-quality bases and adaptor sequences were trimmed using ILLUMIPROCESSOR ver. 1 (https://github.com/fairclothlab/illumiprocessor). We assembled cleaned reads into contigs using TRINITY 2.0.6 (Grabherr et al. 2011), and extracted contigs for each taxon that matched UCE loci. We then assembled two data sets for magpies and treepies, one containing UCE loci represented in all species (complete matrix), and the other containing UCE loci that were present in at least 75% of species (incomplete matrix). We aligned loci using MAFFT (Katoh and Standley 2013), and trimmed uncertain alignment regions using GBLOCKS 0.91 (Castresana 2000) with default parameters, except for the minimum number of sequences for a flank position, which we set at 65% of taxa (Andersen et al. 2018; Moyle et al. 2016).

Mitochondrial DNA (mtDNA) and nuclear introns

We also created separate matrices for treepies and magpies using available sequences of mtDNA and nuclear intron data, with the aim of including two species of treepies (*Platysmurus leucopterus*, *Crypsirina temia*) and one species of magpie (*Urocissa caerulea*) for which we lacked UCE data. We selected three mitochondrial regions (cytochrome *b*, or Cyt*b*; nicotinamide adenine dinucleotide dehydrogenase subunit 2, or ND2; nicotinamide adenine dinucleotide dehydrogenase subunit 3, or ND3), and three nuclear introns (seventh intron of the beta-fibrinogen gene, or βfib7; second intron of the myoglobin gene, or Myo2; fifth intron of the transforming growth factor β2, or TGFβ2) from our previously published sequences (see Fernando et al. 2017) for treepies and magpies. For species with UCE data but no previously published Sanger-sequenced data (i.e., *Dendrocitta bayleii, D. leucogastra*, *D. occipitalis*, *Urocissa ornata*, and *U. whiteheadi*), we extracted mtDNA regions from UCE reads using GENEOUS 8.1.6 (Biomatters, Auckland, New Zealand). We concatenated nuclear and mtDNA sequences to produce combined matrices for treepies and magpies, separately, for use in phylogenetic analyses. We used *Pyrrhocorax* (the oldest branch of the family) as the outgroup taxon to root the trees in both clades.

Phylogenetic analyses

Ultra-conserved elements (UCEs)

We performed maximum likelihood (ML) inference on the complete and incomplete data sets for magpies and treepies separately, using RAxML 8.2.4 (Stamatakis 2014), under a general time-reversible (GTR) model of rate substitution with gamma-distributed rates among sites. Node support was evaluated using 500 rapid bootstrap replicates. We used the 'autoMRE' option in RAxML to test for convergence of bootstrap replicates. We also estimated phylogenies for all multilocus alignments with SVDQUARTETS (Chifman and Kubatko 2014), a method of phylogenetic inference consistent under the multispecies coalescent model, as implemented in PAUP* ver. 4.0a157 (Swofford 2003). We computed the SVDQUARTETS optimal tree and 500 bootstrap replicates, reconciling quartets using the QFM algorithm.

mtDNA and nuclear introns

We estimated phylogenies for treepies and magpies (separately) using the total concatenated data sets of mtDNA and nuclear introns. ML tree searches were performed in RAxML 8.2.6 on the Cyberinfrastructure for Phylogenetic Research portal (Miller et al. 2010), with 5000 nonparametric bootstrap replicates (Felsenstein 1985). Convergence of bootstrap replicates was tested using the ‘autoMRE’ option in RAxML. Time-calibrated Bayesian analyses were conducted in BEAST 2.3.2 (Bouckaert et al. 2014) implemented with BEAGLE (Ayres et al. 2011). To calibrate divergence times, we used a secondary node calibration point from Oliveros et al. (2019b) corresponding to the split for the base of the family Corvidae. We used a birth-death tree prior and an uncorrelated lognormal (UCLN) relaxed clock. Two independent MCMC runs of 10^7 generations were executed with unlinked site models for each partition. Convergence of parameter estimates was examined using TRACER 1.6 (Rambaut and Drummond 2007). We sampled trees every 2000 generations, and discarded the first 25% of trees as burn-in. The remaining trees were summarized to obtain a 50% majority-rule consensus tree.

Since we did not resolve the sister relationship of *Dendrocitta vagabunda* and *D. frontalis* (for which we got >99.9% bootstrap for UCE data) in likelihood and Bayesian analyses of our marker gene data, we incorporated a hybrid phylogenetic-phylogenomic approach as described in Leaché et al. (2014), to obtain a best time-calibrated tree for treepies for the biogeographic analysis. Here, we combined the final posterior distribution of time-calibrated species trees obtained from the BEAST analyses and filtered them using the tree obtained from the UCE incomplete loci as the backbone constraint in PAUP (Swofford 2003) based on topology only. This procedure retained only the topologies in the posterior distribution of trees that were consistent with the UCE backbone constraint imposed by the phylogenomic tree. We then used TREEANNOTATOR 2.3.2 (Bouckaert et al. 2014) to estimate the maximum clade credibility (MCC) tree from the filtered posterior distribution of species trees.

Biogeographic analysis

We used BIOGEOBEARS (Matzke 2013a) implemented in R (R Core Team, 2016) to infer ancestral distributions of treepies and magpies separately. BIOGEOBEARS uses several probabilistic models: DEC-LIKE, a likelihood implementation of Dispersal Extinction Cladogenesis (Ree and Smith 2008), DIVALIKE, a likelihood implementation of Dispersal-Vicariance Analysis (Ronquist 1997; Yu et al. 2010), and BAYAREALIKE, a likelihood implementation of BAYAREA (Landis et al. 2013). BIOGEOBEARS fits them to phylogenetic hypotheses in a likelihood framework given user-defined geographic areas. This program also incorporates +J under each model, a parameter that represents founder-event speciation, which allows daughter lineages to jump into novel areas not occupied by the ancestor (Matzke 2013b).

According to the current species distributions (del Hoyo et al. 2009; eBird 2015), we assigned treepies and magpies to one or more biogeographic regions (treepies: India, Mainland Asia, Sundaland, and Andaman Islands; magpies: Mainland Asia, Sundaland, Sri Lanka, and Taiwan). We set the maximum range size to all four regions in each analysis. The time-calibrated maximum clade credibility tree inferred from marker gene sequences from BEAST was used, and each model's (DEC, DIVA-LIKE, BAYAREA-LIKE; each with and without +j) fit was assessed using the Akaike information criterion (AIC). Jump parameter in the DEC +j model gives it the propensity to explain all biogeographic variations (Ree and Sanmartín 2018). However, we believe that the +j parameter comes in handy in this study in view of the inclusion of insular taxa in both clades.

Results

Molecular data matrices and phylogenetics

Our complete and incomplete UCE data matrices included eight and seven species of the treepie and magpie clades, respectively. The complete matrix for treepies comprised 919 loci and 277,963 bp, whereas that for magpies comprised 1,060 loci and 346,365 bp. The incomplete matrices of treepies and magpies contained 4,375 loci and 1,302,456 bp, and 4,043 loci and 1,711,954 bp, respectively (UCE sequence capture statistics are shown in Appendix II). Our concatenated Sanger-sequenced data matrix for treepies and magpies encompassed 6 loci with 4394 and 4647 bp, respectively.

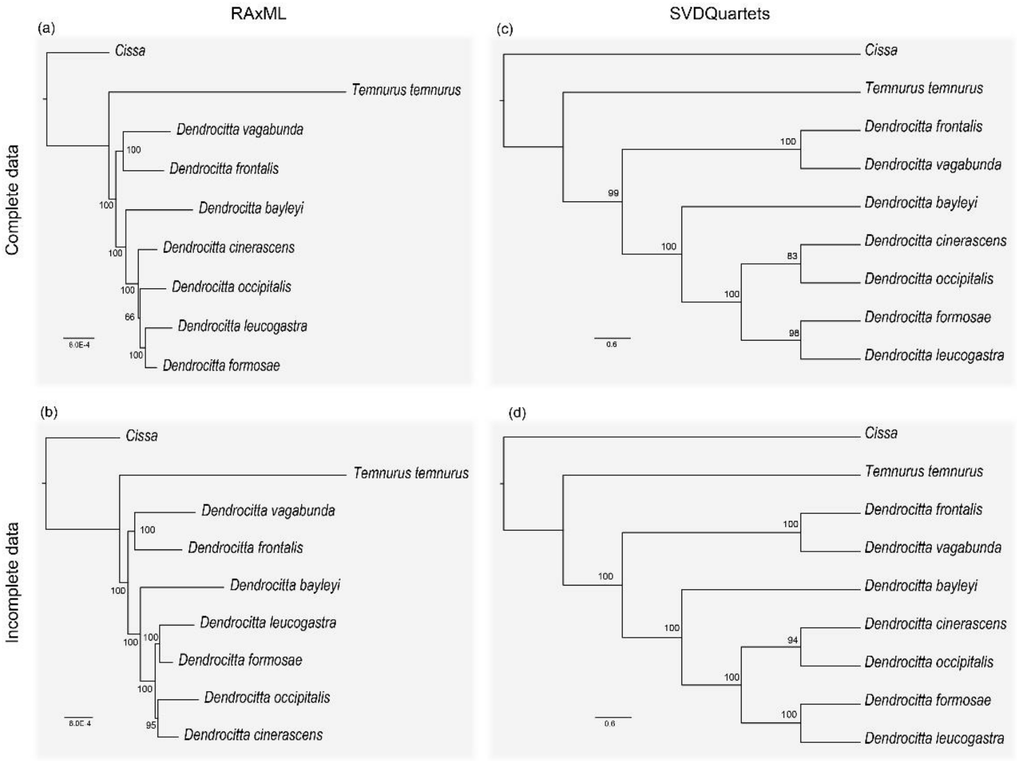

Figure 2.2. Phylogenies of treepies based on ultra-conserved element (UCE) data sets from RAXML (panels a and b) and SVDQUARTETS (panels c and d) analyses. Panels a and c are based on the complete matrix of 919 UCE loci; panels b and d are based on the incomplete matrix of 4375 UCE loci. Node labels represent bootstrap support.

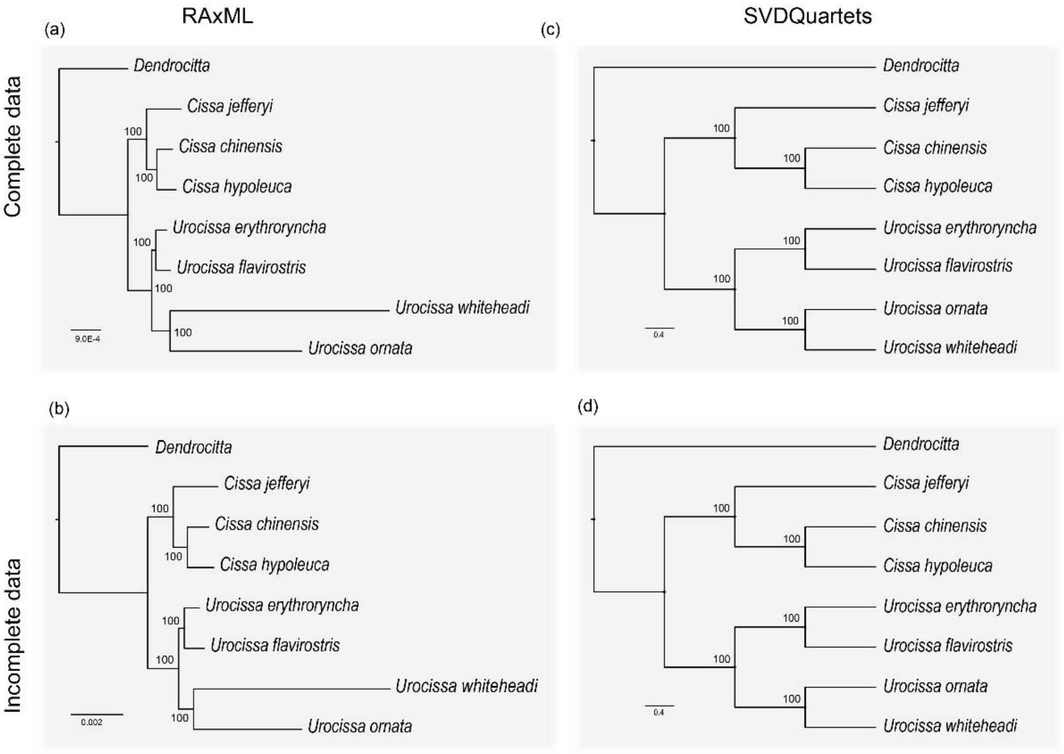

Figure 2.3. Phylogenies of blue/green magpies based on ultra-conserved element (UCE) data sets from RAXML (panels a and b) and SVDQUARTETS (panels c and d) analyses. Panels a and c are based on the complete matrix of 1060 UCE loci; panels b and d are based on the incomplete matrix of 4043 UCE loci. Node labels represent bootstrap support.

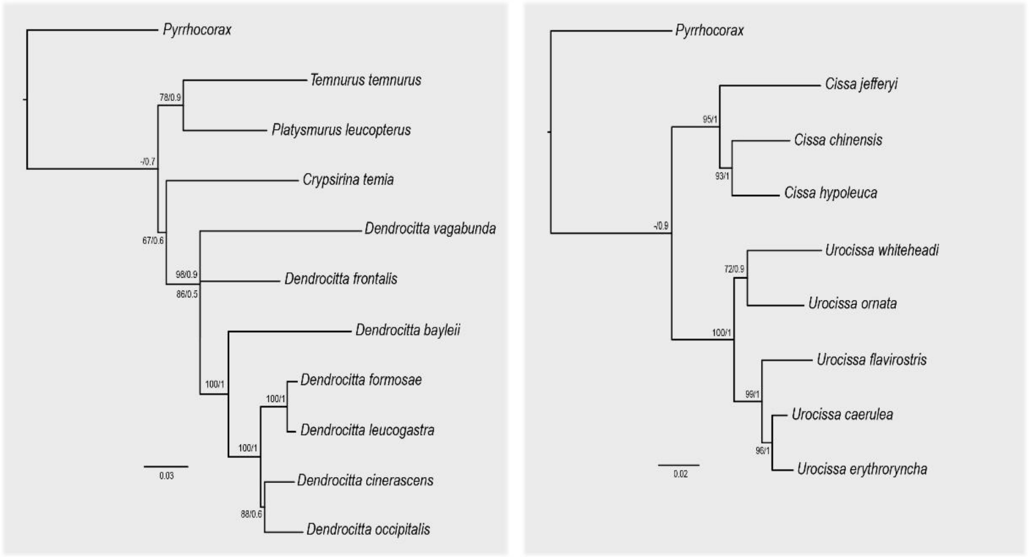

Figure 2.4. *Right* Phylogeny of blue/green magpies based on Bayesian and maximum likelihood (ML) analyses of the combined dataset of mitochondrial DNA and nuclear intron data. Numbers at the nodes refer to Bayesian posterior probability/ML bootstrap support. *Left* Phylogeny of treepies based on Bayesian and ML analyses of the combined dataset of mitochondrial DNA and nuclear intron data. Numbers at the nodes refer to Bayesian posterior probability/ML bootstrap support.

Complete and incomplete data of UCE of treepies produced similar topologies, except in the case of a single poorly supported node (Figures 2.2a and 2.2b); bootstrap support 66%, in the RAXML analysis of the complete data matrix; all other analyses resulted in a topology in which *Dendrocitta cinerascens* and *D. occipitalis* were sister to each other with high nodal support. The results of all UCE analytical approaches for treepies agreed with the outcome of the concatenated Sanger-sequenced, marker-based analysis, except that UCE analyses placed *D. vagabunda* and *D. frontalis* as sister species (bootstrap support 100%), whereas the marker-based analyses did not recover this relationship. In view of these disagreements, we adopted a hybrid phylogenetic-phylogenomic approach, using our incomplete matrix UCE topology for treepies as a backbone constraint with which to obtain a time-calibrated BEAST tree for our downstream biogeographic reconstructions. All analytical approaches of UCE and concatenated mtDNA and nuclear intron sequence data of magpies produced identical topologies (Figures 2.3 and 2.4).

Biogeographic reconstructions and divergence timing

Treepies—DEC was chosen as the best-fit biogeographic model for treepies, and was marginally better supported than the DEC+j model (Table 2.1). This reconstruction revealed that at around 10.0–6.4 Mya, the ancestral range of the treepie clade was in mainland Asia. *Crypsirina* diverged from *Dendrocitta* during the late Miocene (approximately 7.3 Mya), and *Platysmurus* split from *Temnurus* approximately 5.8 Mya.

The analysis further revealed first signs of dispersal of treepies out of mainland Asia (B) at around the Miocene-Pliocene boundary. This lineage (the common ancestor of *Dendrocitta bayleii*, *D. cinerascens*, *D. formosae*, *D. leucogastra*, and *D. occipitalis*) had a broad distribution,

Table 2.1. Model selection summary statistics for treepies from BioGeoBEARS.

Model	LnL	# parameters	*d*	*e*	*j*	AIC	AIC weight
DEC	-20.89	2	0.026	1.00E-12	0	45.77	0.36
DEC+J	-19.96	3	0.02	1.00E-12	0.1	45.93	0.33
DIVALIKE	-21.69	2	0.035	1.00E-12	0	47.38	0.16
DIVALIKE+J	-21.01	3	0.026	1.00E-12	0.079	48.01	0.12
BAYAREALIKE	-26.67	2	0.035	0.12	0	57.34	0.0011
BAYAREALIKE+J	-22.65	3	0.02	0.0000001	0.11	51.3	0.023

Table 2.2. Model selection summary statistics for blue and green magpies from BioGeoBEARS.

Model	LnL	# parameters	*d*	*e*	*j*	AIC	AIC weight
DEC	-16.79	2	0.031	0.016	0	37.58	0.0085
DEC+J	-11.53	3	0.0031	1.00E-12	0.21	29.05	0.61
DIVALIKE	-16.26	2	0.047	1.00E-12	0	36.51	0.015
DIVALIKE+J	-12.16	3	0.014	1.00E-12	0.26	30.31	0.32
BAYAREALIKE	-18.78	2	0.031	0.2	0	41.55	0.0012
BAYAREALIKE+J	-14.2	3	1E-07	0.085	0.094	34.41	0.042

across mainland Asia (B), India (A), part of Sundaland (C), and the Andaman Islands (D), during the early Pliocene (see Figure 2.5); The Andaman population split from the rest of the clade at around the same time. The rest of the group experienced cladogenetic events in the Pleistocene: *D. cinerascens* and *D. occipitalis* were isolated in Sundaland (C), and *D. leucogastra* and *D. formosae* split in mainland Asia (B) and India (A).

Blue/Green Magpies—DEC+j was identified as the best-fit biogeographic model for the blue/green magpie clade (Table 2.2). We incorporated the DEC+j model in our ancestral range reconstruction in view of the inclusion of insular taxa in this clade, despite the recent criticism of AIC-based model selection when assessing these models (Ree and Sanmartín 2018). AIC selected the DEC+j as the best fit model for our analysis. However, DEC gave a similar reconstruction to DEC+j model only except for two nodes in the *Urocissa* clade.

Our time calibration indicated a late Miocene origin for this clade, with time to the most recent common ancestor (TMRCA) at ~7.1 Mya, during which time the taxon inhabited mainland Asia and Sundaland. Among the descendants, the ancestor of *Urocissa* had a mainland-Asian origin, whereas the ancestor of *Cissa* was present on both mainland Asia and Sundaland (see Figure 2.6). Our results further revealed that the common ancestor of *U. ornata* and *U. whiteheadi* inhabited mainland Asia during the late Pliocene (~3.1 Mya); *U. ornata* was isolated in Sri Lanka, and *U. whiteheadi* diversified on the Asian mainland subsequently. The sister clade, comprising *U. caerulea*, *U. erythroryncha*, and *U. flavirostris*, appears to have originated during the early Pleistocene, in mainland Asia. Eventually, a subset of this clade colonized Taiwan and gave rise to *U. caerulea*, and the remaining taxa diversified in mainland Asia. Our results further indicated that the origin and the diversification of green magpies took place in mainland Asia and Sundaland, with much of the speciation within this clade happening during the latter half of the Pliocene.

Discussion

Our phylogenetic hypotheses and biogeographic reconstructions indicated a complex biogeographic history for both of the corvid clades under study. Specifically, both clades appear to have originated in East Asia. The ancestral treepies colonized areas outside of East Asia—both the Indian Subcontinent and Sundaland—around the Miocene-Pliocene boundary; in contrast, parallel colonization events in the blue/green magpie clade occurred later, after the mid-Pliocene. Our results suggest that both clades colonized the Indian Subcontinent during the mid-

Pliocene, reaching all the way to Western Ghats and Sri Lanka by approximately the Late Pliocene.

Relationships of treepies, and blue/green magpie clades

In this study, we have developed a first phylogenetic framework, based on genome-wide UCE data and sequences of mtDNA and nuclear introns, resolving the species-level relationships of both the treepie and the blue/green magpie clades of the family Corvidae. For the magpies, we obtained high nodal support (100% bootstrap) in all analyses of UCE data; analysis of mtDNA and nuclear intron data recovered similar relationships, with >0.9 posterior probabilities for all the nodes and >93% bootstrap support, except in the case of a single node.

We observed slight discordance between topologies obtained from UCE sequences and, mtDNA and nuclear intron data. To force the highly supported relationships from the incomplete UCE data analysis on the Sanger data topology of treepies, we used a constraint method in obtaining a species-level topology, which we incorporated in our biogeographic analysis. We discuss our biogeographic hypotheses testing for the two clades separately.

Origin and diversification of treepies

According to our biogeographic reconstruction, the common ancestor of the treepies ranged across mainland Asia, at ~10.0-6.4 Mya. The ancestral treepies gave rise to the four extant genera (*Crypsirina*, *Dendrocitta*, *Platysmurus*, and *Temnurus*) during the late Miocene within mainland Asia. *Temnurus* was restricted to the Asian mainland whereas *Platysmurus* and *Crypsirina* subsequently extended their ranges to Sundaland, probably after the Miocene, when landmasses of Sundaland were connected to the mainland (den Tex et al. 2010; Hall 2009) during a period of dramatic sea level fluctuations. Our reconstruction did not include *Crypsirina cucullata*, which is distributed in mainland Asia (B).

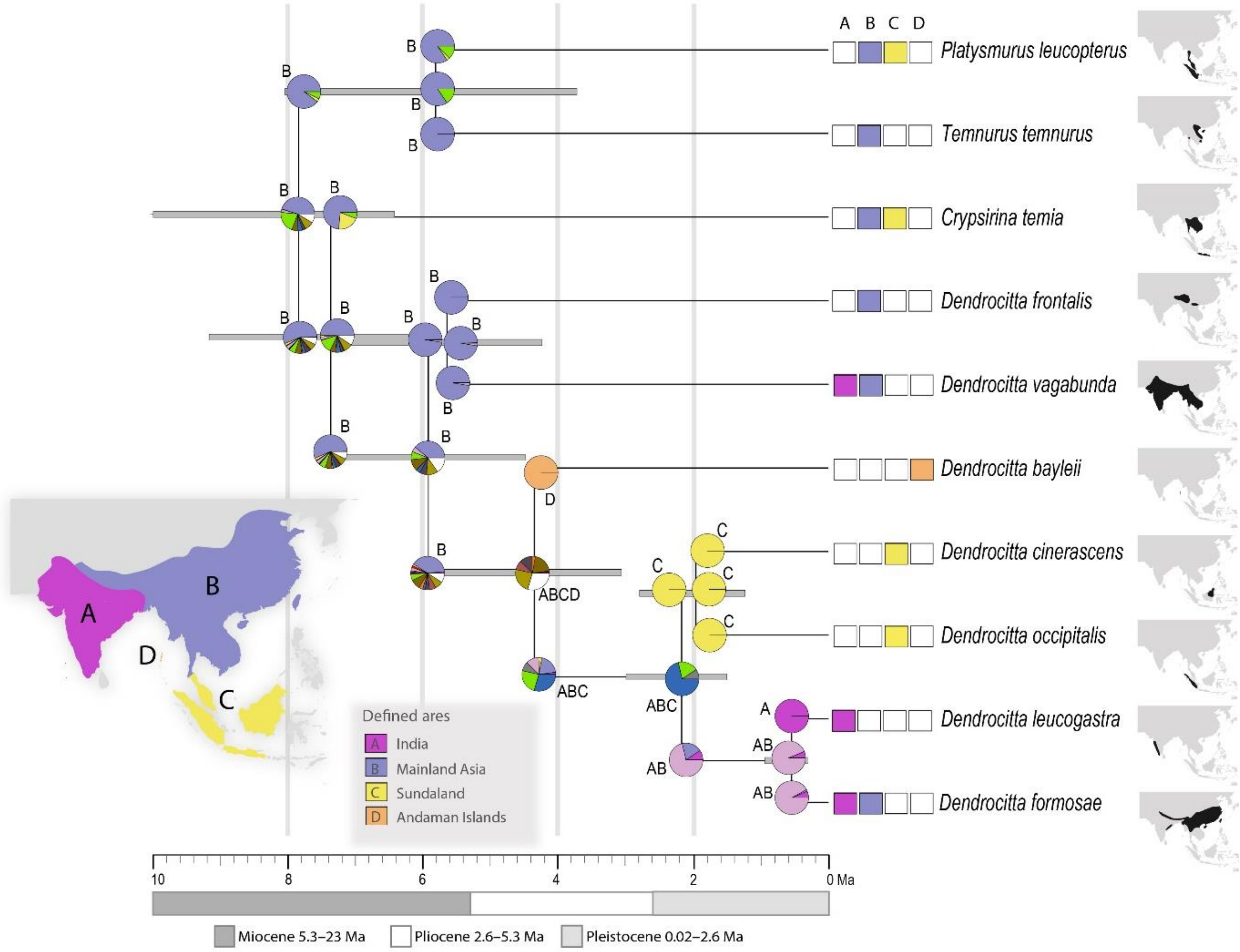

Figure 2.5. Ancestral area estimates for blue/green magpies obtained using the DEC model in BioGeoBEARS. Bars at nodes indicate the highest posterior density (HPD) interval. Ancestral area probabilities before and after cladogenesis are shown by pie charts at nodes and corners, respectively. Letters at the pie charts indicate the area with the highest probability. Colored squares at tips indicate distribution of extant species, which correspond to the colored regions on the map (A = India, B = Mainland Asia, C = Sundaland, D = Andaman Islands). Maps to the right side indicate current distribution of each species.

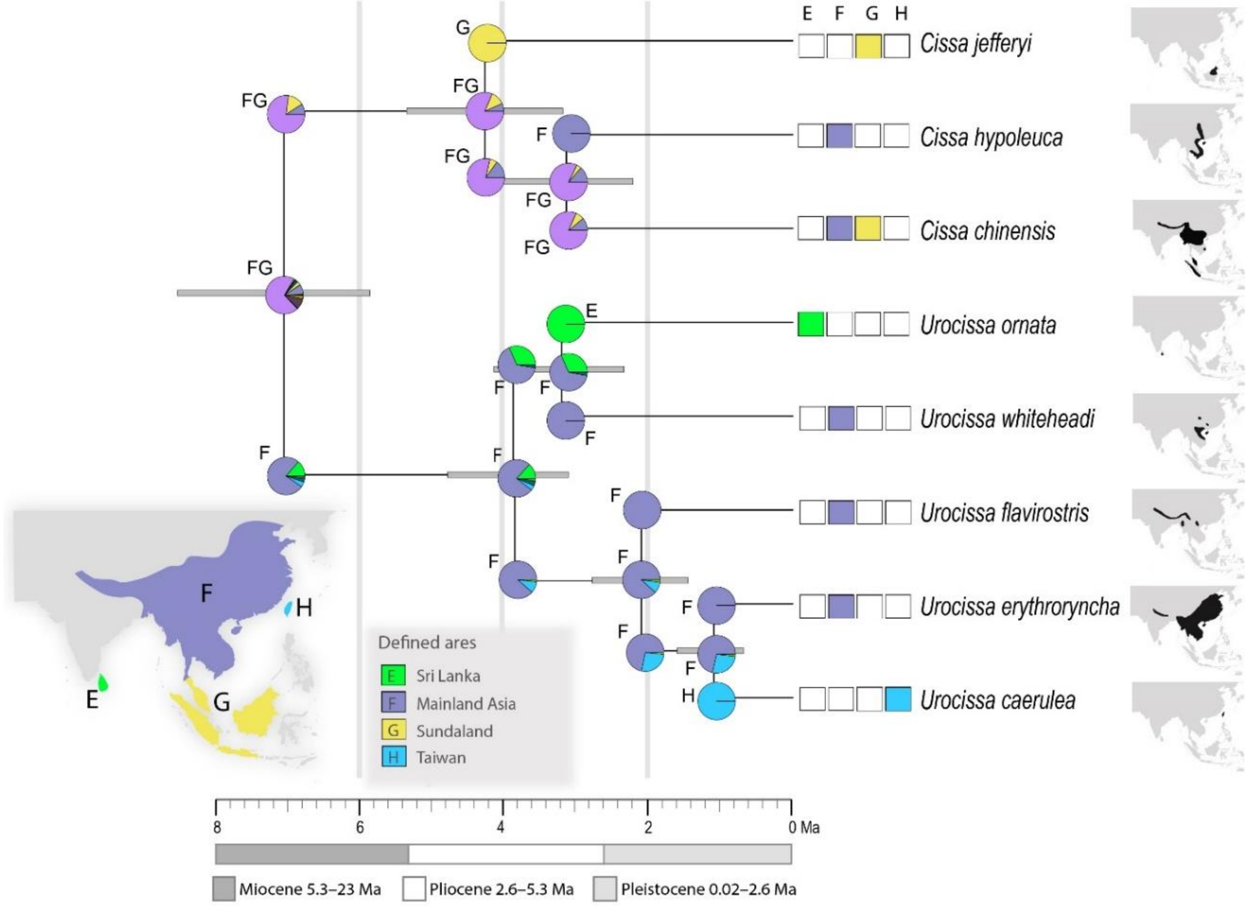

Figure 2.6. Ancestral area estimates for blue/green magpies obtained using the DEC+j model in BioGeoBEARS. Bars at nodes indicate the highest posterior density (HPD) interval. Ancestral area probabilities before and after cladogenesis are shown by pie charts at nodes and corners, respectively. Letters at the pie charts indicate the area with the highest probability. Colored squares at tips indicate distribution of extant species, which correspond to the colored regions on the map (E = Sri Lanka, F = Mainland Asia, G = Sundaland, H = Taiwan). Maps to the right indicate the current distribution of each species.

The relatively species-rich treepie genus *Dendrocitta* showed a more widespread ancestral distribution. The first branching event in this clade probably happened ~6 Mya, giving rise to the common ancestor of *D. frontalis* and *D. vagabunda*; according to our results, this ancestral taxon existed in mainland Asia. Possibly as a consequence of being a habitat generalist, its daughter species (*D. vagabunda*) was able to expand across a wide area (inclusive of much of mainland India), and across many habitat types (dry woodlands to moist broadleaved forest; del

Hoyo et al. 2009). The common ancestor of the sister subclade (comprising *D. bayleii*, *D. cinerascens*, *D. formosae*, *D. leucogastra*, and *D. occipitalis*) expanded its range to the Indian mainland, Sundaland, and the Andaman Islands during the early Pliocene. The avifauna of the Andaman Islands is known to be closest faunistically to that of southwestern Burma (Elwes 1873; Ripley and Beehler 1989). However, the Preparis Strait, which runs from southern Burma to the Andaman Islands, is a deep-water barrier that has been unbroken since the mid-Tertiary (Ripley and Beehler 1989). The only plausible explanation for speciation of birds across the Preparis Strait is considered as dispersal followed by isolation (Ripley and Beehler 1990).

Colonization of the Andaman Islands in the case of treepies may have happened by island-hopping of permanent water barriers during sea-level changes, leading to the evolution of *D. bayleii*. The sister clade inhabited a broad area of India, Sundaland, and the Asian mainland, in the late Pliocene. During the early Pleistocene, Sundaland populations probably diverged from the rest of the populations, giving rise to the two Sundaland taxa, *D. cinerascens* and *D. occipitalis*.

Dendrocitta leucogastra currently inhabit the humid evergreen hill forests of the Western Ghats, an isolated coastal mountain chain in southwestern India. Its sister taxon, *D. formosae*, is widespread, inhabiting most of China and the Himalayan foothills, with an isolated population in the Eastern Ghats of India. Perhaps, the common ancestor of *D. formosae* and *D. leucogastra*, a widespread taxon, existed across the Western Ghats through mainland Asia, connected by a retracting humid forest stretch that fell across the Eastern Ghats during the late Pleistocene times (Karanth 2003). Pleistocene climate oscillations and resultant fragmentation in the humid forests in Eastern Ghats probably caused a disjunction in this ancestral population, giving rise to *D. formosae* in the eastern and *D. leucogastra* in the western parts of the range.

Origin and diversification of blue/green magpies

Our ancestral area reconstruction lacked a single nominal species, *Cissa thalassina*, which is found in Java. This gap in coverage does not affect our biogeographic analysis thanks to its distribution in the same area (Sundaland) as its sister taxon, *C. jefferyi*. Our results suggest that this clade originated in mainland Asia and Sundaland during the late Miocene, when Sundaland was probably a single land mass (Hall 2009); The ancestral population eventually split, giving rise to blue magpies (*Urocissa*) and green magpies (*Cissa*) by the mid-Pliocene.

The origin and the diversification of green magpies probably took place in the same regions (mainland Asia and Sundaland); seemingly, much of the speciation in this clade happened during the latter half of the Pliocene. The blue magpies, however, are absent from the Sundaland, yet they went on to colonize the Indian Subcontinent and Taiwan. The group experienced its first split during the mid-Pliocene, creating the subclade comprising the common ancestor of *Urocissa ornata* and *U. whiteheadi*, which probably ranged all the way across the Indian Subcontinent to Sri Lanka. *Urocissa ornata* inhabits the tropical broadleaf evergreen forests of Sri Lanka, where its range is restricted to the central mountains and foothills of the wet zone. *Urocissa whiteheadi* is found in tropical broadleaf evergreen forests in the lowlands and foothills of Hainan, China (del Hoyo et al. 2009; Madge and Burn 1994). This massive disjunction between the current ranges of these sister taxa suggests that their common ancestor inhabited an area comprising much of mainland Asia and the Indian Subcontinent during the mid-Pliocene times.

However, given the absence of modern blue magpie taxa in mainland India, our analysis was not capable of reconstructing an ancestral area of the clade within India. Fossil records of flora and fauna indicate a major vegetational shift in India, with warm humid tropical climates in lowland areas in the early and middle Miocene shifting to cooler and drier conditions in the late Miocene and early Pliocene (Patnaik 2016). The uplift of the Himalayan range, and intensification of the Asian monsoons were mainly responsible for this climatic change (Patnaik 2016), and as a result wet evergreen forests in northern India were displaced by deciduous forests (Quade et al. 1995). We suggest, with caution, that *U. ornata* (or its ancestral populations), probably once inhabited mainland India; however, given vegetational and climate change, the taxon was forced southwards, until it lost all of its Indian range, and evolved in isolation in Sri Lankan rainforests.

Most speciation events of taxa in the wet zone of Sri Lanka pre-date the Quaternary period (Cadle et al. 1990; Schulte II et al. 2002), which coincides with our timeline for the splitting of *U. ornata* from *U. whiteheadi.* According to our results, the other *Urocissa* subclade, comprising *U. caerulea*, *U. erythroryncha*, *U. flavirostris,* and their ancestors, perhaps originated in mainland Asia during early Pleistocene. *Urocissa flavirostris* and *U. erythroryncha* diversified in mainland Asia, whereas *U. caerulea* is likely the result of isolation on Taiwan. During Pleistocene glaciations, sea levels were lower (Chang 1989), and the Taiwan Strait was probably exposed as a broad land-bridge connecting the mainland (Chang 1989; Rohling et al. 1998), thus encouraging the colonization process.

Colonization of the Indian Subcontinent

Our biogeographic analyses for two corvid clades in the tropical Asia indicate first signs of dispersal of both clades into the Indian subcontinent during the mid-Pliocene (~4 mya). Timing of these colonization events, and our well-resolved phylogeny suggest strongly that the subcontinental treepie and blue magpie taxa are a subset of the diverse avifaunal lineages in Southeast Asia and the Himalayas, similar to the cases of many other avian families (Karanth 2003; Robin et al. 2017). Past work on subcontinental biogeography (Karanth 2003) discuss four potential hypothetic dispersal routes that the wet-zone species took to reach the Western Ghats and Sri Lanka from mainland Asia or northeastern India: (1) the Aravalli range, (2) the Brij region, (3) the Vindhya-Satpura ranges, and (4) the Eastern Ghats. Our biogeographic reconstruction suggests that the common ancestor of *Urocissa ornata* and *U. whiteheadi* probably existed on the Indian Subcontinent during the late Pliocene (~3.5 mya) at the earliest, and the same story applies to wet-zone *Dendrocitta* taxa. Interestingly, at this point in time (i.e. late Pliocene and afterwards), humid forests existed only along the Eastern Ghats dispersal route, and the rest of the dispersal routes were taken over by the dry-zone (Karanth 2003). Consequently, the ancestral treepies and blue magpies most likely dispersed across India, to Western Ghats and Sri Lanka via the Eastern Ghats dispersal route.

CHAPTER 3

Climatic niche reconstructions give new insights to the evolution of the New World jays (family Corvidae)

Abstract

Evolution of species' climatic niches through time has become an area of intensive study; the ultimate goals being (1) to understand the associations between climatic niche evolution and lineage diversification, and (2) to provide ecological explanations for current species distribution patterns and predict how distributional patterns will be impacted by future climate changes. The New World jays (NWJs) form a well-studied bird lineage within the family Corvidae, however, little understanding exists of the effects of climate on the diversification process in this clade, despite the availability of large amounts of occurrence data and well resolved phylogenetic hypotheses. In this study, we attempt to reconstruct ancestral climate niches of New World Jays (NWJs) by mapping temperature and humidity niches on to a comprehensive and well-resolved phylogenetic framework. We employed an improved methodology that explicitly incorporates the uncertainty associated with knowledge of climate niches of species, by considering an accessible area for the species, to avoid overinterpretation of niche changes throughout the evolutionary history. Our ancestral reconstructions indicated that humidity niches are more dynamic compared to temperature niches, and that different clades exhibit different degrees of niche conservatism versus niche dynamism. We attempted to relate niche dynamism in lineages to species' ecology, geological history, and distributional patterns. Thus, our results provide a synthetic view of ecological niche and its evolution over time in the history of the NWJs.

Introduction

Understanding the factors that influence species' geographic distributions has long been of intense interest in ecology and biogeography (Chesson 2000; MacArthur 1984). Environmental conditions are considered as important extrinsic influences that shape these distributions across diverse spatial and temporal scales (MacArthur 1964). During the past decade, the evolution of species' climatic niches through time has become an area of intensive study, the goal being to understand associations between climatic niche evolution and lineage diversification (García-Navas and Rodríguez-Rey 2018; Nyari and Reddy 2013; Peterson et al. 1999; Ribeiro et al. 2017). On shorter timescales, understanding patterns of climatic niche evolution could also provide ecological explanations for current distributions of species, and predictions of how distributional patterns will be impacted by future changes in climate.

Phyloclimatic studies–i.e., analyses of climatic niche evolution in phylogenetic contexts–often involve phylogenetic comparative frameworks that combine a phylogenetic hypothesis with either ecological niche model (ENM) outputs (Elith et al. 2011; Graham et al. 2004; Peterson et al. 2011), or with raw climate data corresponding to species' known occurrences (Ackerly et al. 2006; Evans et al. 2005). Quantifying niches from ENMs is probably the most commonly used approach, but depend perilously on extrapolation routines in the ENM algorithms (Owens et al. 2013). More generally, empirical estimates of ecological niches are often incompletely characterized (Owens et al. 2013; Saupe et al. 2018) owing to at least three factors: (1) existing abiotic conditions not being fully representative, (2) biotic interactions that may limit species' environmental usage, and (3) dispersal limitations that limit exploration of geographic and environmental space (Soberón 2007; Peterson et al. 2011). Saupe et al. (2017)

demonstrated that phylogenetic analyses of incompletely characterized niches inflate estimates of evolutionary change over time, leading to incorrect reconstructions of ancestral states. Ribeiro et al. (2017), in an analysis of niche evolution and diversification in *Geositta* miners, used explicit consideration of species-specific accessible area (**M**) hypotheses (Soberón and Nakamura 2009) to account for incomplete knowledge of climate occupancy, such that errors in estimates of evolutionary change are minimized.

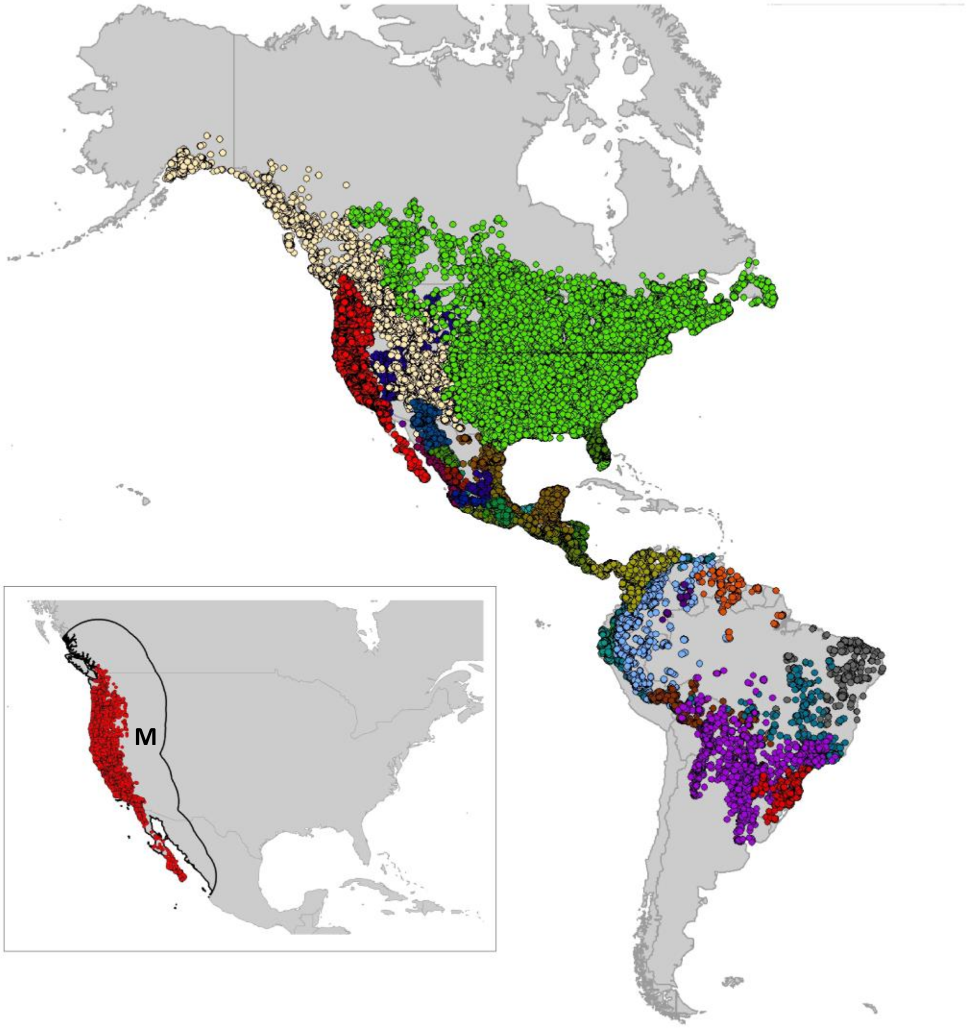

Figure 3.1. *Right* Geographic distribution of the NWJs clade: sampled occurrence points used in niche reconstruction analyses are indicated by red dots. *Left* an example showing **M** (dispersal limitations) for *Aphelocoma californica*.

The New World jays (NWJs) are a well-studied bird lineage in the family Corvidae, distributed broadly across the Americas (Figure 3.1). It is a monophyletic group that includes ~36 species in seven genera: *Aphelocoma*, *Calocitta*, *Cyanocitta*, *Cyanocorax*, *Cyanolyca*, *Gymnorhinus*, and *Psilorhinus* (Goodwin 1976; Madge and Burn 1994; Zusi 1987). The NWJ clade is, arguably, one of the best-studied bird lineages in terms of evolutionary history, biogeography, and behavioral ecology (Bonaccorso and Peterson 2007; Brown 1963, 1974; Fernando et al. 2017; Woolfenden 1975). However, little understanding exists of effects of climate on the diversification process in this group, despite the availability of large amounts of occurrence data, highly-resolved phylogenies, and broad interest in the ornithological community for this group. Hence, here, we examine climatic niche evolution in the NWJs, using ancestral reconstruction and phylogenetic comparative methods, a well-resolved phylogenetic hypothesis, and an improved methodology that accounts explicitly for uncertainty related to climate niche.

Methods

Phylogenetic hypothesis

Our ancestral reconstruction was based on the latest phylogenetic hypothesis for NWJs, derived from next-generation sequencing of ultra-conserved elements (UCEs), using 3142 loci. We included 45 NWJ taxa in this analysis (provided by John McCormack lab at Occidental Collage).

Occurrences and climate data

Primary occurrence data were assembled for 45 NWJ taxa from eBird (2015). We quality-controlled the occurrence data via careful comparisons with distributional maps (BirdLife International 2018; Madge and Burn 1994; Pitelka 1951). Our occurrence data were plotted on maps and vetted by specialists in the group to detect and remove any outliers that could represent errors or extralimital occurrences.

Climate data at 10’ resolution (~18 km at the Equator) were drawn from the MERRAclim dataset, a high-resolution global dataset of remotely-sensed climatic variables relevant to species’ distributions (Vega et al. 2017). We used two relatively uncorrelated bioclimatic variables, mean annual temperature and specific humidity, in our analysis. We defined **M** hypotheses (Soberón and Nakamura 2009) for each taxon based on their geographic distributions and biological requirements (Figure 3.1). We used the distribution of occurrence data within an **M** area to determine certainty/uncertainty of niche limits of a taxon. This explicit consideration of certainty/uncertainty related to climate niche was implemented as a useful approach in avoiding overinterpretation of the information available about the niche.

Character matrices

The ranges of tolerances across all NWJ species for temperature and humidity were divided into 15 and 19 bins, respectively. Each bin was set to 1 for presences and 0 for absences. If the limit of the presences matched the environmental limit of the species’ **M** area, the rest of the bins (i.e., those more extreme) were classified as uncertain. Since suitable bin ranges could change depending on the size of the bins, we classified bins on either side as uncertain if only one bin flanked the suitable range (see Appendix III). Via this procedure, we obtained character matrices for the two bioclimatic variables. These matrices were considered as summaries of the state of knowledge regarding the current climate niches of each of the NWJ taxa. We followed this method since distinguishing between environments manifested or not manifested within **M** is vital in avoiding overestimation of actual evolutionary change (Saupe et al. 2017).

Figure 3.2. Summary of ancestral niche reconstruction output under parsimony analysis. *Top* temperature and *Bottom* humidity niches of each ancestral node of the NWJ clade.

Climatic niche optimization

Using the two-character matrices, we traced evolution in each bin for every node in the phylogeny as means of reconstructing the climatic niches piecemeal. These reconstructions were done using routines in Mesquite v. 3.2 (Maddison and Maddison 2017). We performed both parsimony and maximum likelihood (ML) analyses: parsimony reconstruction methods find the ancestral states that require the least number of character changes given the tree and observed character distribution, whereas ML methods recover ancestral states using stochastic evolutionary models that maximize the probabilities of the observed states (Schluter et al. 1997; Pagel 1999). We performed ML analysis under the Mk1 model; in our ML output, we took probability >0.8 as “present,” (2) probability <0.2 as “absent,” and (3) probability between 0.2–0.8 as “uncertain.”. We used reconstructed temperature and humidity occupancies for each node (Figure 3.2) in the tree to analyze degrees of change at a given node (compared to its most recent ancestor), and overall to understand patterns of evolutionary change in the climatic niche (Figures 3.3 and 3.4).

Results

Phylogenetic hypothesis used in this analysis recovered that the NWJs comprise a monophyletic group, and identified five major clades: (1) Clade A: *Cyanolyca*; (2) Clade B: *Cyanocitta* and *Gymnorhinus*; (3) Clade C: *Aphelocoma*; (4) Clade D: some *Cyanocorax*, plus *Calocitta* and *Psilorhinus*; and (5) Clade E: remaining species of *Cyanocorax*.

The two different approaches that we employed—parsimony and ML—recovered similar general patterns for the evolution of NWJ climate niches. However, disagreements were observed at a few nodes, and the ML reconstruction was accompanied by greater uncertainty compared to the parsimony analysis. Thus, we interpret our results based on the parsimony reconstruction.

Temperature niches

Our climate reconstruction for mean annual temperature showed that most past and present NWJ taxa (extant and extinct) tend to have maintained an unchanged climate niche in terms of temperature across numerous speciation events, throughout their evolutionary history. However, certain ancestral nodes indicated signs of substantial temperature niche expansions and retractions (see Figure 3.1). Overall, we recovered three expansions and ten retractions, within a phylogenetic framework that consisted of a total of 43 internal nodes.

We observed significant changes in temperature niches in the evolutionary history of clade A, compared to the rest of the NWJ clades (Figure 3.3); all of the events are retractions with a mix of retractions from warmer and colder borders. A drastic niche expansion into colder climates can be observed in the evolution of the common ancestor of clade B (comprising *Gymnorhinu*s and *Cyanocitta*), with the broadest gain of temperature occupancy anywhere in the evolutionary history of NWJs. Two other significant retraction events were observed in clade C, in the speciation events of *Aphelocoma coerulescens* and the common ancestor of the clade containing *A. sumichrasti* and *A. woodhouseii*, from colder and warmer climates respectively.

The first niche expansion event (into higher temperature) in the history of NWJ clade was observed in the speciation of the ancestor of clades, D and E (Figure 3.3). A significant retraction from warmer conditions was noted in transition from node 36 to 40 (clade E in Figure 3.3). Downstream evolutionary events for clade E portrayed a relatively conserved temperature niche, with only a single niche retraction from warmer climates during the speciation of *C. sanblasianus* (Figure 3.3). The only niche change in clade D was observed during the evolution of *C. cristatellus*, where the species has retracted its niche from cold climates.

Humidity niches

Ancestral reconstructions for specific humidity (Figure 3.4) indicated that the humidity niche is relatively more dynamic compared to the temperature niche in NWJs. The humidity niche reconstruction revealed seven expansion and 19 retraction events in the course of NWJ evolution; only one event was manifested as a niche shift (expansions and retractions; Figure 3.4). Out of 43 nodes assessed, only 10 nodes (discounting uncertainties) showed a conserved humidity niche as compared to their ancestors.

In clade A, all observed niche changes were associated with retraction events. The slight shift towards low humid climates during the evolution of the common ancestor of clades B and C (node 4) is the first humidity niche change observed in the evolutionary history of NWJs. The most extreme niche retraction event was associated with the evolution of *Gymnorhinus* (clade B), where the humidity niche of its ancestral niche was retracted from high humid climates. Whereas, clades, C, D and E show different degrees of niche expansion and retraction events.

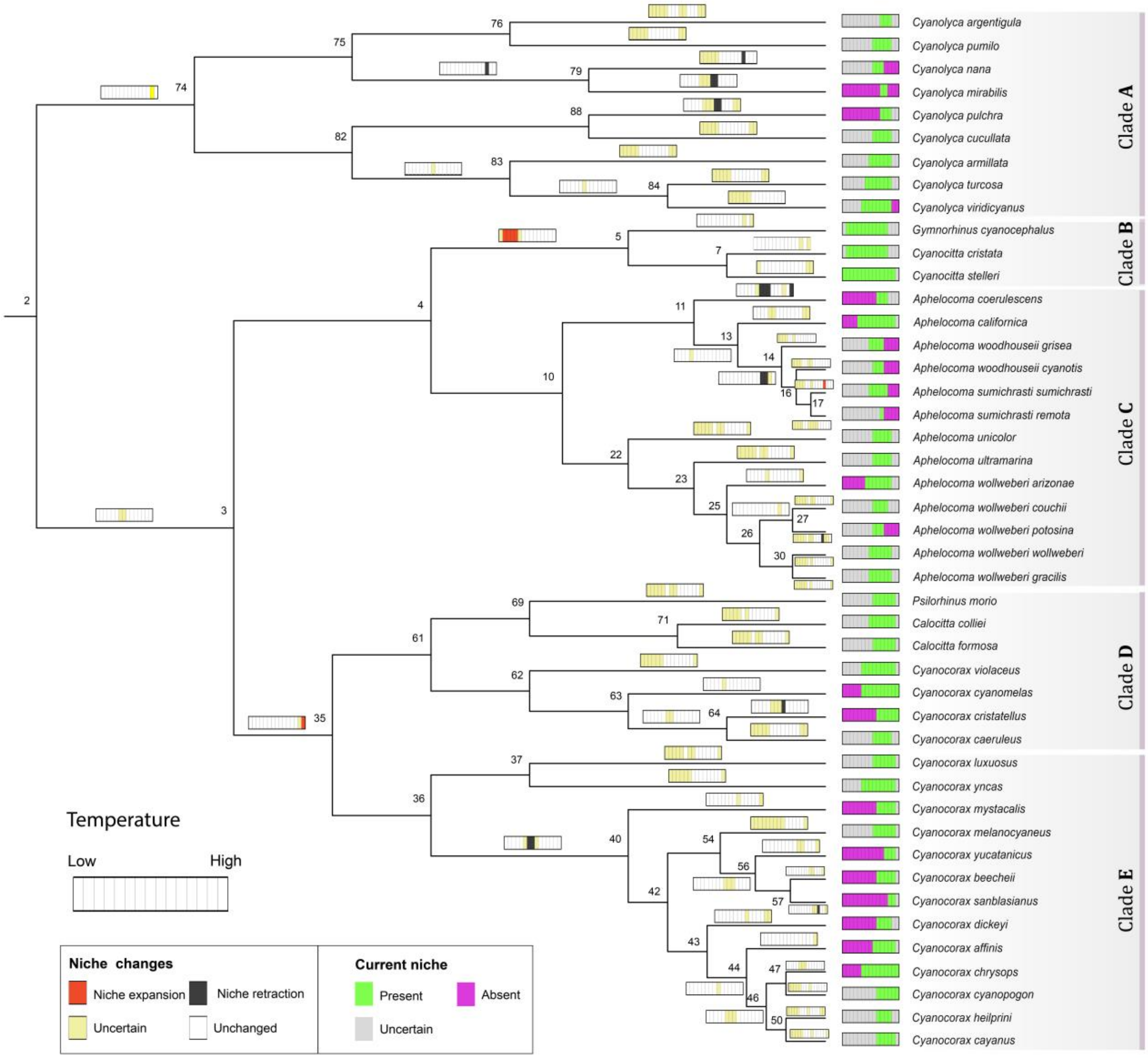

Figure 3.3. Temperature niche reconstruction under parsimony analysis. Boxes on the right represent current temperature niches of the NWJ species. Boxes at nodes indicate the degrees of temperature niche change at a given node compared to its most recent ancestor.

Discussion

In this study, we examined evolutionary patterns in the climate niche of NWJs, by reconstructing ancestral character states for mean annual temperature and specific humidity, using the most recent and comprehensive phylogenetic hypothesis for the clade. Both ML and parsimony reconstruction approaches demonstrated similar evolutionary trends for ancestral climate niches of the NWJs, with many parallels and only a few disagreements. The ML reconstruction showed a comparatively greater number of uncertainties, in terms of reconstructing presences and absences in climate bins. This result could be a consequence of (1) our extreme caution in scoring absences within the **M** area (see Methods for details), and/or (2) the narrow probability ranges we considered as true presences ($p > 0.8$) or true absences ($p < 0.2$) in our reconstructions of ancestral states for climate bins. Still, adopted these interpretation criteria to avoid overinterpretation of our results; the former aided in coping with the issue of pseudo-absences, and the latter helped us distinguish between reconstructed presences and absences with high confidence. Given the greater degree of uncertainty associated with the ML approach, and the general agreement between the two sets of results, we discuss in detail only the results obtained by the parsimony analysis.

In general, our ancestral reconstructions indicated that temperature niches evolve at a relatively slower rate compared to humidity niches. We categorized climate niche changes observed in NWJs into three types: (a) niche expansions (red boxes in Figures 3.3 and 3.4), (b) niche retractions (black boxes in Figures 3.3 and 3.4), and (c) niche shifts (both expansions and retractions at the same node). Without explicit consideration of accessible area for each species, reconstructed niche expansion can be a consequence of (1) the species’ niche truly expanding, or (2) overcoming a dispersal barrier, giving the species access to new climate conditions that were already part of the species’ original niche. Deciding whether these reconstructed niche evolution events were true events of niche evolution, or mere artifacts of changes in **M**, requires careful consideration of dispersal and access of species; our explicit consideration of **M** for each species, and consequent gaps in information, represent a useful approach to avoiding this overinterpretation of niche changes.

Out of the two climatic dimensions we considered, humidity can be considered as less evenly and predictably distributed across space, compared to temperature, which is often closely related to elevation (Pepin et al. 2015). Geographic barriers such as mountains can affect movements of air masses, resulting in noticeable differences in humidity and precipitation between windward and leeward sides. To understand the likely association between diversification and climate, taking the current species distributional patterns into consideration is important. NWJs are broadly distributed across both North and South America. Of the two NWJ lineages that reached South America, genus *Cyanolyca* (Clade A in Figure 2) includes species that inhabit humid montane forest that range from Mexico to Bolivia. The clade is comprised of nine allopatric species with highly subdivided ranges (Hellmayr 1934) that appear to have originated with formation of geographic barriers that promoted speciation (Bonaccorso 2009). Our humidity niche reconstruction indicated that six of the eight splits within this clade were associated with non-directional niche retractions (withdrawing from both high and low humid conditions), whereas three retractions were high-magnitude withdrawals (losing at least 2 climate bins) from the humidity niche of the immediately ancestral node. One possibility is that the non-directional retractions are artifacts of dispersal limitations: glacial climate fluctuations in montane regions leading to repeated formation and disappearance of sky-islands could be one explanation, forming dispersal corridors between once-fragmented range areas. However, we took good care in delimiting **M** areas for these species, and temperature niche reconstructions for the same clade resulted in just two retraction scenarios (losses of 1 climate bin each).

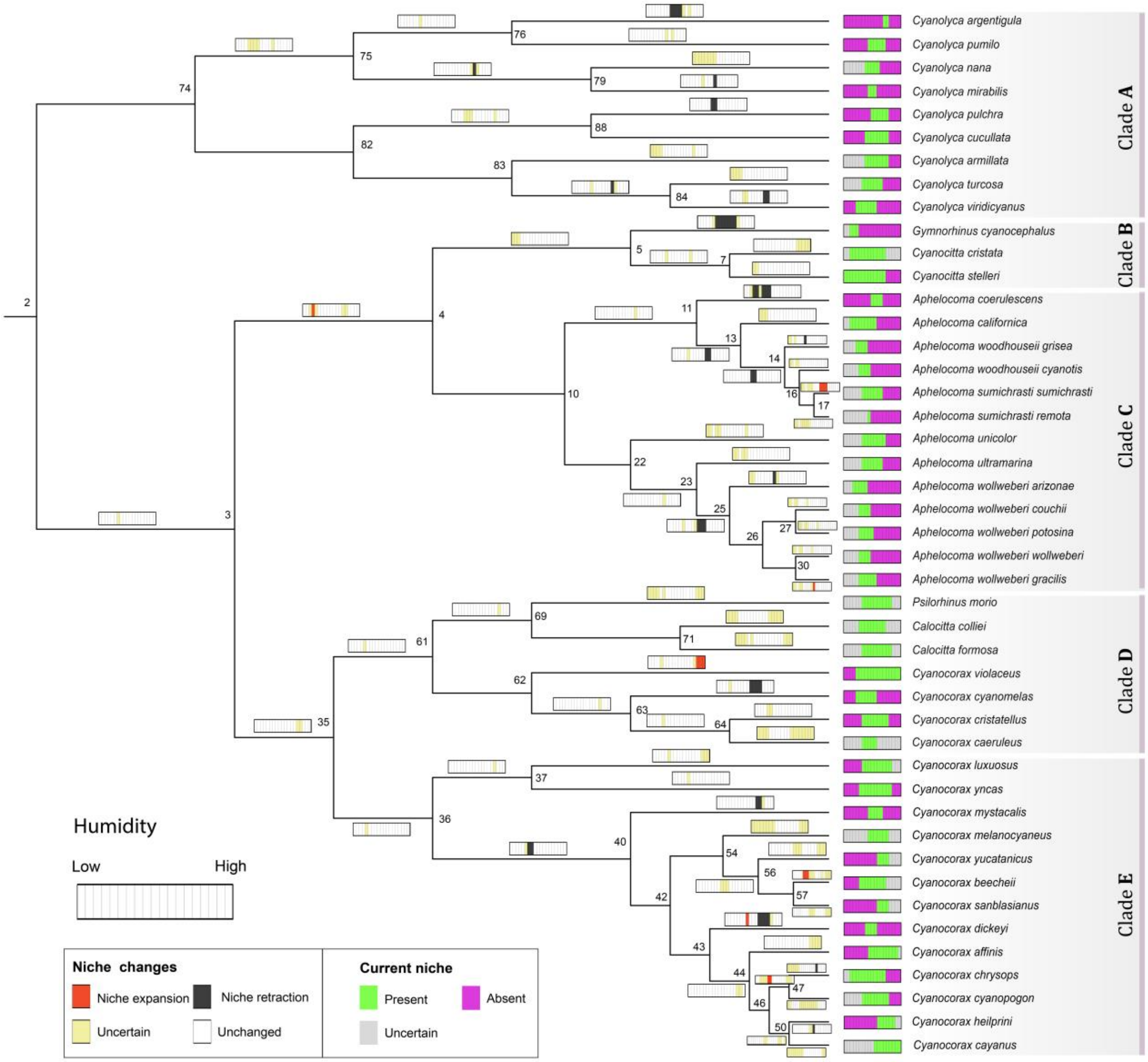

Figure 3.4. Humidity niche reconstruction under parsimony analysis. Boxes on the right represent current humidity niches of the NWJ species. Boxes at nodes indicate the degrees of humidity niche change at a given node compared to its most recent ancestor.

A dramatic temperature niche expansion was observed in the climate niche reconstructions for Clade B, comprising *Gymnorhinus* and *Cyanocitta*. Obviously, this situation represents a true niche expansion, in where the niche breadth of the clade actually increased, as evident in broad current distributions of the component taxa, compared to the distribution of its sister clade (Clade C) taxa unified. Another interesting observation in Clade B was the similarly broad temperature tolerances of all three extant species, but the substantial amount of humidity niche variation between *Gymnorhinus* and *Cyanocitta*.

Clade C includes the *Aphelocoma*, which shows diverse distributions in terms of geography (Pitelka 1951); current species' distributions are in cloud forest, pine-oak forest, woodland, scrub, deserts, and even mangroves (Peterson and Vargas 1993). Our temperature niche reconstruction of the clade indicates two significant niche retraction events. The retraction event associated with the speciation event of *A. coerulescens* shows a dramatic retraction from colder climates and a slight retraction from hot climates. Similar retraction was noted in humidity, where the niche has been retracted from low humid climates. As evident in both temperature and humidity changes, this situation possibly represents a true niche retraction, wherein the niche breadth of the clade actually decreased. Being a habitat specialist, living mainly in scrub woodlands of peninsular Florida, the restricted distribution of *A. coerulescens* supports the observed niche retraction event.

Temperature niche reconstruction in clades D and E demonstrated a scenario in which niche conservatism prevails through numerous speciation events. Temperature niches remained unchanged, except only in the case of three retraction events. Taxa within these clades are good dispersers, and show broad current distributions across most of tropical South and Central America. Perhaps, their common ancestor, which had broad climate niche tolerances, initially occupied a broad range, with subsequent allopatric speciations. Under such circumstances, the original climate niche could remain unchanged across many speciation events (Peterson et al. 1999). One requirement for such a phenomenon to take place would be a relatively evenly distributed climate across the ancestral landscape; current mean annual temperature patterns for tropical South America seem to fulfill this condition. Validity of this hypothesis can be further tested through detailed biogeographic analysis.

In summary, we attempted to reconstruct ancestral climate niches of NWJs, in terms of temperature and humidity niche reconstructions, in a well-resolved phylogenetic framework. In effect, we tried to observe how two dimensions of the climate niche behave through evolutionary time in NWJs. Our results revealed that humidity niches are more dynamic, compared to temperature niches, and that different clades exhibit different degrees of niche conservatism, or niche dynamism. Finally, we attempted to relate differences in niche to species' ecology, geological history, and distributional patterns. The result is a synthetic view of ecological niche and its evolution over time in the history of the NWJs.

CHAPTER 4

Climatic niche stability versus dynamism and geographic range evolution in treepies and blue/green magpies (family Corvidae)

Abstract

In this study, we attempted to reconstruct the climatic niches of two non-sister clades (treepies and blue/green magpies) of the family Corvidae that are distributed across the tropical and subtropical forests of southern and eastern Asia. Their subsequent origin at around the same time period as well as similar current distributional patterns made them ideal candidates to examine the implications of evolving niches in two closely related clades under the effects of dramatic geological and climatic changes. Our climate reconstructions indicated, in general, temperature niches in both treepies and magpies seem to be more dynamic than the humidity niches, indicating, perhaps, temperature acts as a more significant factor in shaping species' distributions and diversification in the tropics. Moreover, the observed temperature niche modifications associated with speciation events in both clades may relate to past climatic changes in the region. We attempted to relate environmentally driven evolutionary patterns to biogeographic processes in an attempt to understand species distributions across spatial and temporal scales.

Introduction

Understanding patterns of climatic niche evolution in species has become an area of intensive study in the past few decades (Cavender-Bares et al. 2011; Eaton et al. 2008; Kozak and Wiens 2006; Pie et al. 2017). Two major hypotheses linking niche evolution and speciation have been proposed, yet these ideas contrast drastically: one predicts that speciation is greatest in lineages with rapidly evolving climatic niches (Kozak and Wiens 2007; Moritz et al. 2000); a counter-hypothesis predicts that diversification is higher when climatic niches evolve more slowly (Cadena et al. 2012; Kozak and Wiens 2006). Hence, the role of climatic niche change in diversification remains unclear. Furthermore, studying climatic niche evolution has become imperative to understand patterns of current species diversity and distributions, to evaluate the effects of climate change on species' distributions and extinctions (Cahill et al. 2013; Latinne et al. 2015; Peterson et al. 2001), and to predict possible biological invasions (Broennimann and Guisan 2008; Broennimann et al. 2012).

Changes in species' climatic niches have been evaluated in many taxa via different approaches (Duran et al. 2013; McNyset 2009; Peixoto et al. 2017; Pie et al. 2017), demonstrating different evolutionary patterns in different groups. Consequently, to understand the evolutionary trends of climatic niche dynamics, one needs to focus on smaller clades (exhibiting less extreme variation in terms of evolutionary history and geography), with an approach that minimizes errors in niche estimates (Saupe et al. 2018). Additionally, closely related clades are likely to have similar niches (Peterson et al. 1999); detecting changes amongst such taxa is interesting and intriguing in terms of understanding such changes and their causes and effects on geographic distributions.

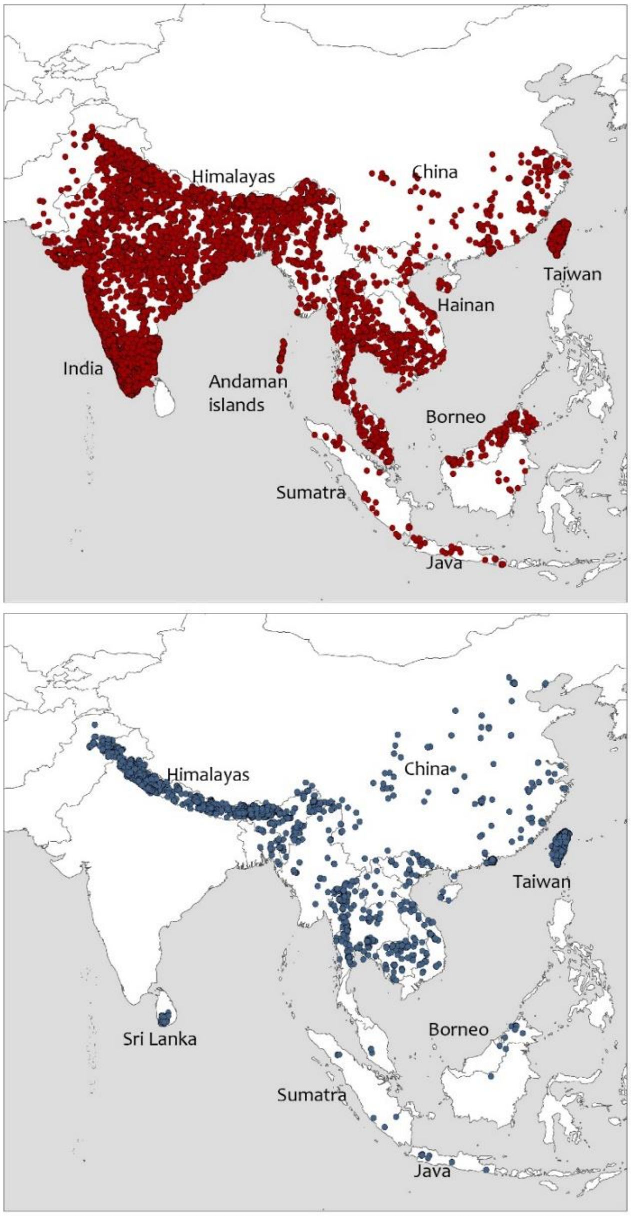

Figure 4.1. *Top* Geographic distribution of treepies, *Bottom* Geographic distribution of magpies: sampled occurrence points used in niche restrictions are indicated by colored dots.

Distributed across the tropical and subtropical forests of southern and eastern Asia (Figure 4.1), treepies and blue/green magpies are two non-sister clades that branch off sequentially (as the 2nd and 3rd deepest splits, respectively) within the crown group of the family Corvidae (Fernando et al. 2017; Jønsson et al. 2016). The magpies include five species of blue magpies in genus *Urocissa*, and four species of green magpies in genus *Cissa* (Madge and

Burn 1994; Van Balen et al. 2013). Treepies inhabit South and Southeast Asia and comprise four genera (*Dendrocitta*, *Crypsirina*, *Temnurus*, and *Platysmurus*) and 11 species (Jønsson et al. 2016). Both clades have originated during the late Miocene in East Asia, and in East Asia and Sundaland, respectively, and have subsequently diversified into the Indian Subcontinent (unpublished chapter 2).

Tropical South and Southeast Asia has a complex geological and climatic history (Bird et al. 2005). These processes have apparently altered spatial distributions of terrestrial habitats in this region dramatically through time, promoting speciation and lineage diversification (Bird et al. 2005; Esselstyn et al. 2009). Since environmental conditions are important extrinsic factors that shape species' distributions across spatial and temporal scales (MacArthur 1984), historical biogeography probably interacts with phylogenetic patterns of niche variation in species (Borcard et al. 1992; Freckleton and Jetz 2009). However, limited knowledge exists on the influence of climatic variation on the diversification and distribution of birds in this region. Owing to their distributional patterns in southern and eastern Asia accompanied by manageable species numbers, treepies and blue/green magpies form two independent systems of parallelly evolved yet closely related clades, ideal for studying climatic niche dynamics in a phylogenetic context. In this study, we investigate how climatic niches have evolved in treepies and blue/green magpies over time, and how past climatic fluctuations and geological events have shaped species' distributions within these two clades using novel ancestral niche reconstruction and comparative phylogenetic methods.

Methods

Phylogenetic hypotheses

We used the best-supported topologies (separately for treepies and magpies) from our previous study, derived from a hybrid phylogenetic-phylogenomic approach (paper submitted), that incorporated ultra-conserved elements (UCEs), and mitochondrial DNA and nuclear introns. We conducted time-calibrated Bayesian analyses in BEAST 2.3.2 (Bouckaert et al. 2014), implemented with BEAGLE (Ayres et al. 2011). A secondary node calibration point (Oliveros et al. 2019b), corresponding to the split for the base of the family Corvidae, was used to estimate divergence times. We used a birth-death tree prior and an uncorrelated lognormal (UCLN) relaxed clock. Two independent MCMC runs of 100 million generations each were executed with unlinked site models for each partition. Convergence of parameter estimates was examined using TRACER 1.6 (Rambaut and Drummond 2007). Trees were sampled every 2000 generations, and the first 25% of trees was discarded as burn-in. We summarized the remaining trees to obtain a 50% majority-rule consensus tree. All species represented in the phylogenies (10 treepies and 8 magpies) were considered in the niche reconstructions.

Input data

We assembled occurrence data for treepies and magpies from eBird (2015) and the Global Biodiversity Information Facility (GBIF; http://www.gbif.org). For quality control, we compared the occurrence data with species distributional maps (del Hoyo et al. 2009; Goodwin 1976; Madge and Burn 1994) and removed any records that could represent errors or extralimital occurrences. Climate data at 2.5’ resolution was drawn from the MERRAclim dataset, a high-resolution global dataset derived from remotely sensed data sources (Vega et al. 2017). We used

15 variables, 9 related to temperature and 6 related to humidity, in our analysis. We did not consider bio 8, 9, 18 and 19 in the analysis because they included odd spatial artifacts.

Climatic niche reconstructions

Based on each species' geographic distributions and natural history, we delimited hypotheses of accessible areas **M** (Barve et al. 2011; Soberón and Nakamura 2009; Soberón and Peterson 2005) for each species. We incorporated these areas in characterizing sets of conditions available to a species that constitute species' niche limits for each variable following Owens et al. (2020). This approach reduces risk of overestimation of amounts or rates of ecological niche evolution of the taxa under consideration (Saupe et al. 2018) as it does not identify evolutionary change when niche limits are uncertain. We prepared tables of binned niche character values, performed ancestral niche reconstructions, and identified niche evolution for treepies and blue/green magpies using the package nichevol (Cobos et al. 2020) in R 3.6.3 (R Core Team 2020). The niche reconstructions were performed under both maximum parsimony and maximum likelihood methods. To visualize, we represented reconstructed ancestral niches and evolutionary change of niches in our phylogeny; for certain sister species, we projected the observed niche reconstructions and changes into geographic space with respect to today's climatic conditions.

Results

We reconstructed climatic niches of treepies and blue/green magpies separately for all the available bioclimatic variables used; however, here, we describe in detail niche evolution for (a) mean annual temperature (bio1), and (b) mean annual specific humidity (bio12), which are relatively uncorrelated variables. Ancestral reconstructions for the remaining climatic variables (that are related to temperature and humidity) are presented in the Appendices (Appendix IV).

For both treepie and magpie clades, parsimony and maximum likelihood (ML) approaches yielded similar niche reconstructions, though, with slight discrepancies. ML reconstructions were associated with more uncertainty (compared to that of the parsimony method), resulting in less obvious evolutionary niche dynamics. As a consequence, we chose to discuss the outcomes of our parsimony analysis, while presenting the ML reconstructions for both clades in the Appendices (Appendix V).

Treepies

Temperature niches—Reconstruction of the temperature niche (in the form of mean annual temperature) for treepies showed several niche expansion and retraction scenarios throughout the clade's course of evolution (Figure 4.2); six of the 18 speciation events were associated with temperature niche modifications, although most were quite minor in magnitude. The niche shift observed in the late Pleistocene transition from the most recent ancestor to *Dendrocitta formosae* is one example of dramatic expansion of the temperature tolerance of the lineage towards colder climates accompanied by a minor retraction from the warmer climates. Another instance of a drastic niche expansion was reconstructed at around the Miocene-Pliocene boundary associated with the speciation event that gave rise to the common ancestor of *D. frontalis* and *D. vagabunda*; out of the two daughter species, the former further expanded its niche towards warmer conditions, while the latter withdraws slightly from its ancestral warm temperature tolerance.

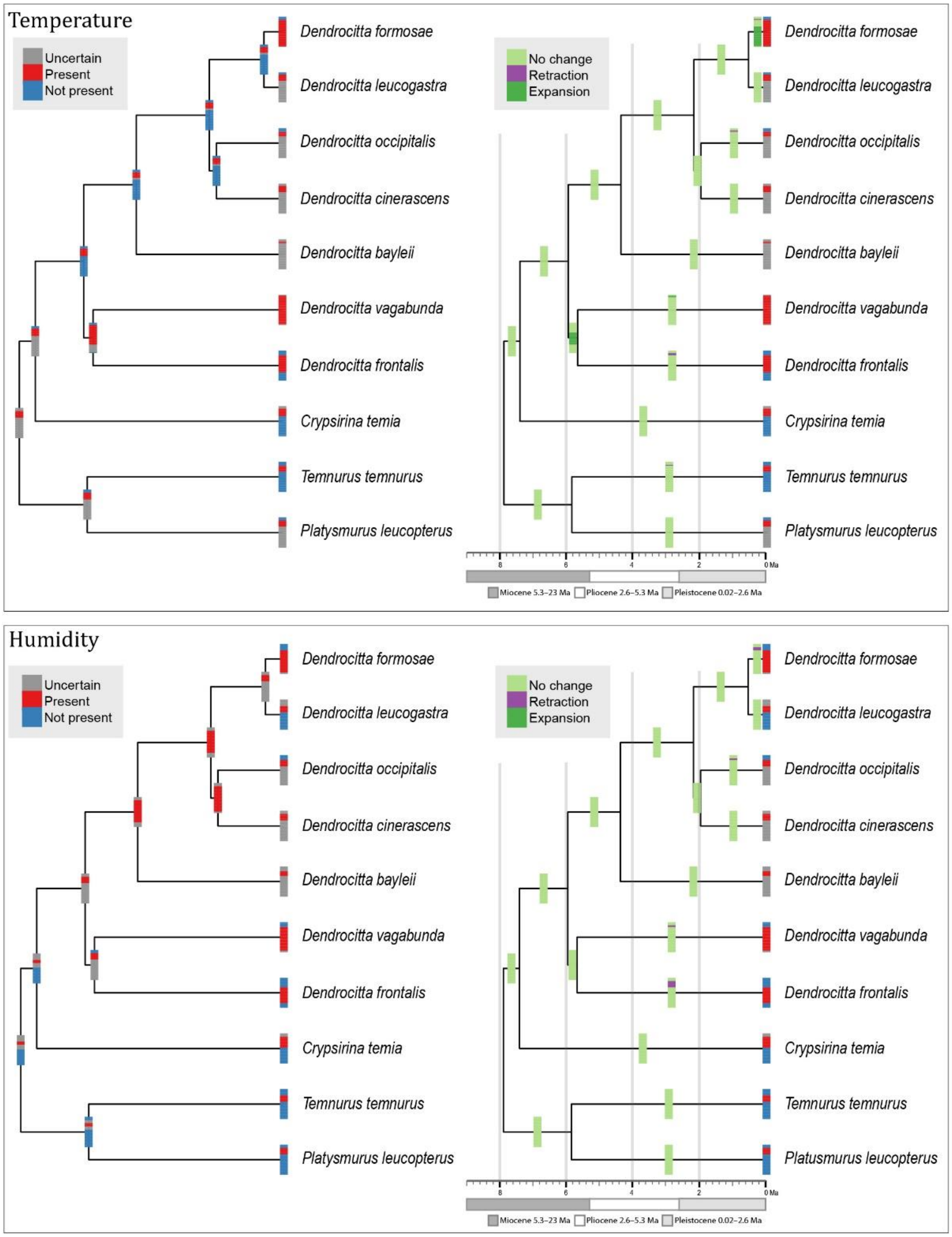

Figure 4.2**.** Climatic niche reconstruction in treepies; *top*: temperature niche, *bottom*: humidity niche. Bars at the nodes represent the reconstructed niches in each ancestor and bars at the branches represent the niche change (expansion or retraction) from ancestor to descendent. Each species' current niche is represented by the bars at the tips.

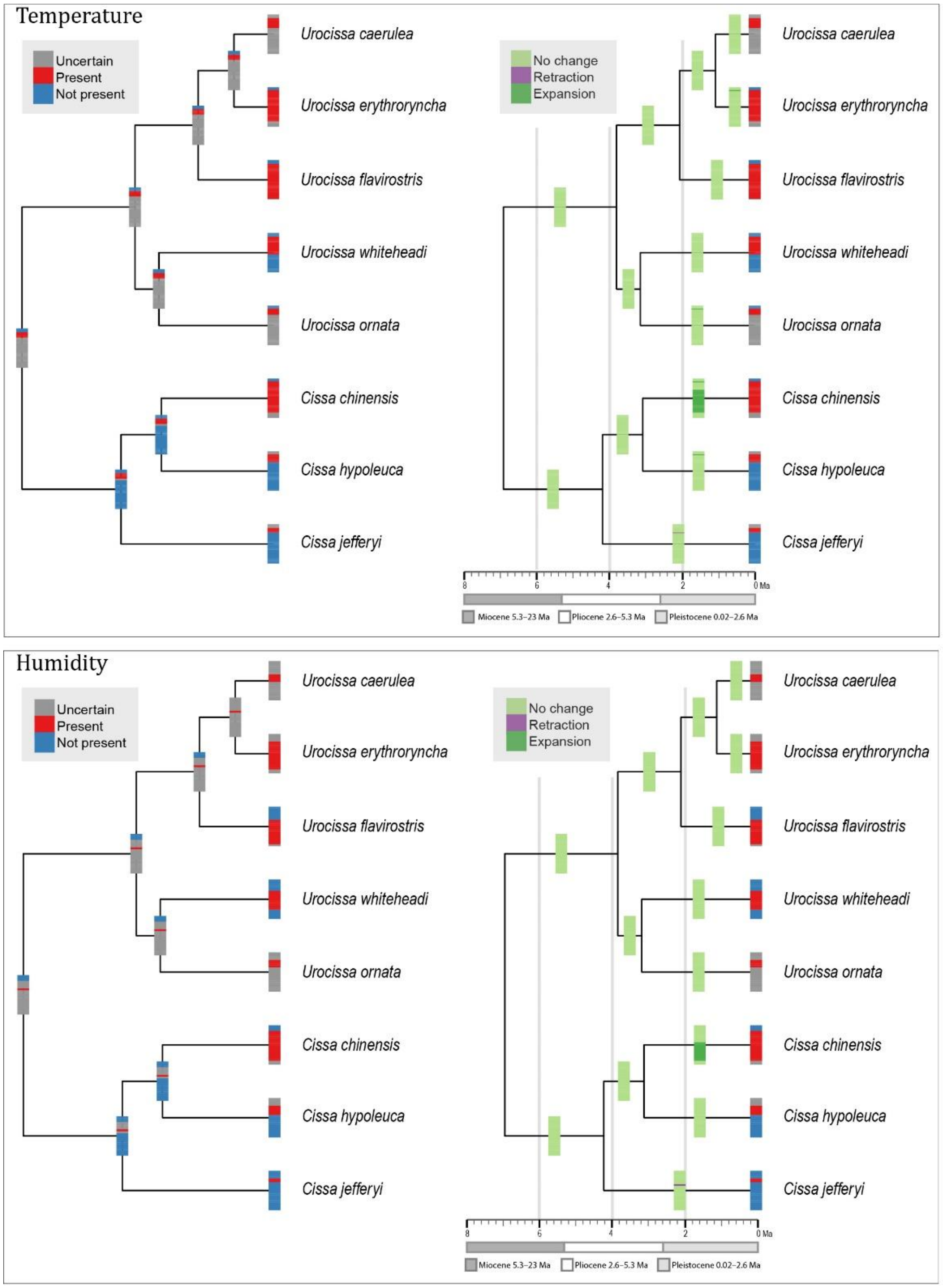

Figure 4.3. Climatic niche reconstruction in magpies; *top*: temperature niche, *bottom*: humidity niche. Bars at the nodes represent the reconstructed niches in each ancestor and bars at the branches represent the niche change (expansion or retraction) from ancestor to descent. Each species' current niche is represented by the bars at the tips.

furthermore, two faint retractions of the temperature niche (from warmer climates) were observed during the speciation events of *D. occipitalis* and *Temnurus temnurus*. Some small-scale modifications in the climatic niche were reflected as substantial changes in species' distributional area, when projected onto geographic space based on current global climatic conditions (see e.g, niche retraction in *D. frontalis*; Figure 4.4).

Humidity niches—Compared to temperature niches, the reconstructed humidity niche (mean annual specific humidity) for the treepie clade was more conserved; only four out of the 18 diversification events were accompanied by any niche differentiation (Figure 4.2). All observed niche modifications were of retractions from high humidity, as seen in the speciation process of *D. formosae*, *D. frontalis*, *D. occipitalis*, and *D. vagabunda*. For the most part, the treepie clade has maintained a stable humidity niche while undergoing diversification and speciation.

Magpies

Temperature niches—Our niche reconstruction of mean annual temperature for the magpies reveals that the clade has undergone several niche changes throughout its evolutionary history (Figure 4.3); out of the 14 speciation events, five were associated with changes in temperature niche. The most extreme temperature niche expansion was associated with the speciation process of *Cissa chinensis*; this expansion came in the form of a dramatic gain in cold tolerance and a slight gain in warm tolerance, relative to its immediate ancestor. *Urocissa erythrorhyncha*, *U. ornata*, and *C. hypoleuca* exhibited slight expansions into warmer climates. The only retraction episode in the temperature niche evolution of magpies was during the speciation event of *C. jefferyi*, in terms of cold tolerance.

Humidity niches—Similarly as with treepies, the humidity niche of magpies showed fewer evolutionary modifications compared to the temperature niche; out of 14 speciation events, only two showed changes in humidity niche dimensions. A substantial humidity niche expansion occurred in the same speciation event (associated with *Cissa chinensis*) as with the temperature niche. Furthermore, *Cissa jefferyi* showed a niche retraction from low humidity conditions during its speciation event.

Discussion

In this study, we attempted to reconstruct the climatic niches of two non-sister clades (treepies and blue/green magpies) of the family Corvidae that are distributed across the tropical and subtropical forests of southern and eastern Asia. This region has a complex geological and climatic history, which is thought to have altered the spatial distribution of terrestrial habitats dramatically during the Cenozoic era (Morley 2012). Such changes in habitat, perhaps, impacted speciation and diversification patterns of birds in this region. Being two tropical lineages that belong in the same family, with subsequent origins at around the same time period (~7–8 million years; Chapter 2), and with similar distributional patterns, treepies and blue/green magpies form ideal candidate clades with which to examine the implications of evolving niches in two closely related clades under the effects of dramatic geological and climatic changes.

According to our climate reconstructions, in general, temperature niches in both treepies and magpies seem to be more dynamic than the humidity niches. This observation is contrary to our previous studies on New World jays in which we found temperature niches to be more conserved. NWJs are a group of corvids that have radiated successfully in the Americas, across tropical, subtropical, and temperate environments. Perhaps, temperature acts as a more significant factor in shaping species' distributions and diversification in the tropics than in the temperate regions. Consequently, the observed temperature niche modifications associated with speciation events may relate to past climatic changes in the region. Interestingly, all observed humidity niche changes were associated with temperature niche transformations, in both clades.

Species' biogeographic history plays an important role in their niche evolution (Borcard et al. 1992; Freckleton and Jetz 2009). It is worth noting that all areas displayed as suitable for species (as regards reconstructed environmental space and distributional potential) may not have been actually occupied by the ancestral species; mainly due to (a) accessibility issues, (b) habitat alterations, and (c) limitations imposed by biotic interactions, each of which probably constrained species' distributions in the past. Hence, in reality, one may not observe species' distribution across all areas predicted as suitable by niche models, even at present. Therefore, interpretations concerning climatic niche evolution and historical biogeography should be made with caution.

Treepies—The niche reconstruction for the mean annual temperature of treepies showed two significant expansion events during their evolutionary history (Figure 4.2), both being expansions into colder climates. During the speciation process that lead to *Dendrocitta formosae*, a notable shift in the temperature (as compared to the ancestral niche) can be witnessed in the form of a drastic expansion towards colder climates and a slight withdrawal from warmer temperatures, associated with a humidity niche retraction from high humid climates (Figure 4.2). These niche modifications appear to have accumulated in *D. formosae* during the late Pleistocene

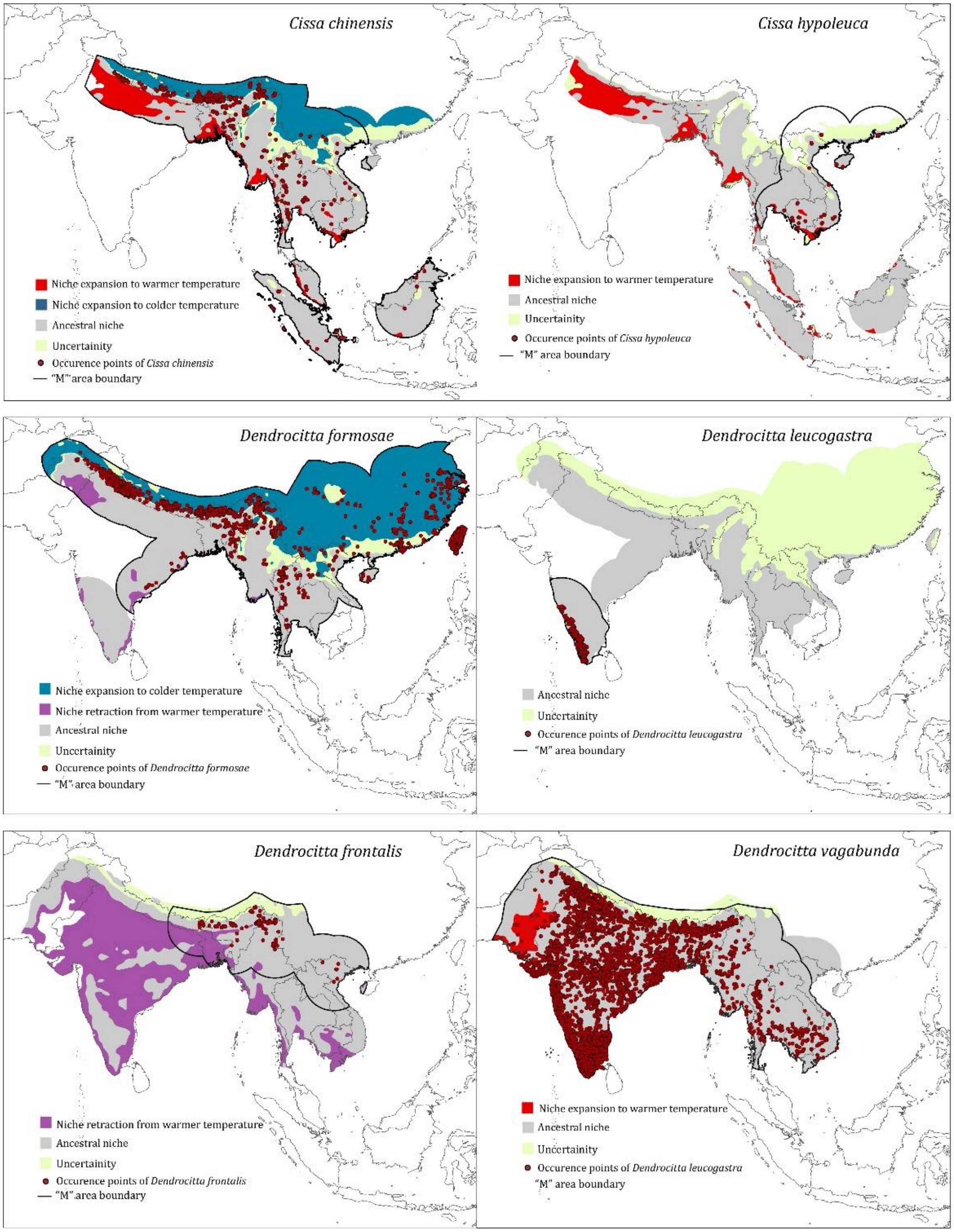

Figure 4.4. Temperature niche evolution in the sister species, *top*: *Cissa chinensis* and *C. hypoleuca* magpies, *middle*: *Dendrocitta formosae* and *D. leucogastra* and, *bottom*: *D. frontalis* and *D. vagabunda* treepies. All the niche changes displayed are with respect to today's distribution of climatic conditions.

soon after the ancestral population diverged to form the two sister taxa (*D. leucogastra* being the other). Our results further suggest that the ancestral species probably resembled *D. leucogastra* in terms of its ecology, but was a widely distributed taxon that ranged across the tropical Indomalayan region (Figure 4.4); this species obviously favored humid forests, and thus existed along the forest stretch in the Eastern Ghats during the late Pleistocene (Karanth 2003), connecting Western Ghats with mainland Asia. Pleistocene climate oscillations and resultant fragmentation of the humid forests in Eastern Ghats probably caused a disjunction in this ancestral population, giving rise to *D. leucogastra* in the western and *D. formosae* in the eastern parts of the range. At around the same time period, cool-temperate forest coverage spread across northeastern China (Stebich et al. 2009). The observed significant niche modifications in *D. formosae* (both in temperature and humidity) could probably be due to physiological adaptations of this lineage that ensured its existence and enhanced its dispersal capability in across ever-transforming habitats.

The ancestral temperature niche of the genus *Dendrocitta* experienced a massive change during the evolution of the ancestral species of *D. frontalis* and *D. vagabunda*, which is an expansion into colder climates that occurred during the late Miocene. *Dendrocitta vagabunda* is a widespread taxon that inhabits most of India, also extending eastwards across lowland Southeast Asia. *Dendrocitta frontalis*, in contrast, is a species that inhabits dense mixed-humid forests in the Eastern Himalayas, northern Myanmar, southern China, and northern Vietnam. The most recent common ancestor of these two taxa extended its geographic range into Himalayas (Chapter 2), and perhaps expanded its temperature niche in the same time period. Our temperature niche reconstruction further indicated a slight expansion into warmer climates, and a slight retraction from warmer climates, respectively, in *D. vagabunda* and *D. frontalis*. Our projections of the reconstructed ancestral niches and niche modifications (for these taxa) in geographic space revealed that slight changes in climatic tolerances can lead to large-scale modifications in distributional potential of species (Figure 4.4).

Our humidity niche reconstruction indicates a drastic niche retraction from humid climates during the evolution of *D. frontalis*. Fossil evidence suggests that during the mid-Miocene much of India was covered in humid forests that was continuous with Southeast Asian forests (Karanth 2003). However, change in climate as caused by the evolution of Asian monsoons due to phased uplift of the Himalayas and the Tibetan Plateau (Zhisheng et al. 2001) probably resulted in the gradual retraction of these forests. Thus, the ancestor of the two species, perhaps, a taxon that inhabited humid climates, diversified, giving rise to daughter species that were more adapted to drier climates.

Our reconstructions for temperature and humidity niches showed retractions from higher temperatures and high humidity during the evolution of *D. occipitalis*, a taxa currently distributed on the island of Sumatra in Indonesia. During the Pliocene and Pleistocene, Sundaland formed a continuous subcontinental landmass connecting the Indonesian islands with the Asian mainland (Haile 1973; Hall 2009; Sartono 1973; Tjia 1980). Our previous biogeographic reconstructions (Chapter 2) indicate that the ancestor of both *D. cinerascens* and *D. occipitalis* (currently distributed in Borneo) inhabited Sundaland during the early Pleistocene, perhaps when these islands were connected in period of lowered sea levels. With rising sea levels and consequent vicariance, the two island populations perhaps speciated into *D. cinerascens* and *D. occipitalis*.

Magpies—Our ancestral reconstruction for magpies indicated a substantial expansion in the temperature niche into colder climates, during the evolution of *Cissa chinensis*; the same speciation event was also accompanied by a slight expansion into warmer climates. However, once projected onto geographic space under current climatic conditions, this slight expansion of the temperature niche into warmer climates converts to massive gains in terms of suitable distributional area for this species, much more than does the expansion into colder temperatures (Figure 4.4), indicating the importance of prevalent climatic conditions and their distributions for the success of a species.

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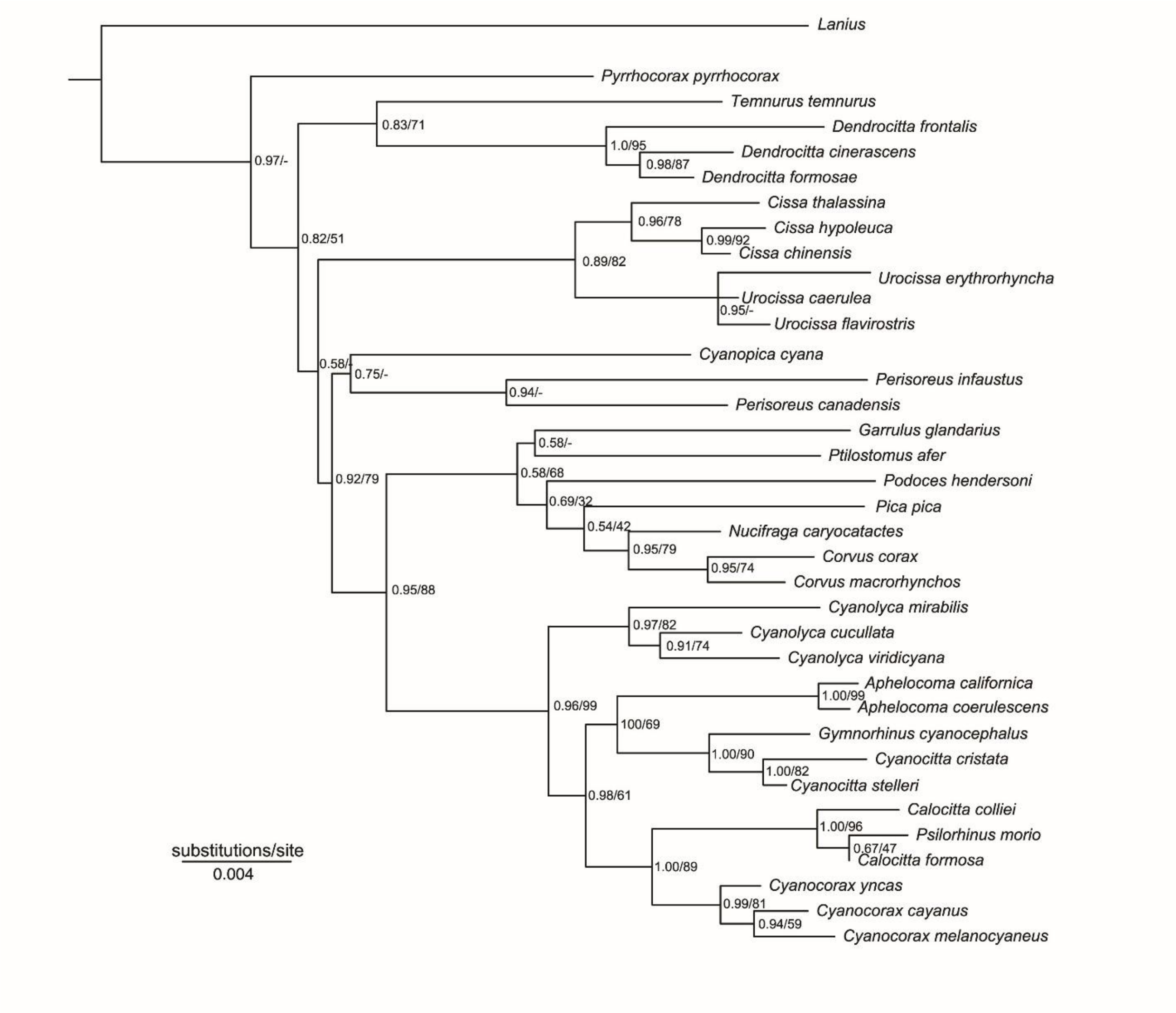
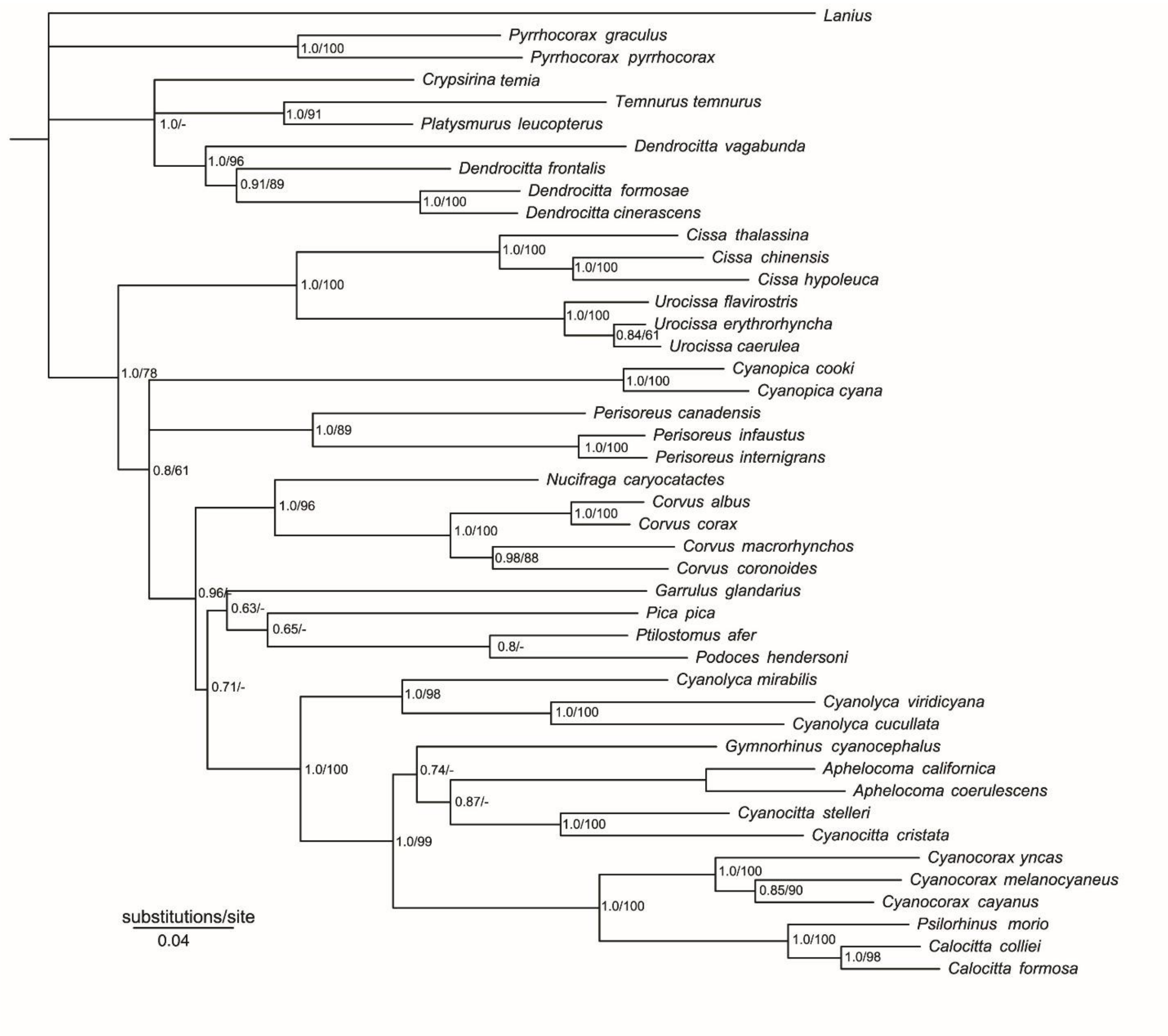
Appendix I. Detailed phylogenies.



Phylogeny based on BA and ML analyses of the combined nuclear data set. Numbers at the nodes refer to Bayesian posterior probability/ML bootstrap support



Phylogeny based on BA and ML analyses of the combined mitochondrial data set. Numbers at the nodes refer to Bayesian posterior probability/ML bootstrap support.

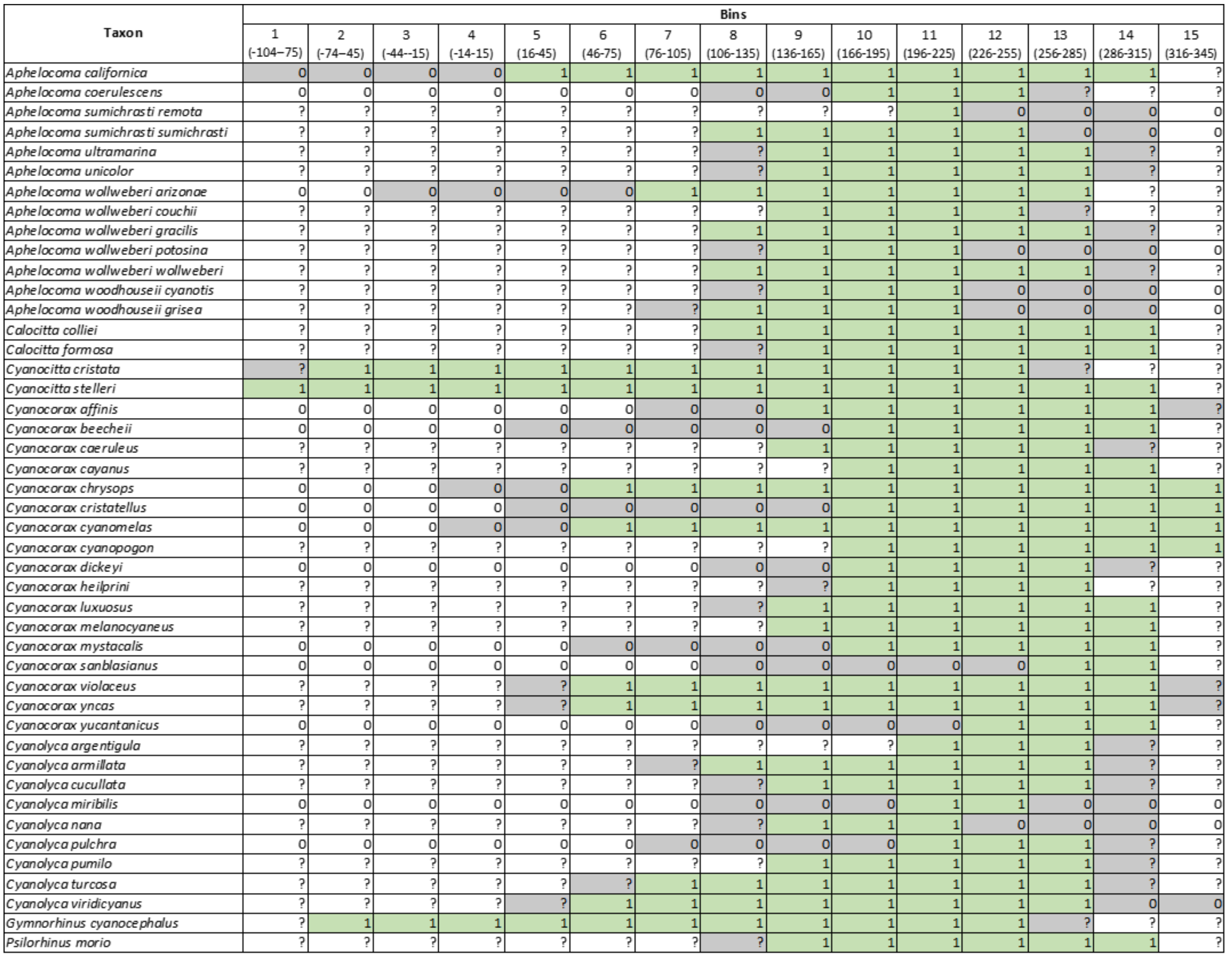
Appendix II. Sampling and contig characteristics.

Species	Sample number	No of UCE contigs	Mean and (range) UCE contig length (bp)
Treepies			
*Dendrocitta bayleii**	AMNH Birds SKIN-677100	3761	293.5 (201–973)
Dendrocitta cinerascens	LSUMZ birdsTissues 38662	4571	552.9 (201–1415)
Dendrocitta formosae	KU Birds 119295	4481	545.9 (201–1387)
Dendrocitta frontalis	KU Birds 124847	4439	509.9 (201–2699)
*Dendrocitta leucogastra**	YPM VZ YPM ORN 024483	4050	323.4 (201–911)
*Dendrocitta occipitalis**	YPM VZ YPM ORN 041001	3773	313.5 (201–899)
*Dendrocitta vagabunda**	CM Birds S15216	4120	350.2 (201–1354)
*Temnurus temnurus**	LACM Birds 24756	2094	242.4 (201–812)
Blue and green magpies			
Cissa chinensis	KU Birds 122970	4462	530.5 (201–1266)
Cissa hypoleuca	KU Birds 116798	4461	516.1 (201–2774)
Cissa jefferyi	LSUMZ 19185	4478	601.1 (203–3268)
Urocissa erythroryncha	KU Birds 98934	4198	563.1 (201–1644)
Urocissa flavirostris	KU Birds 124738	4592	559.6 (202–3252)
*Urocissa ornata**	YPM VZ YPM ORN 020259	2320	261.7 (201–547)
*Urocissa whiteheadi**	MCZ Orn 238481	2740	275.2 (201–877)

* Toepad samples

Appendix III. Summary of the Mesquite input data.

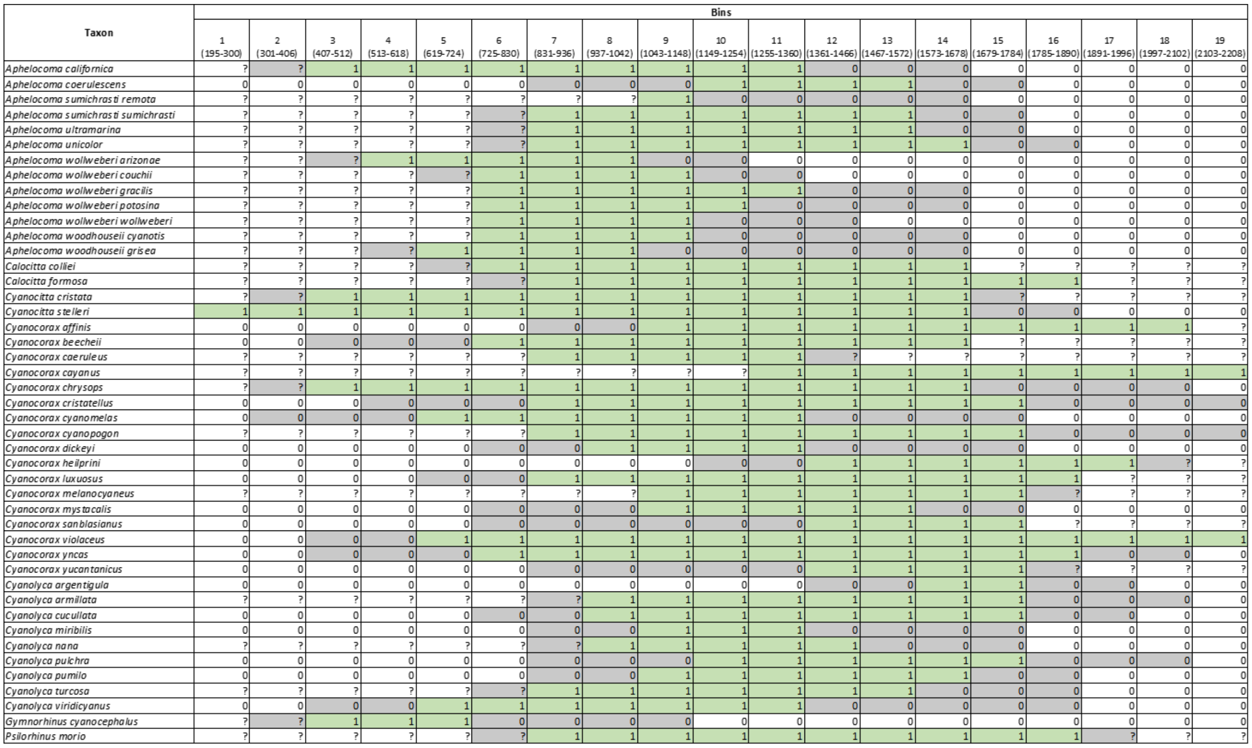
Temperature niches of each terminal taxa of the NWJ clade



Taxon	Bins														
	1 (-104–75)	2 (-74–45)	3 (-44--15)	4 (-14-15)	5 (16-45)	6 (46-75)	7 (76-105)	8 (106-135)	9 (136-165)	10 (166-195)	11 (196-225)	12 (226-255)	13 (256-285)	14 (286-315)	15 (316-345)
Aphelocoma californica	0	0	0	0	1	1	1	1	1	1	1	1	1	1	?
Aphelocoma coerulescens	0	0	0	0	0	0	0	0	0	1	1	1	?	?	?
Aphelocoma sumichrasti remota	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0
Aphelocoma sumichrasti sumichrasti	?	?	?	?	?	?	?	1	1	1	1	1	0	0	0
Aphelocoma ultramarina	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?
Aphelocoma unicolor	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?
Aphelocoma wollweberi arizonae	0	0	0	0	0	0	1	1	1	1	1	1	1	?	?
Aphelocoma wollweberi couchii	?	?	?	?	?	?	?	?	1	1	1	1	?	?	?
Aphelocoma wollweberi gracilis	?	?	?	?	?	?	?	1	1	1	1	1	1	?	?
Aphelocoma wollweberi potosina	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0
Aphelocoma wollweberi wollweberi	?	?	?	?	?	?	?	1	1	1	1	1	1	?	?
Aphelocoma woodhouseii cyanotis	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0
Aphelocoma woodhouseii grisea	?	?	?	?	?	?	?	1	1	1	1	0	0	0	0
Calocitta colliei	?	?	?	?	?	?	?	1	1	1	1	1	1	1	?
Calocitta formosa	?	?	?	?	?	?	?	?	1	1	1	1	1	1	?
Cyanocitta cristata	?	1	1	1	1	1	1	1	1	1	1	1	?	?	?
Cyanocitta stelleri	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?
Cyanocorax affinis	0	0	0	0	0	0	0	0	1	1	1	1	1	1	?
Cyanocorax beecheii	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?
Cyanocorax caeruleus	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?
Cyanocorax cayanus	?	?	?	?	?	?	?	?	?	1	1	1	1	1	?
Cyanocorax chrysops	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Cyanocorax cristatellus	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Cyanocorax cyanomelas	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Cyanocorax cyanopogon	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1
Cyanocorax dickeyi	0	0	0	0	0	0	0	0	0	1	1	1	1	?	?
Cyanocorax heilprini	?	?	?	?	?	?	?	?	?	1	1	1	1	?	?
Cyanocorax luxuosus	?	?	?	?	?	?	?	?	1	1	1	1	1	1	?
Cyanocorax melanocyaneus	?	?	?	?	?	?	?	?	1	1	1	1	1	1	?
Cyanocorax mystacalis	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?
Cyanocorax sanblasianus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?
Cyanocorax violaceus	?	?	?	?	?	1	1	1	1	1	1	1	1	1	?
Cyanocorax yncas	?	?	?	?	?	1	1	1	1	1	1	1	1	1	?
Cyanocorax yucantanicus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?
Cyanolyca argentigula	?	?	?	?	?	?	?	?	?	?	1	1	1	?	?
Cyanolyca armillata	?	?	?	?	?	?	?	1	1	1	1	1	1	?	?
Cyanolyca cucullata	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?
Cyanolyca miribilis	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Cyanolyca nana	?	?	?	?	?	?	?	?	1	1	1	0	0	0	0
Cyanolyca pulchra	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?
Cyanolyca pumilo	?	?	?	?	?	?	?	?	1	1	1	1	1	?	?
Cyanolyca turcosa	?	?	?	?	?	?	1	1	1	1	1	1	1	?	?
Cyanolyca viridicyanus	?	?	?	?	?	1	1	1	1	1	1	1	1	0	0
Gymnorhinus cyanocephalus	?	1	1	1	1	1	1	1	1	1	1	1	?	?	?
Psilorhinus morio	?	?	?	?	?	?	?	?	1	1	1	1	1	1	?

0	Absence within M	1	Presence
0	Absence outside M	?	Uncertain

Humidity niches of each terminal taxa of the NWJ clade



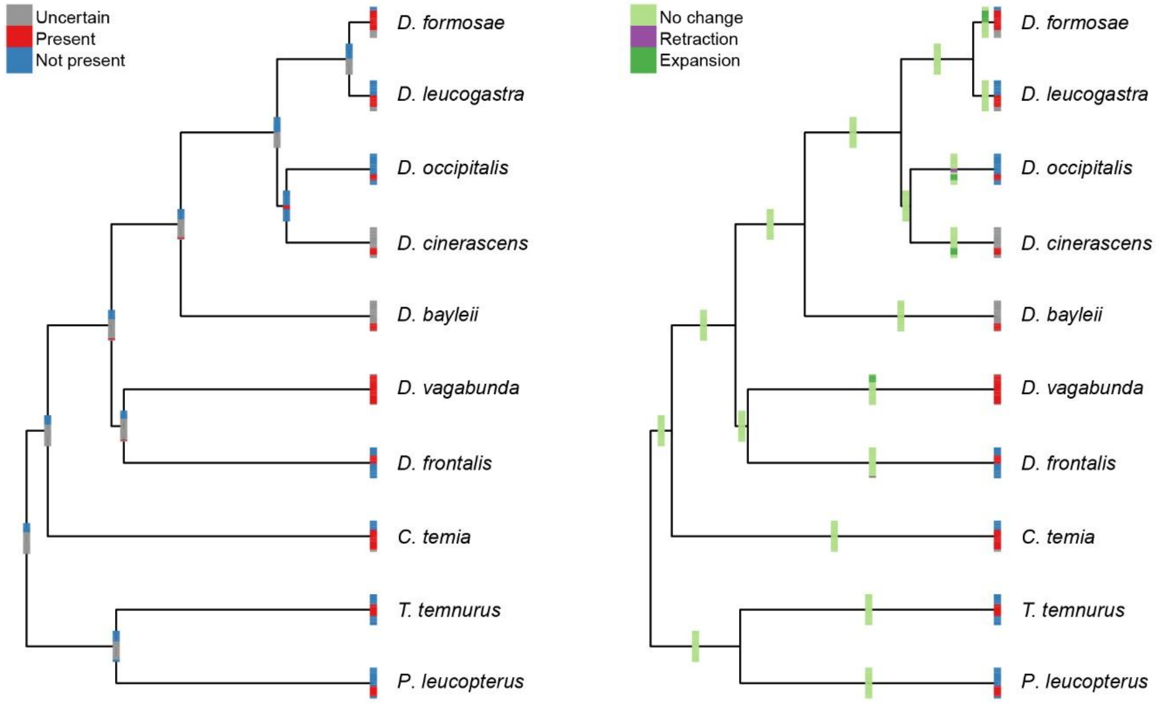
Taxon	Bins																		
	1 (195-300)	2 (301-406)	3 (407-512)	4 (513-618)	5 (619-724)	6 (725-830)	7 (831-936)	8 (937-1042)	9 (1043-1148)	10 (1149-1254)	11 (1255-1360)	12 (1361-1466)	13 (1467-1572)	14 (1573-1678)	15 (1679-1784)	16 (1785-1890)	17 (1891-1996)	18 (1997-2102)	19 (2103-2208)
Aphelocoma californica	?	?	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Aphelocoma coerulescens	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Aphelocoma sumichrasti remota	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	0	0	0	0
Aphelocoma sumichrasti sumichrasti	?	?	?	?	?	?	1	1	1	1	1	1	1	0	0	0	0	0	0
Aphelocoma ultramarina	?	?	?	?	?	?	1	1	1	1	1	1	1	0	0	0	0	0	0
Aphelocoma unicolor	?	?	?	?	?	?	1	1	1	1	1	1	1	1	0	0	0	0	0
Aphelocoma wollweberi arizonae	?	?	?	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Aphelocoma wollweberi couchii	?	?	?	?	?	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Aphelocoma wollweberi gracilis	?	?	?	?	?	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Aphelocoma wollweberi potosina	?	?	?	?	?	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Aphelocoma wollweberi wollweberi	?	?	?	?	?	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Aphelocoma woodhouseii cyanotis	?	?	?	?	?	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Aphelocoma woodhouseii grisea	?	?	?	?	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Calocitta colliei	?	?	?	?	?	1	1	1	1	1	1	1	1	1	?	?	?	?	?
Calocitta formosa	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	?	?	?
Cyanocitta cristata	?	?	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	?	?
Cyanocitta stelleri	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Cyanocorax affinis	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	?
Cyanocorax beecheii	0	0	0	0	0	1	1	1	1	1	1	1	1	1	?	?	?	?	?
Cyanocorax caeruleus	?	?	?	?	?	?	1	1	1	1	1	?	?	?	?	?	?	?	?
Cyanocorax cayanus	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1
Cyanocorax chrysops	?	?	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Cyanocorax cristatellus	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0
Cyanocorax cyanomelas	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Cyanocorax cyanopogon	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	0	0	0	0
Cyanocorax dickeyi	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Cyanocorax heilprini	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	?	?
Cyanocorax luxuosus	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	?	?	?
Cyanocorax melanocyaneus	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	?	?	?	?
Cyanocorax mystacalis	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
Cyanocorax sanblasianus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	?	?	?	?
Cyanocorax violaceus	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyanocorax yncas	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Cyanocorax yucantanicus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	?	?	?	?
Cyanolyca argentigula	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Cyanolyca armillata	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	0	0	0	0
Cyanolyca cucullata	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0
Cyanolyca miribilis	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Cyanolyca nana	?	?	?	?	?	?	?	1	1	1	1	1	0	0	0	0	0	0	0
Cyanolyca pulchra	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0
Cyanolyca pumilo	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Cyanolyca turcosa	?	?	?	?	?	?	1	1	1	1	1	1	1	0	0	0	0	0	0
Cyanolyca viridicyanus	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Gymnorhinus cyanocephalus	?	?	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psilorhinus morio	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	?	?	?

0 Absence within M
1 Presence
0 Absence outside M
? Uncertain

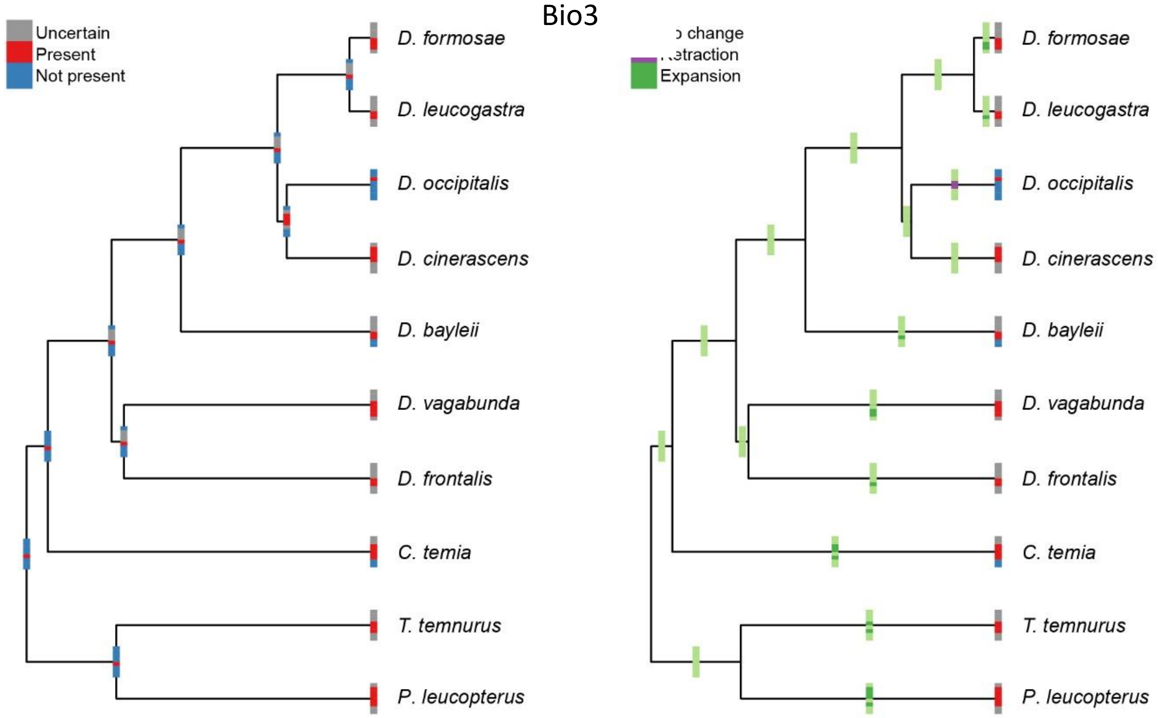
Appendix IV. Climatic niche reconstructions for rest of the bioclimatic variables under parsimony approach.

Treepies:

Bio2



Bio3



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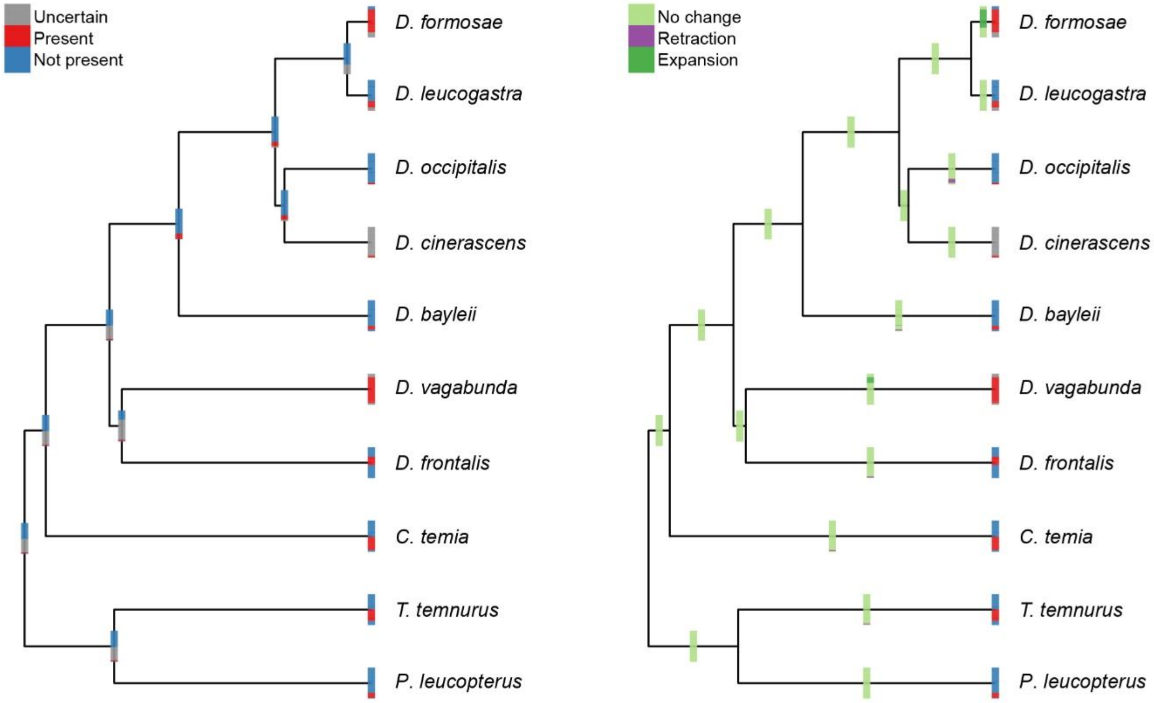
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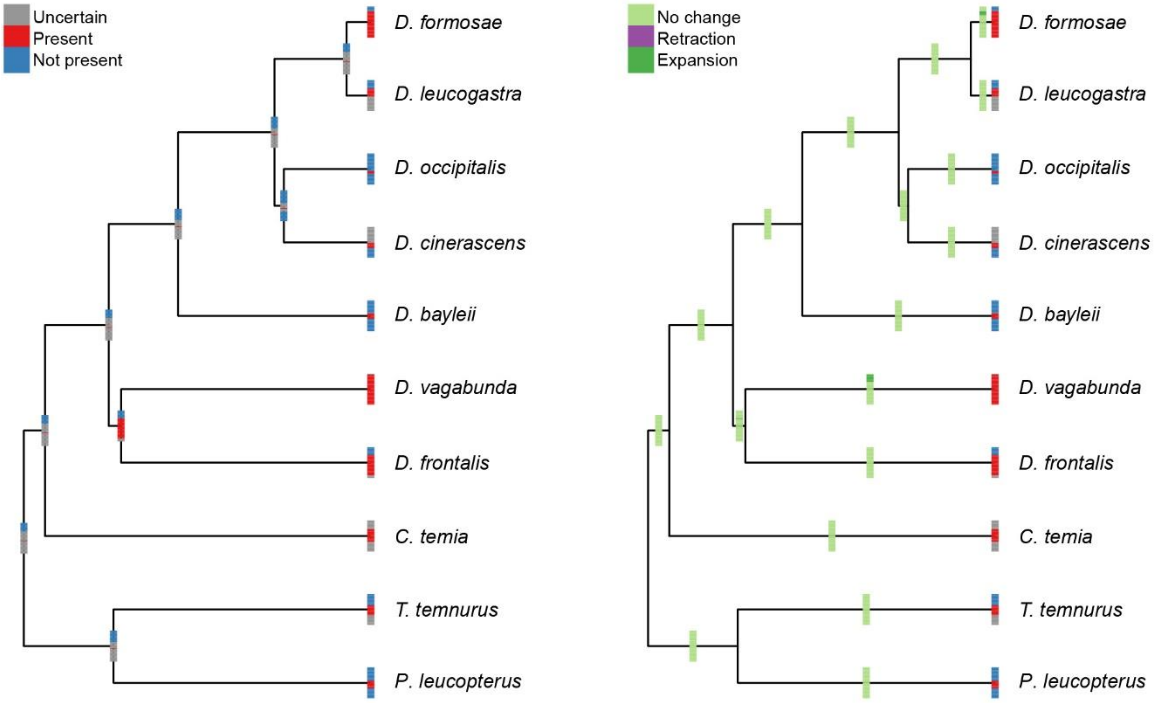
Present
Not present
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio5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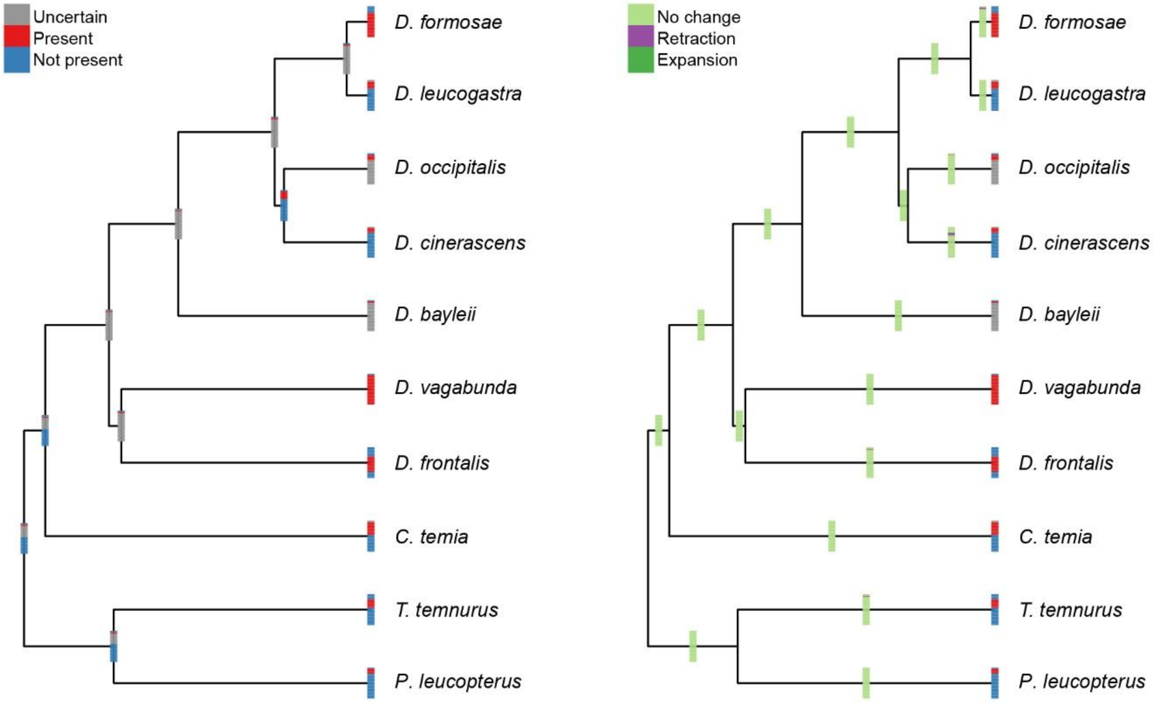
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio6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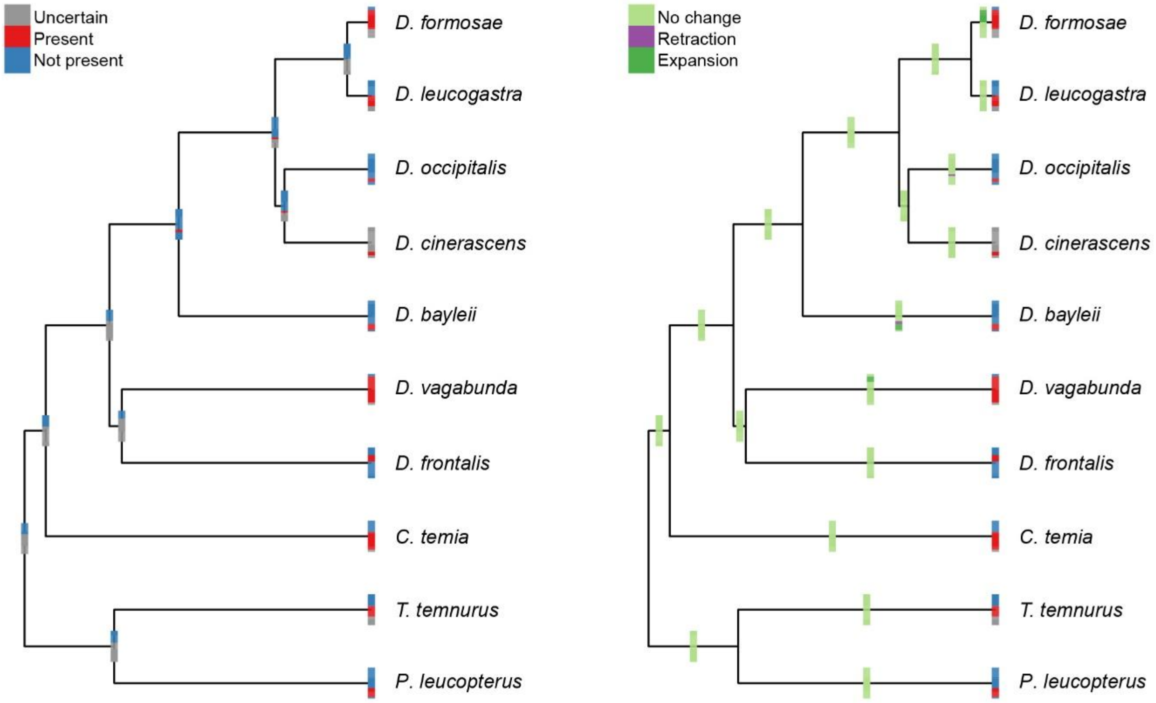
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio7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C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
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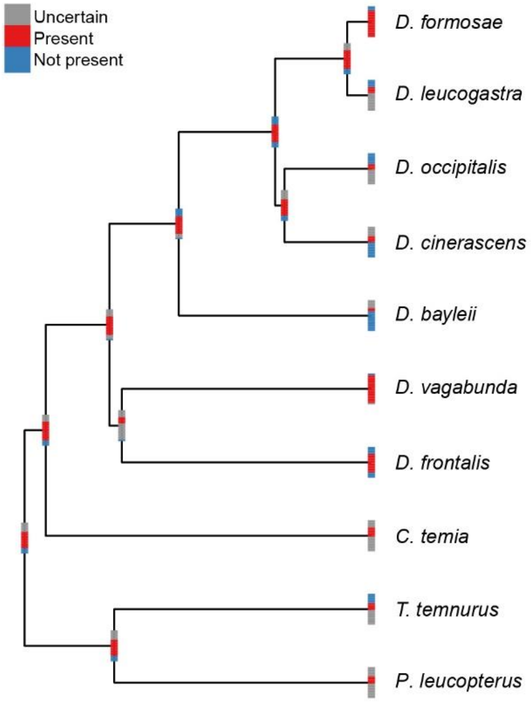
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio10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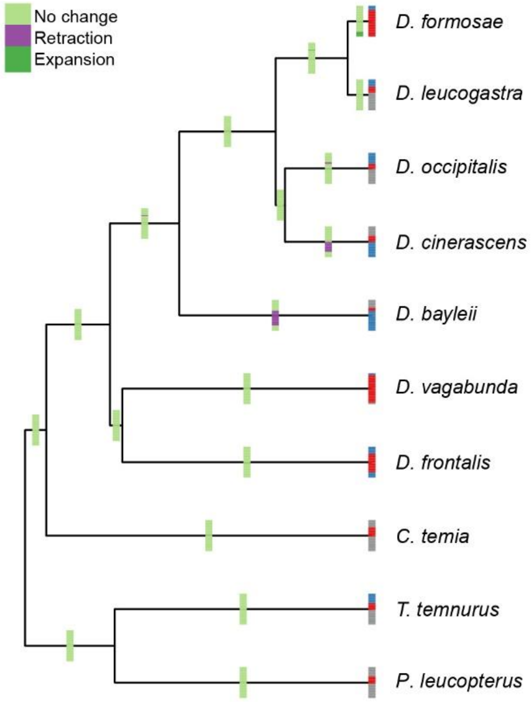
T. temnurus
P. leucopterus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Retraction
Expansion
D. formosae
D. leucogastra
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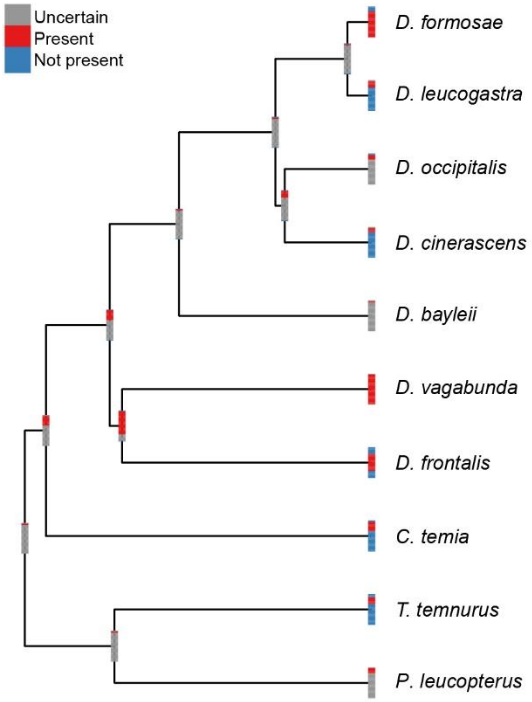
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio11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Not present
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D. leucogastra
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D. cinerascens
D. bayleii
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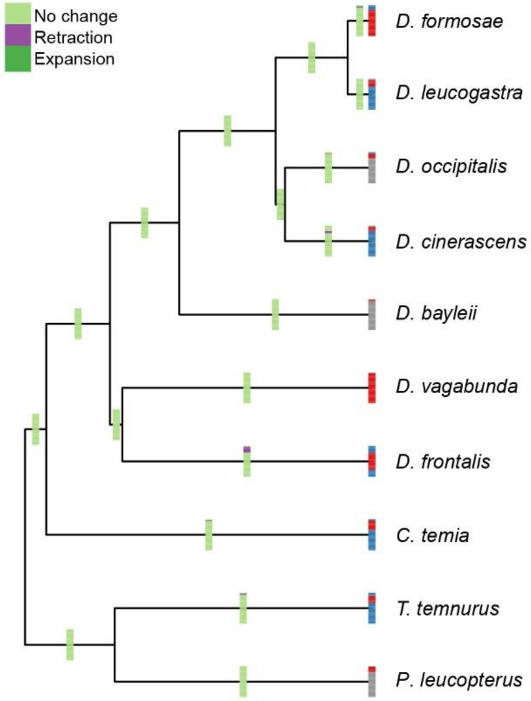
C. temia
T. temnurus
P. leucopterus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Retraction
Expansion
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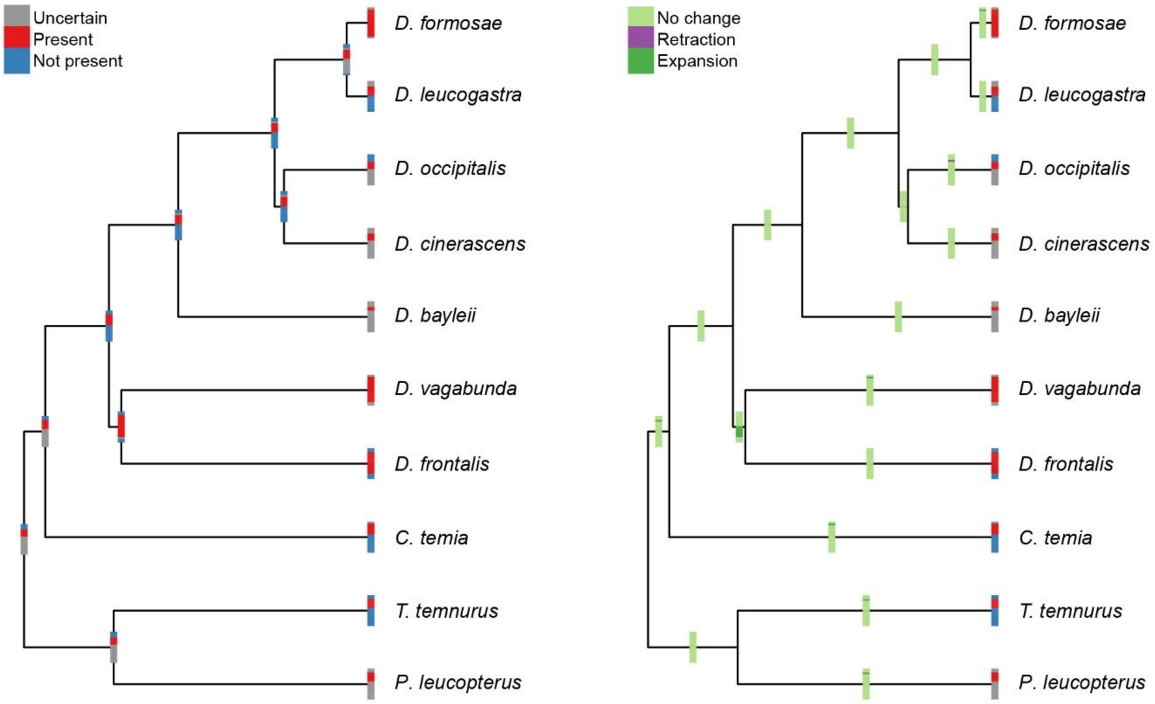
C. temia
T. temnurus
P. leucopterus

Bio13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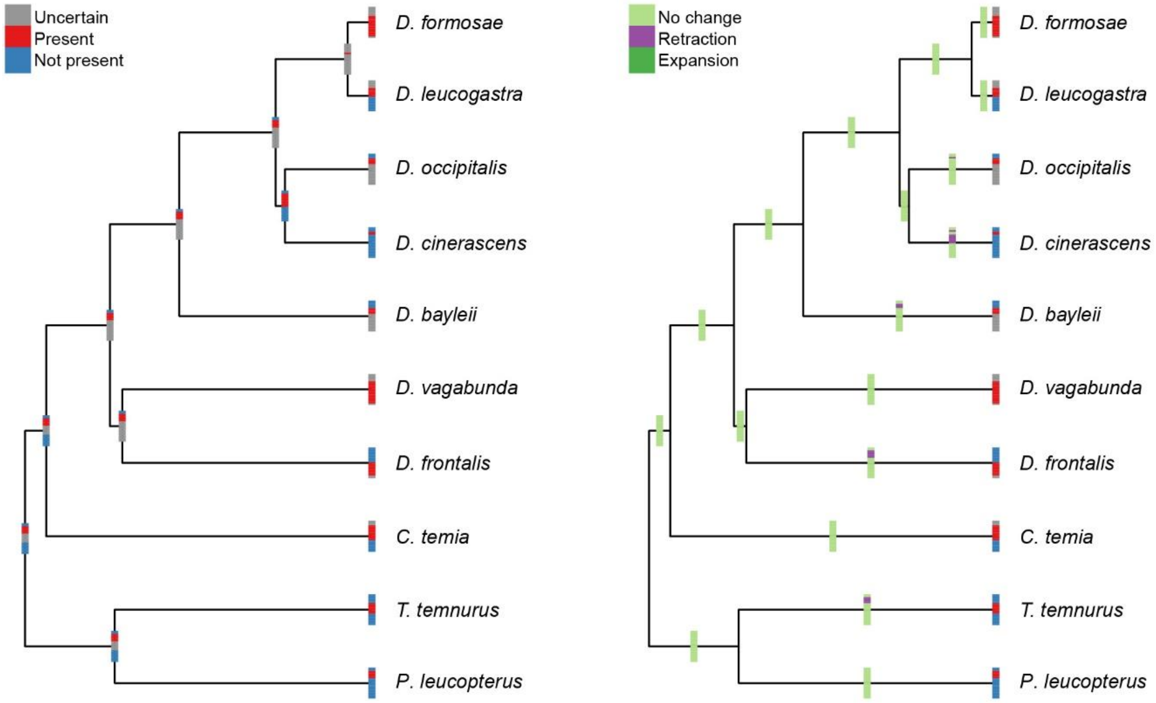
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio14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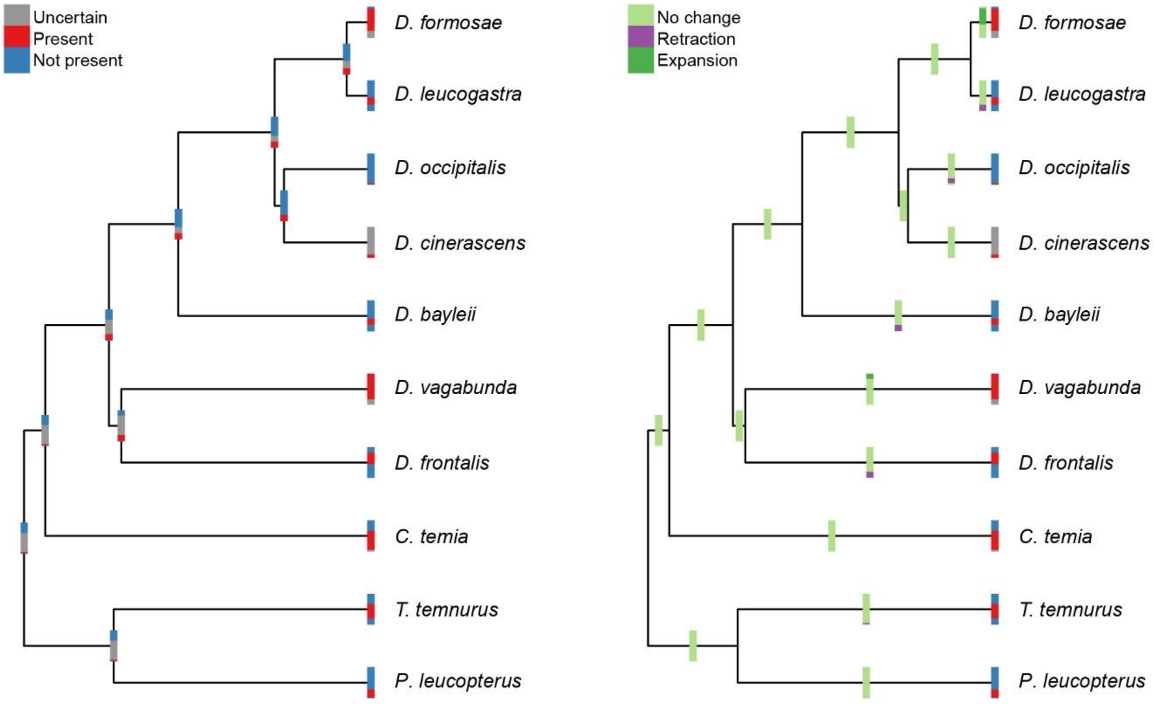
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio15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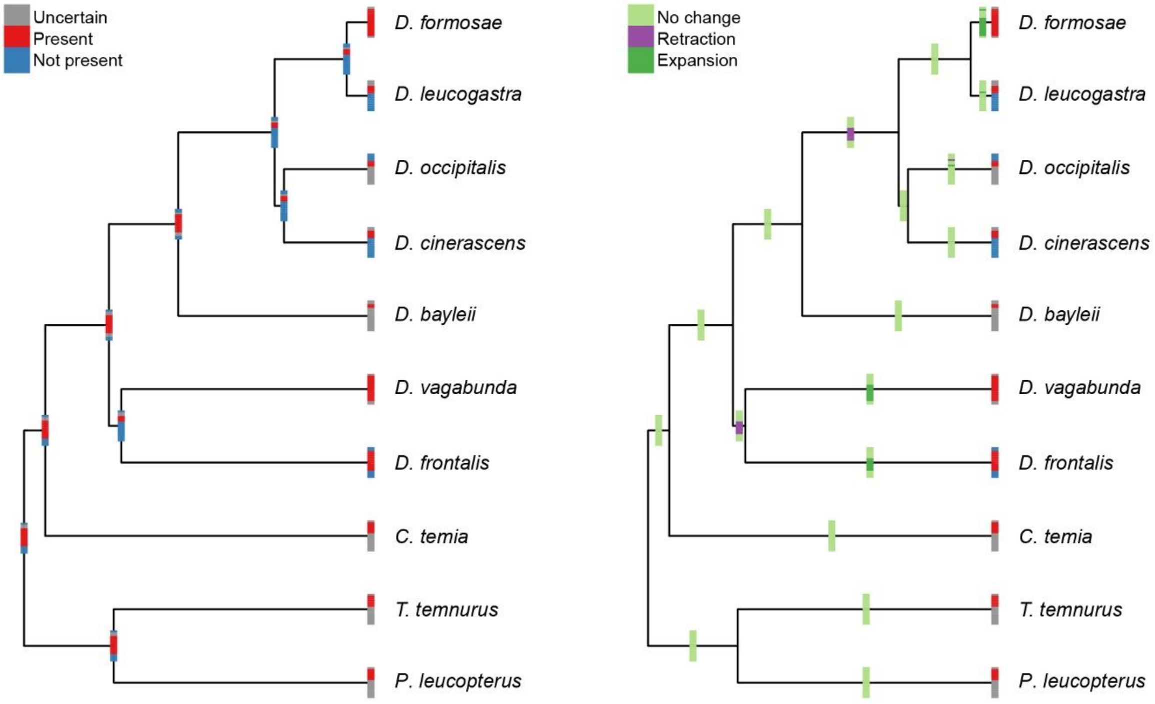
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio16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Present
Not present
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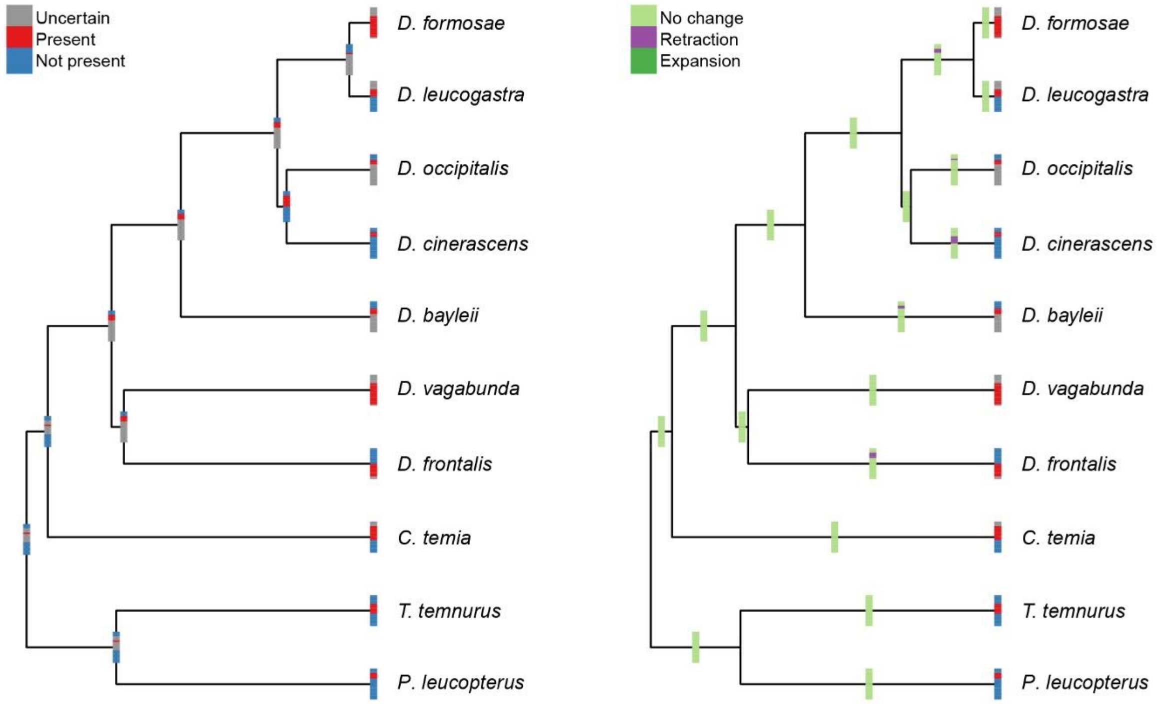
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Bio17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Not present
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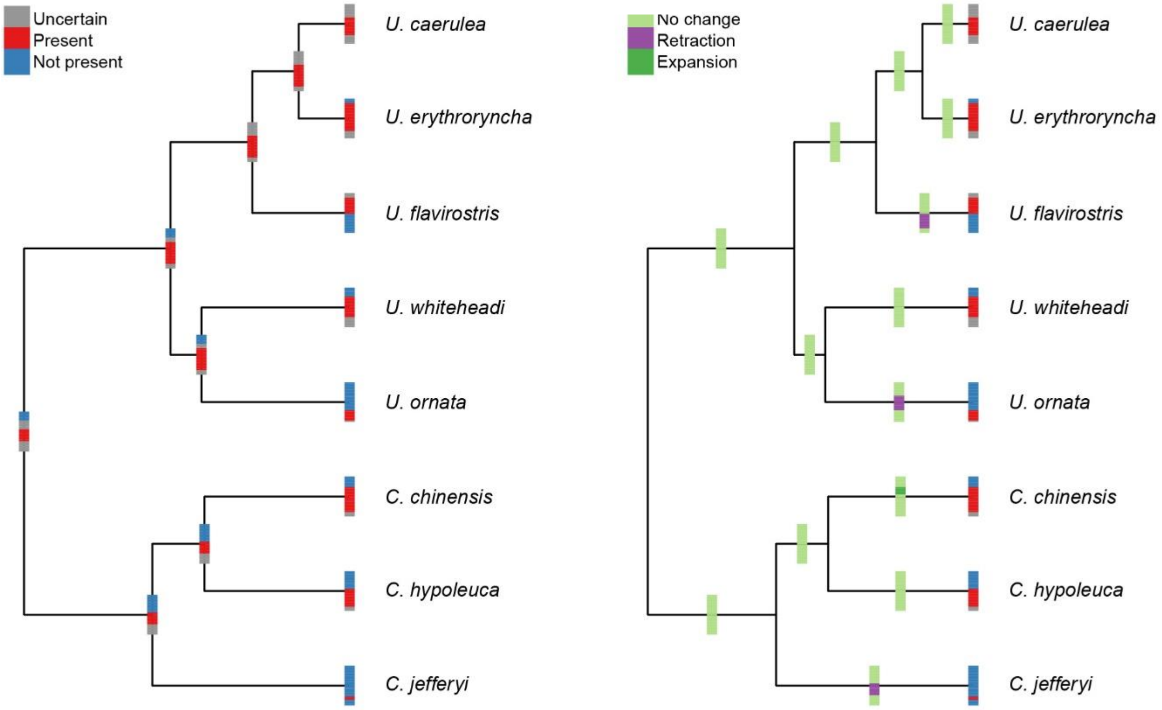
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus
No change
Retraction
Expansion
D. formosae
D. leucogastra
D. occipitalis
D. cinerascens
D. bayleii
D. vagabunda
D. frontalis
C. temia
T. temnurus
P. leucopterus

Magpies:

Bio2



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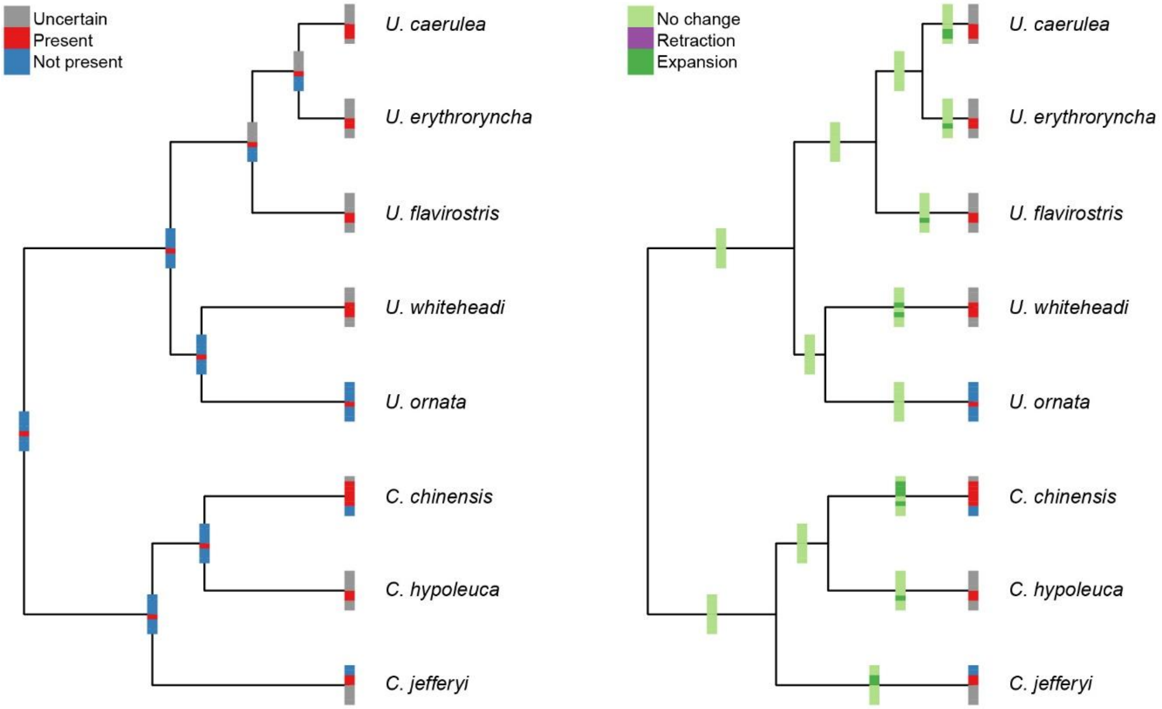
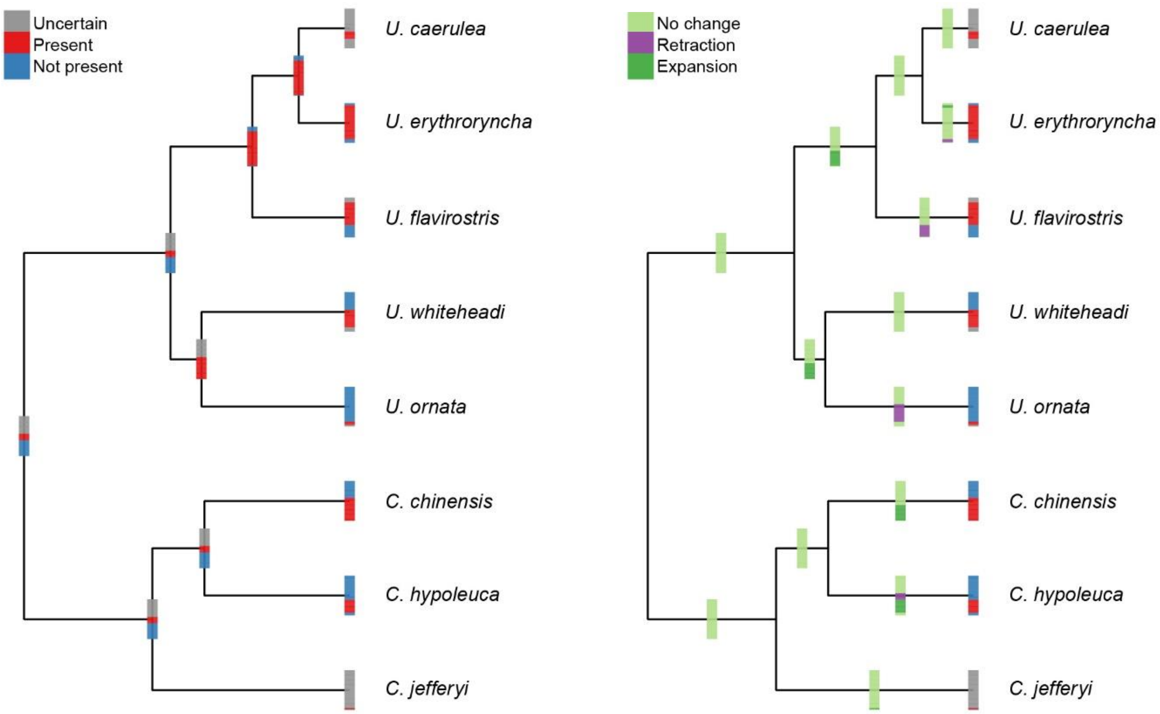


Bio4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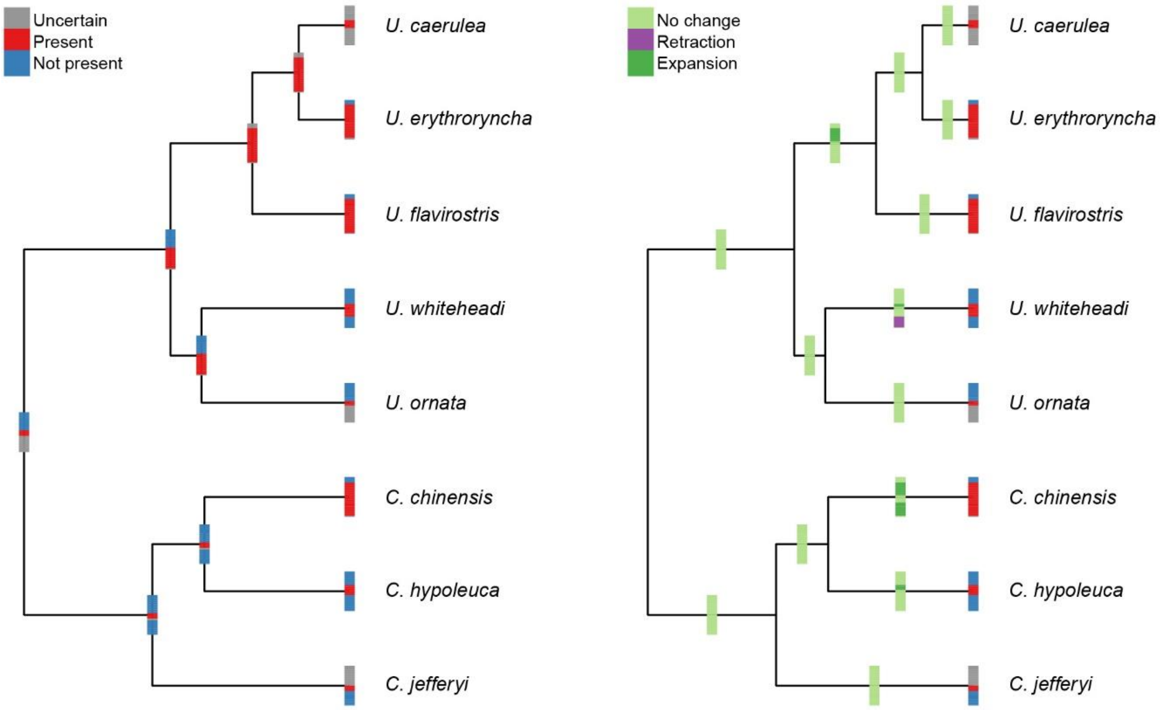
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi
No change
Retraction
Expansion
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio5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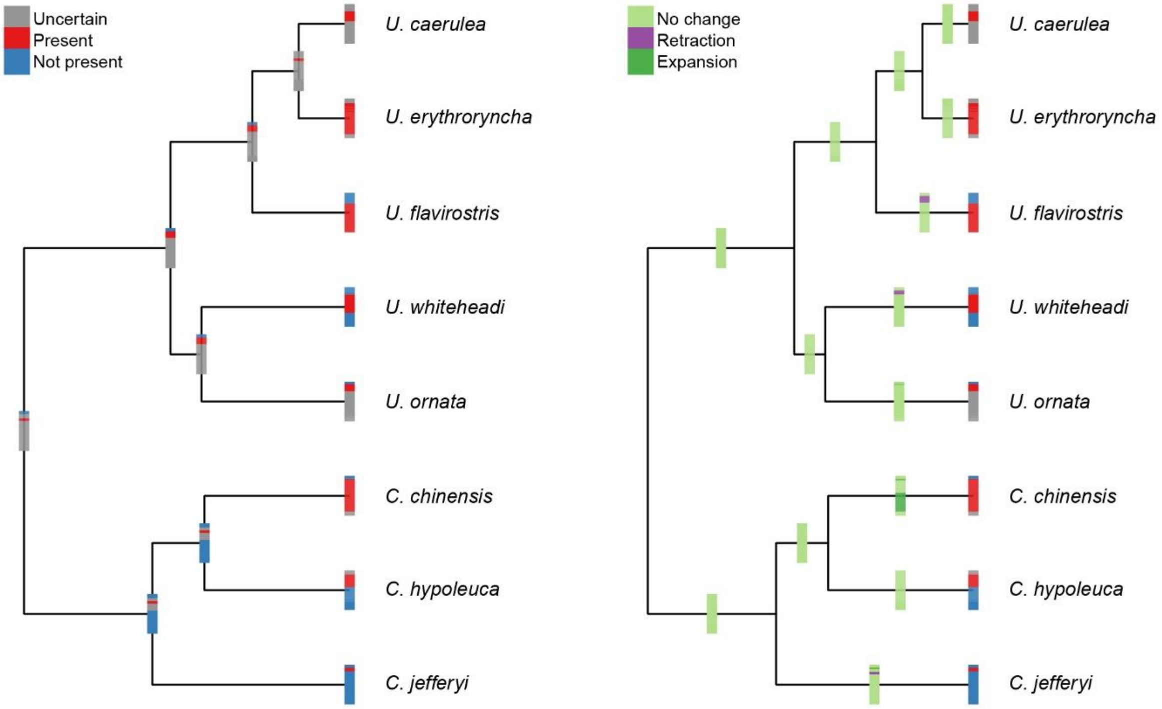
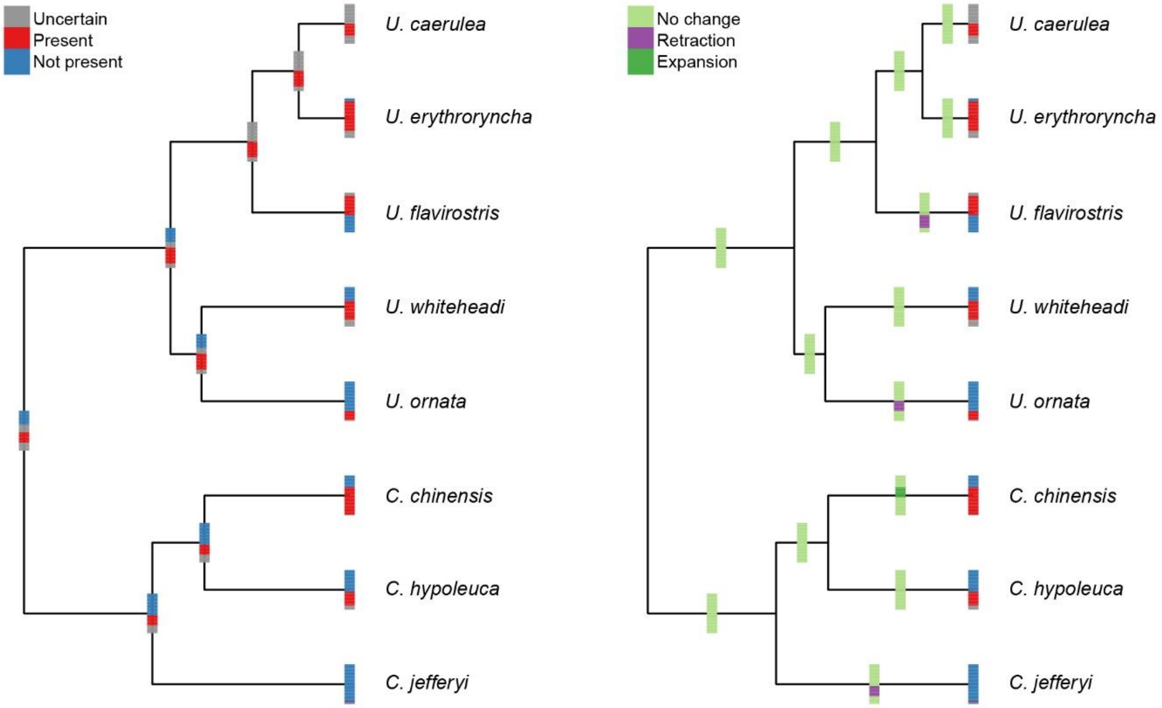
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi
No change
Retraction
Expansion
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

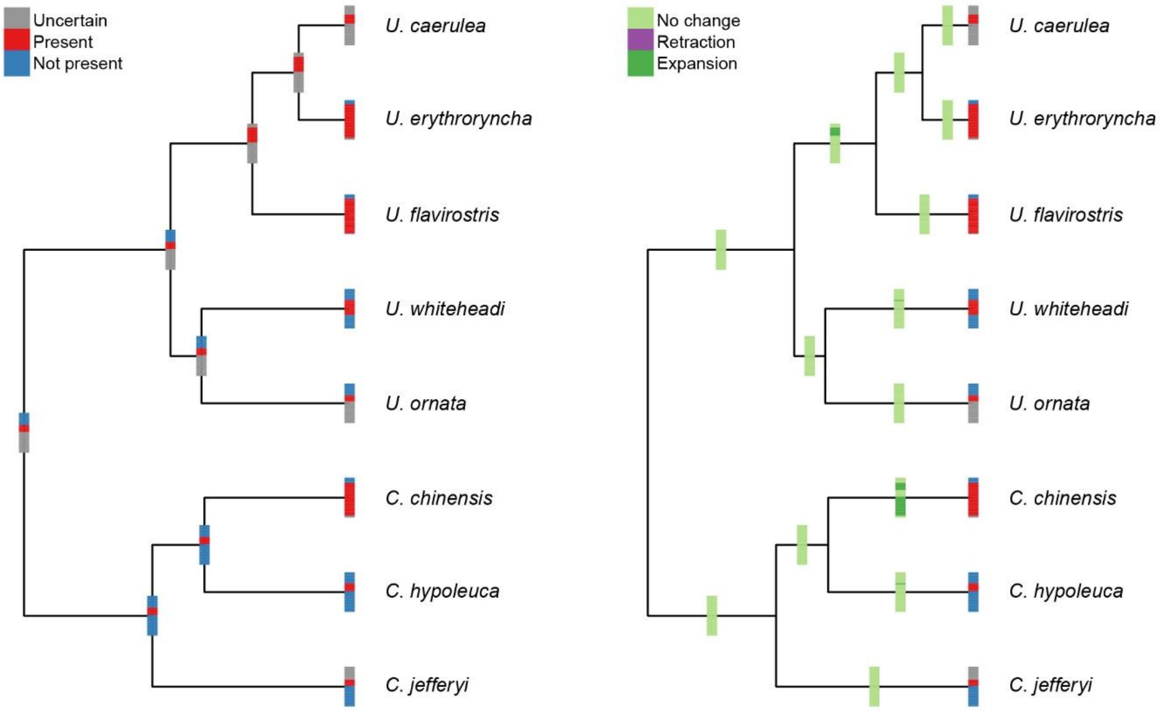
Bio6


Uncertain
Present
Not present
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi
No change
Retraction
Expansion
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio7


Uncertain
Present
Not present
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi
No change
Retraction
Expansion
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio10


Uncertain
Present
Not present
No change
Retraction
Expansion
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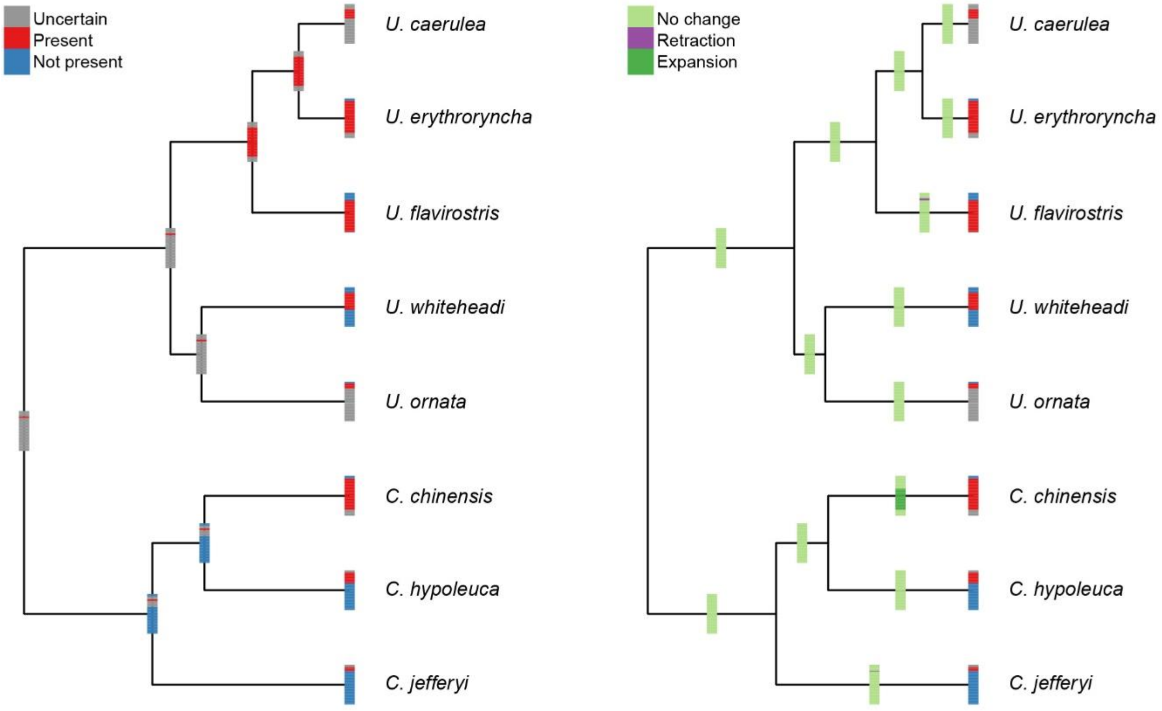
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio11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No change
Retraction
Expansion
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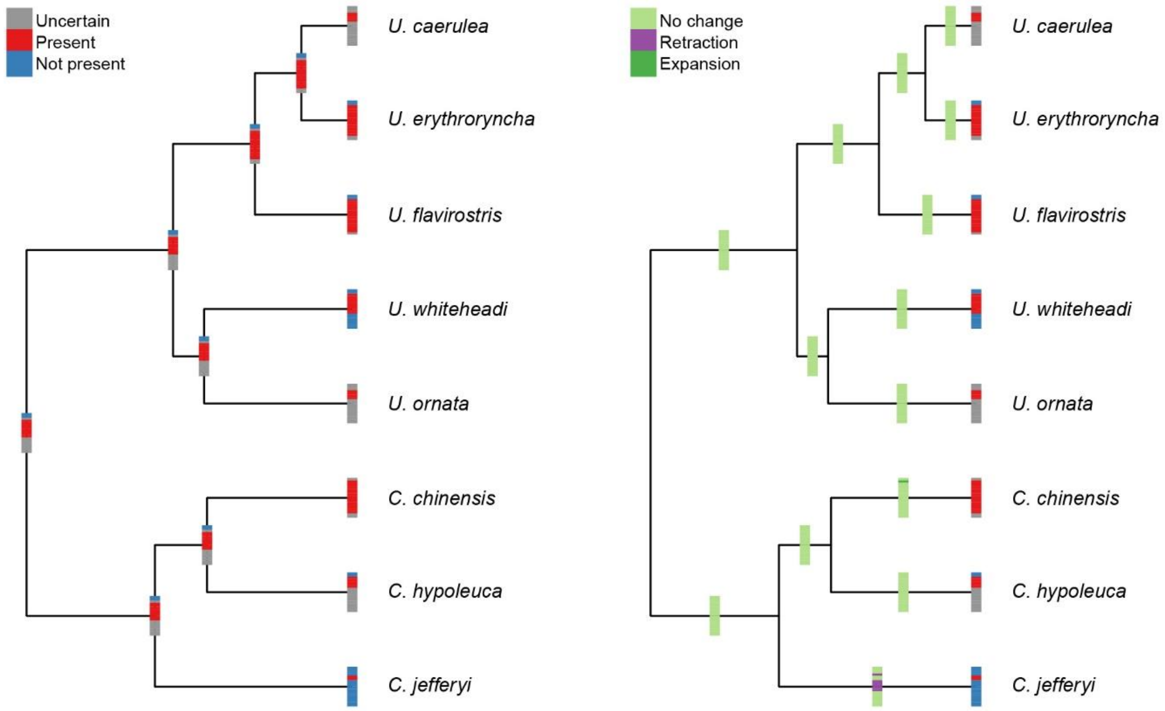
C. chinensis
C. hypoleuca
C. jefferyi
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi


Bio13
Uncertain
Present
Not present
No change
Retraction
Expansion
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U. whiteheadi
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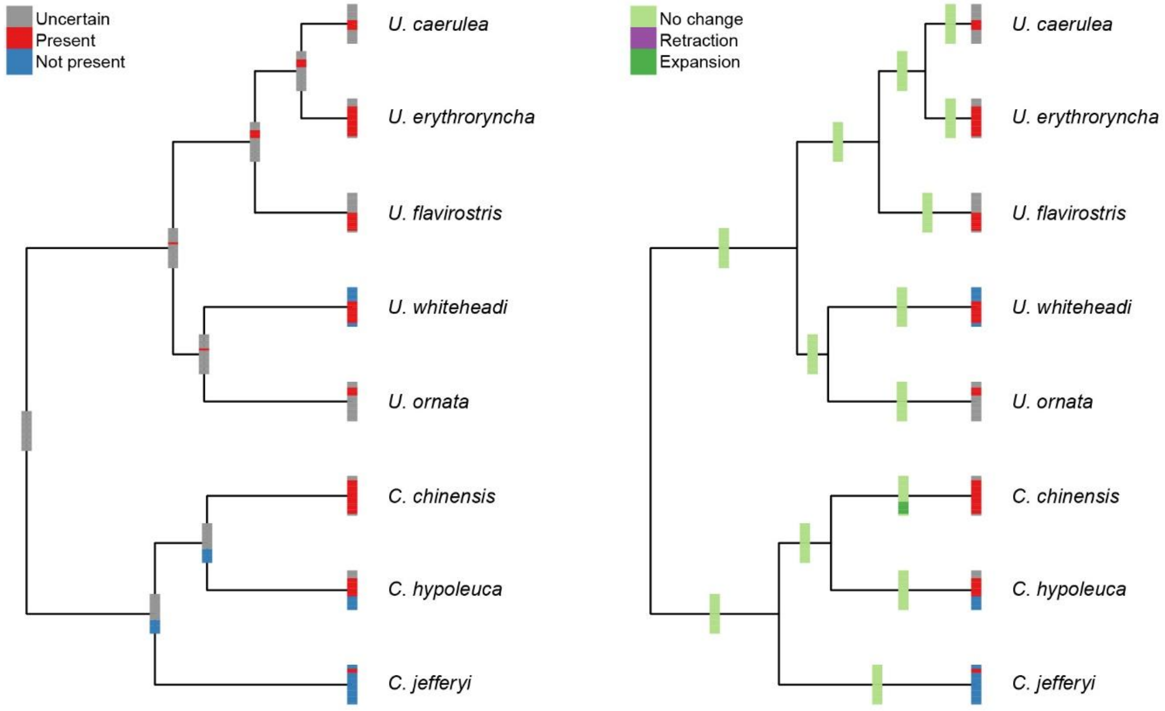
C. hypoleuca
C. jefferyi


Bio14
Uncertain
Present
Not present
No change
Retraction
Expansion
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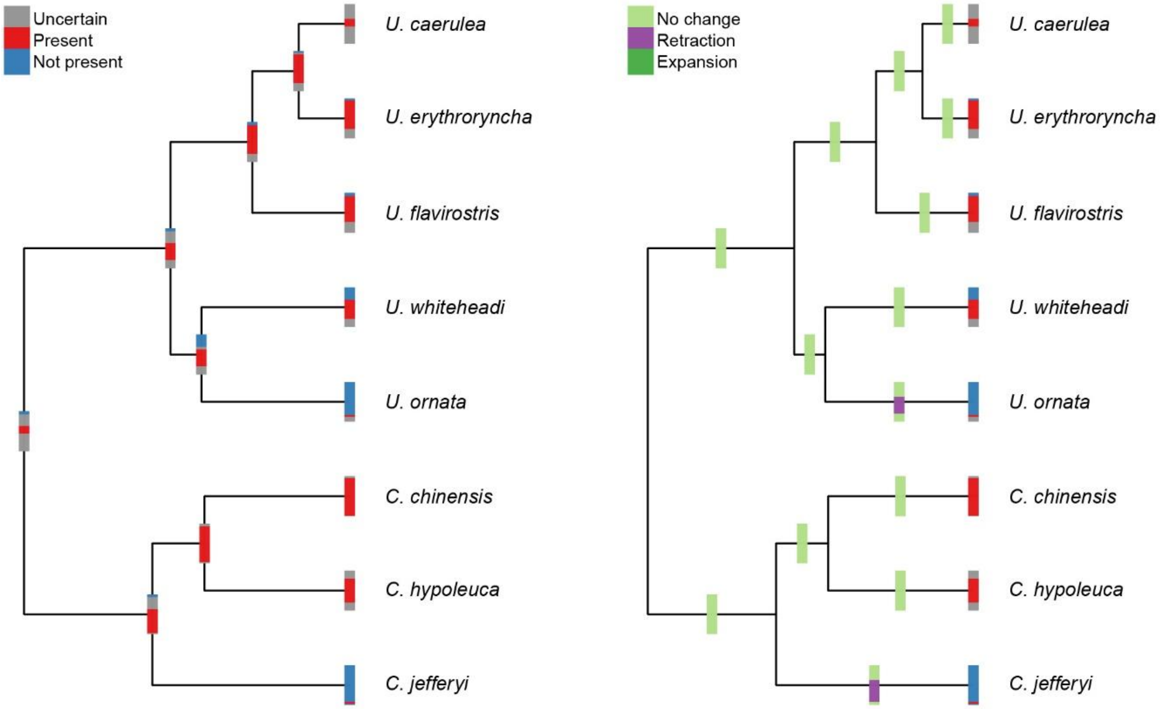
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio15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Present
Not present
No change
Retraction
Expansion
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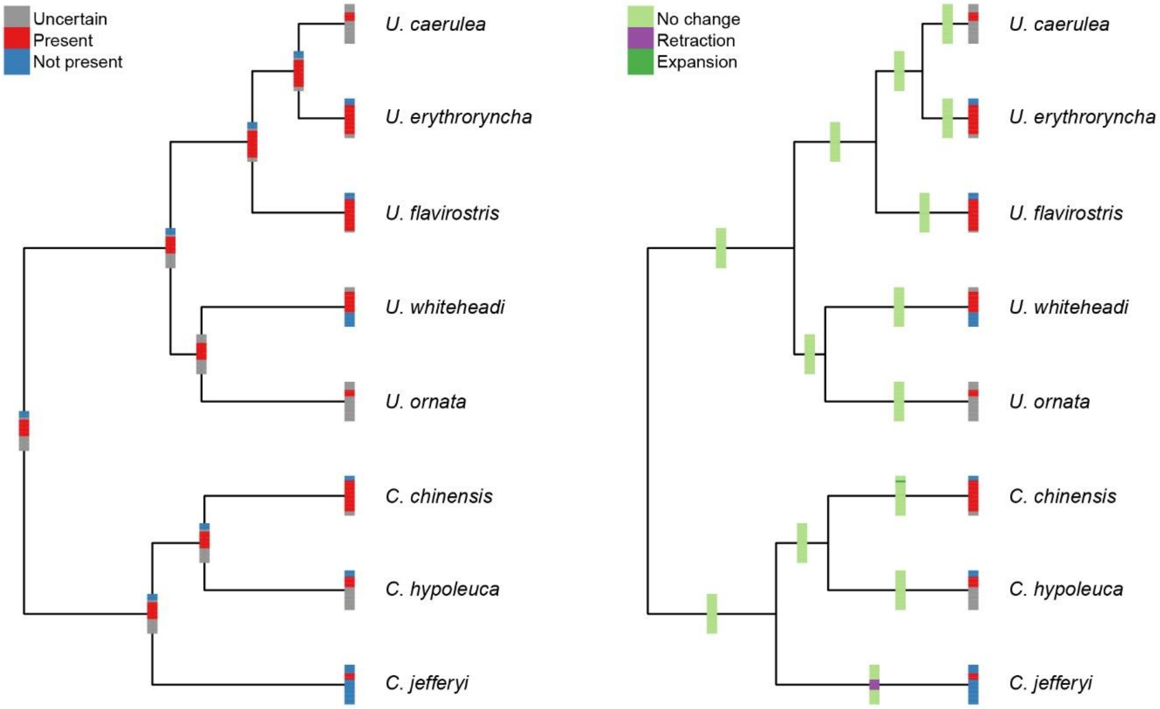
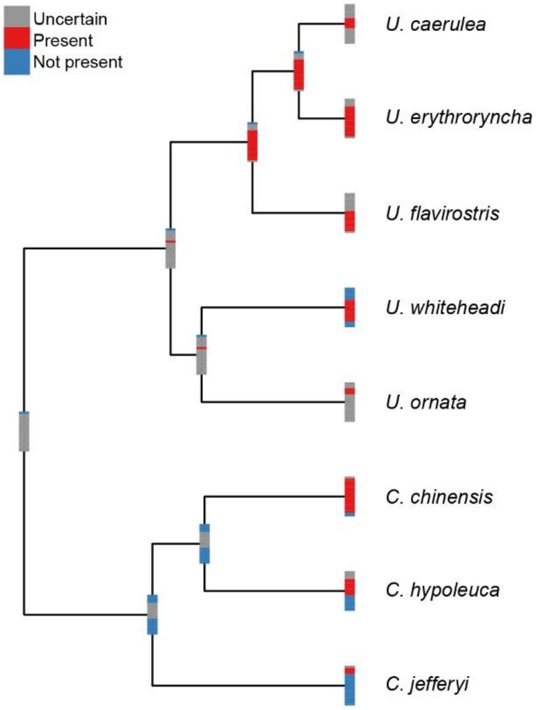
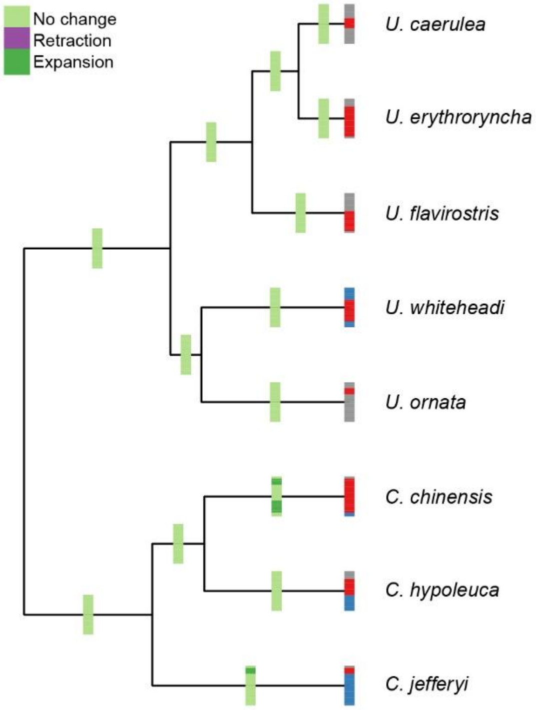
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio16

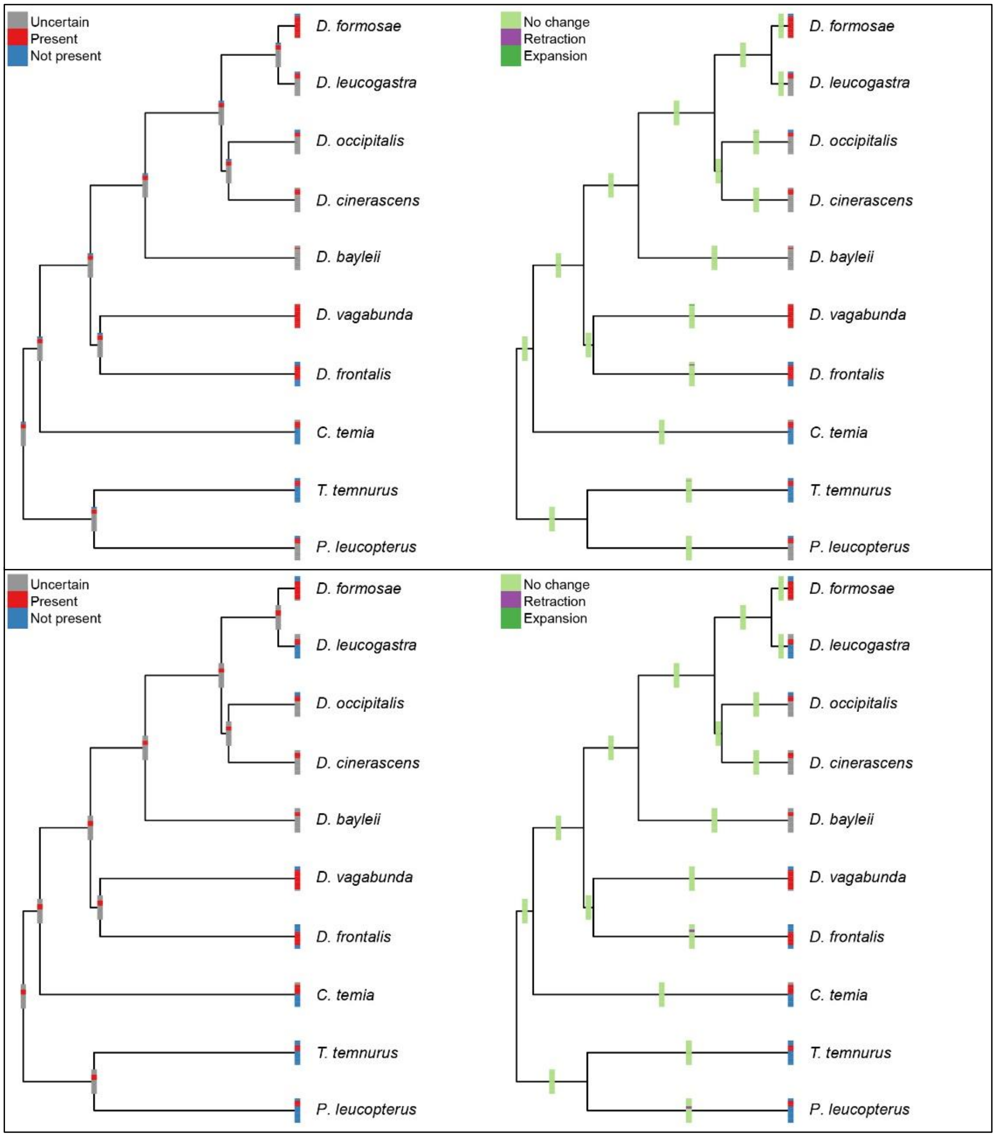

Uncertain
Present
Not present
No change
Retraction
Expansion
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Bio17

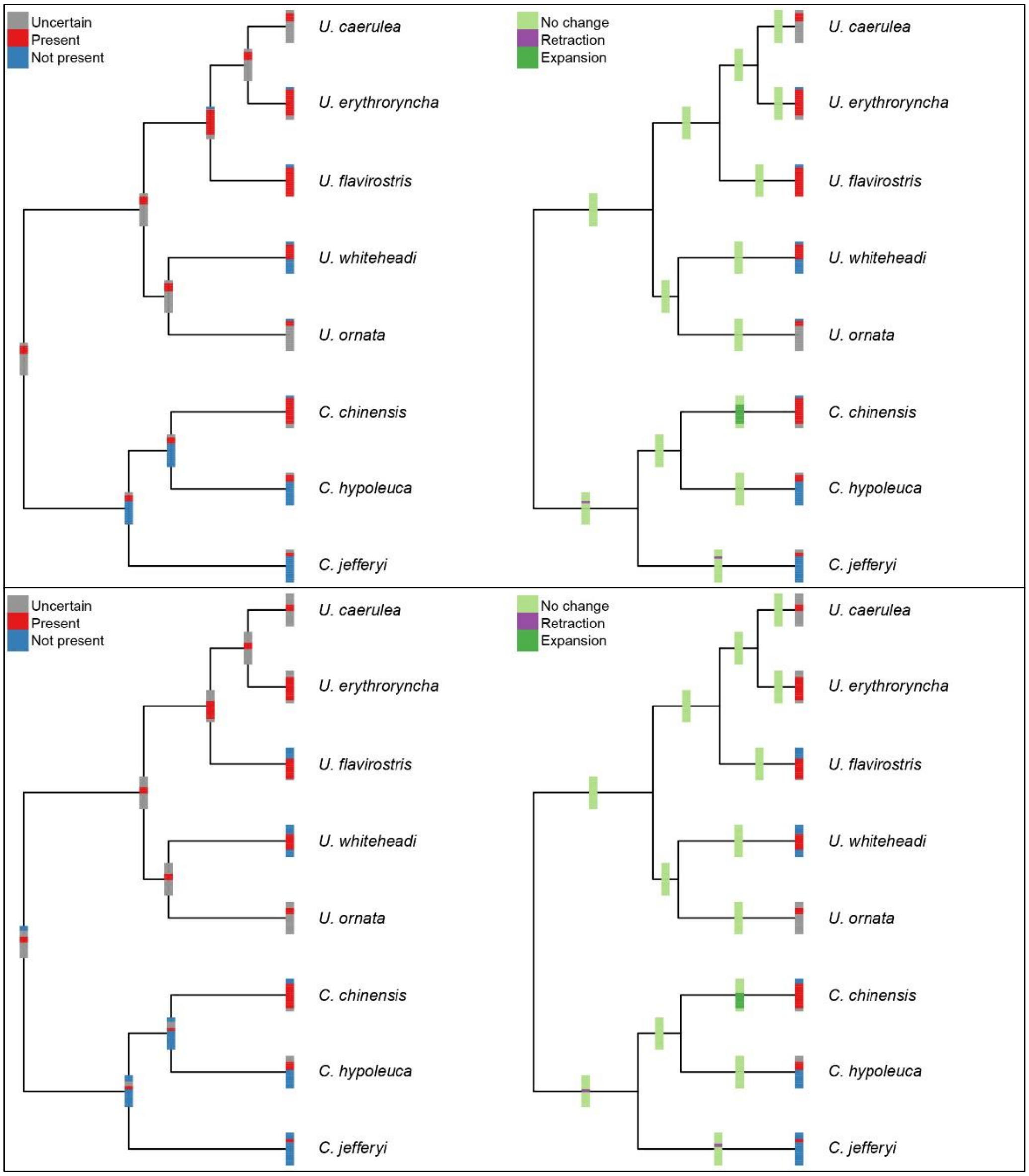

Uncertain
Present
Not present
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi


No change
Retraction
Expansion
U. caerulea
U. erythroryncha
U. flavirostris
U. whiteheadi
U. ornata
C. chinensis
C. hypoleuca
C. jefferyi

Appendix V. Climatic niche reconstructions in treepies and blue/green magpies under maximum likelihood approach.



Climatic niche reconstruction in treepies; *top*: temperature niche, *bottom*: humidity niche. Bars at the nodes represent the reconstructed niches in each ancestor and bars at the branches represent the niche change (expansion or retraction) from ancestor to descendent. Each species' current niche is represented by the bars at the tips.



Climatic niche reconstruction in magpies; *top*: temperature niche, *bottom*: humidity niche. Bars at the nodes represent the reconstructed niches in each ancestor and bars at the branches represent the niche change (expansion or retraction) from ancestor to descendent. Each species' current niche is represented by the bars at the tips.