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Contrasting phylogeographic signatures in two Australo-Papuan bowerbird species complexes (Aves: Ailuroedus)

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The Australo-Papuan catbird genus *Ailuroedus* has a complex distribution and a contested taxonomy. Here, we integrate phylogenetic analysis of DNA data and morphology to study the group's biogeography and to re-examine its taxonomy. We couple phylogeographic and abiotic data to examine differences between the major groups defined in our phylogenetic analysis. Our results are consistent with *Ailuroedus* catbirds being divided into two species complexes, one distributed in humid forests in the lowlands on New Guinea and another in comparably drier and colder forests mainly in mid-mountains on New Guinea and Australia. Vicariant events during the Pliocene are surmised to have been the major force in shaping the contemporary phylogeographical signature of this genus. Several previously suggested vicariant events, such as fragmentation of xeric forests in Australia and the uplift of the central mountain range on New Guinea, are reinforced as important Pliocene barriers for tropical forest taxa in this region. Interaction between Pleistocene climatic fluctuations and differences in habitat requirements may explain a higher and more recent population structures in the mid-mountain catbird complex and the lack of representatives from the lowland clade in the comparably drier Australia. Phylogeographical patterns in both catbird complexes, respectively, both comply and deviate from other lowland and mid-mountain taxa in the region. This highlights that taxon-specific properties, such as their historical spatial and ecological distributions, capacity to disperse and tolerance to habitat changes, affect the phylogeographical histories of organisms. Within both species complexes, the genetic differentiation between several geographically isolated populations was found to exceed those commonly observed for avian sister species. As these genetically distinct taxa also were found to be morphological diagnosable, we suggest a revised classification of the genus *Ailuroedus*, where we recognize three species within the lowland complex and seven species within the mid-mountain complex.

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Introduction

New Guinea is the largest and highest tropical island on earth (Allison 2007), as well as being a 'high biodiversity' wilderness area (Mittermeier *et al.* 2003). A complex topology with several mountain ranges and habitats ranging from lowland savannahs and rainforests, to alpine

grasslands and glaciated mountains has resulted in high levels of endemism in the flora and fauna (e.g. Pratt & Beehler 2014). In general, restricted range species and subspecies are replaced by sister taxa in adjacent regions, but several genera of birds also exhibit strong patterns of altitudinal replacement (Diamond 1972; Norman *et al.* 2007; Irestedt *et al.* 2009; Driskell *et al.* 2011). The New Guinean bird fauna has its strongest biogeographical connection with Australia, but there is also a distinct Asian component (Pratt & Beehler 2014).

Most disjunct allopatric distributions in New Guinea are best explained by past vicariant events where microplates of different origin and the rise of various mountain regions are reflected in deep splits between related taxa (Hall 2002; Heads 2001a,b; Heads 2013). Conversely, more shallow splits between related taxa are thought to be the result of expansions and contractions of suitable habitats in the Pleistocene due to fluctuations in sea levels and temperature (e.g. Murphy & Legge 2007; Williams *et al.* 2008; Kearns *et al.* 2011). In addition, molecular phylogeographical studies have corroborated the existence of several late Pliocene and early Pleistocene dispersal barriers for birds (McGuigan *et al.* 2000; Dumbacher *et al.* 2003; Zwiers *et al.* 2008; Deiner *et al.* 2011). Arguably, the most important such barrier is the 1300-km-long central mountain range (which has many peaks being over 3000 m in elevation) that separates the northern lowlands from the southern ones. The impact of this barrier has been demonstrated by the genetic divergence observed between northern and southern forms in several lowlands and mid-mountain taxa (McGuigan *et al.* 2000; Dumbacher & Fleischer 2001; Rawlings & Donnellan 2003; Zwiers *et al.* 2008). Most of these divergences are estimated to have occurred during the Pliocene which complies well with the current knowledge of the formation of the central mountain range (Hall 2002; Cloos *et al.* 2005). In some taxa (Irestedt *et al.* 2013), divergences between northern and southern populations are estimated to be considerably younger, which reflects the importance of this barrier for organisms that have colonized the island more recently.

In this study, we use catbirds (genus *Ailuroedus*) within the bowerbird family Ptilonorhynchidae, to study phylogeographical patterns within New Guinea and between Australia and New Guinea. Catbirds were chosen as a model group as: (i) the genus is part of the basal oscine radiation centred in the Australo-Papuan plate (Barker *et al.* 2002, 2004; Ericson *et al.* 2002, 2003); and (ii) the two species complexes that occur in New Guinea are often found at slightly different altitudes, and may thus have responded differently to past earth history events. The White-eared Catbird (*Ailuroedus buccoides*) is currently divided into four subspecies (Frith & Frith 2004; Dickinson & Christidis 2014) that are distributed throughout the lowlands (up to 800 m and locally to 1200 m) on New Guinea and some adjacent islands (Dickinson & Christidis 2014). The Black-eared Catbird (*Ailuroedus melanotis*) is generally a mid-mountain species (altitudes between 600 and 1800 m and exceptionally to 2250 m), and has a more scattered distribution with eight subspecies in New Guinea and two in Australia (Frith & Frith 2004) (cf. Dickinson & Christidis 2014). The third species in this genus, the Green Catbird (*Ailuroedus crassirostris*), is endemic to eastern Australia and is sometimes considered conspecific with *Ailuroedus melanotis* (Christidis & Boles 2008; Dickinson & Christidis 2014; cf. Frith & Frith 2004; Schodde & Mason 1999).

By examining the variation in mitochondrial and nuclear DNA within a spatio-temporal framework, we test the generality of previously proposed biogeographical hypotheses for lowland and mid-mountain taxa in New Guinea. We use locality information from museum collections to obtain altitude, temperature and precipitation data, in order to test if there are significant differences in habitat requirements between these two clades. By integrating our molecular data with morphological data, we also re-evaluate species delimitations in the catbirds.

Material and methods

Sampling and molecular procedures

For the molecular analyses, we aimed at dense geographical coverage and sampled six individuals of *Ailuroedus crassirostris*, 41 individuals from the mid-mountain *Ailuroedus melanotis* complex, and 34 individuals from the lowland *Ailuroedus buccoides* complex (Appendix S1), including all described subspecies. *Ptilonorhynchus violaceus* (satin bowerbird) was used as outgroup to root the trees. Total DNA was obtained from toe pads or fresh tissue. Standard laboratory procedures were used for the DNA samples from fresh tissue.

The use of museum study skin samples in phylogenetics and population genetics has increased dramatically, in recent years. Most of these studies have provided solid results, but a few of these studies (e.g. Jønsson *et al.* 2011b) have been shown to be based partly on erroneous sequence data (chimeric or pseudogenes). The source of these erroneous sequences are in most cases of two types; (i) the sequences are partly PCR contaminations, which may happen when the pre-PCR work has not been conducted in PCR-free environments (i.e. laboratories without proper separation of post- and pre-PCR sections), and (ii) the target fragment sizes during amplification have been too large (fragment sizes where no or very few copies exists in degraded museum sample). Measurements of concentration and fragment length with Bioanalyser 2100 (Agilent

Technologies) show that the DNA quality in study skin samples varies greatly among museum samples. However, these measurements demonstrate that the average fragment length in the DNA from study skins almost always exceeds 125 bp and has a reasonable concentration of fragments that are longer than 200 bp (even for samples that are more than 100 years old). Extensive work with study skins samples at Swedish museum of Natural history corroborates these measurements and support that a vast majority of museum study skin samples produce authentic sequences when target regions are shorter than approximately 225 bp for mitochondrial DNA and 200 bp for nuclear DNA. A careful inspection of Electropherograms and substitutions patterns is although always necessary as poor primer design may lead to a better fit to background DNA or other regions in the genomes.

In this study, we follow the recommendation above and the procedures described in Irestedt *et al.* (2006) and Ohlson *et al.* (2012), with the exception that we have amplified shorter pieces of DNA. We have sequenced three loci, the mitochondrial cytochrome b gene and the nuclear ornithine decarboxylase (ODC) intron 6 and 7, and nuclear myoglobin (myo) intron 2.

Sequence edition, phase, recombination test and variation

Sequences were aligned using CLUSTAL W (Thompson *et al.* 1994) in MEGA5 (Tamura *et al.* 2011). All the alignments were inspected and corrected visually. For nuclear introns, we codified double peaks present in both strands in the electropherograms of the same individual as ambiguous sites according to the IUPAC code. The gametic phase of heterozygote individuals was resolved using the algorithm PHASE (Stephens *et al.* 2001) with the default settings in DNASP 5 (Librado & Rozas 2009) and 0.8 as the minimum probability. Individuals with lower probabilities were removed from further analyses. We used the PHI test in SPLITSTREE4 (Bruen *et al.* 2006; Huson & Bryant 2006) to check for recombination in nuclear introns. This test was used due to its power to distinguish recombination events from homoplasies (Bruen *et al.* 2006). We implemented summary statistics for each mitochondrial phylogroup to quantify the level of variation and demography: the nucleotide diversity per site (π), the haplotype diversity (hd) and number of haplotypes (h) were calculated in DNASP 5.

Phylogeographic structure

We employed Bayesian inference to estimate the phylogenetic relationships among *Ailuroedus* lineages based on the mitochondrial gene using MRBAYES 3.1.2 (Huelsenbeck & Ronquist 2001) at the Cipres Science Gateway (Miller *et al.* 2010). The best fit substitution model was GTR+*I* which was selected using MRMODELTEST 2.2 (Nylander, 2004) based on the Akaike information criterion (AIC), in conjunction with PAUP* (Swofford, 1998). Two independent Bayesian runs of 10 million generations with four chains of Markov chain Monte Carlo (MCMC) each were performed. The first million generations were discarded as burn-in, after which trees were sampled every 500 generations. Chain convergence (Effective Sample Size – ESS values > 200) was checked using the likelihood plots for each run using TRACER 1.6 (http://beast.bio.ed.ac.uk/Tracer). The Potential Scale Reduction Factor was also used to check chain convergence and burn-in; values close to one indicate good convergence between runs (Gelman & Rubin 1992).

We also generated median-joining networks (Bandelt *et al.* 1999) using NETWORK 4.6.1.2 (www.fluxus-engineering.com) for each locus for both lowland and mid-mountain clades in order to study the relationships between haplotypes and their geographic distribution. In addition, to check the level of population genetic structure for each locus among the mitochondrial phylogroups (Fig. 1), for both lowland and mid-mountain clades, we performed a three hierarchical level analysis of molecular variance (AMOVA; Excoffier *et al.* 1992) using ARLEQUIN 3.5.1.2 (Excoffier & Lischer 2010). Significance of AMOVA was obtained by 1000 permutations. To verify whether genetic (uncorrected mitochondrial p-distances) and geographic distance between localities are correlated for each clade, as well as to identify evidence of isolation by distance, we implemented the Mantel test in IBDWS 3.23 (Jensen *et al.* 2005). Significance of the Mantel test was inferred by 10 000 permutations. We obtained geographic distance matrices using the Geographic Distance Matrix Generator 1.2.3 (Ersts 2007).

Divergence time estimation

Divergence time estimates were obtained by implementing a Bayesian relaxed clock model in BEAST 1.8.1 (Drummond *et al.* 2012) based on the mitochondrial gene, and using the CIPRES Science Gateway. We used a relaxed clock with an uncorrelated lognormal distribution (Drummond *et al.* 2006) as indicated by hLRT test, UPGMA starting tree and birth–death process. We applied the same substitution models as used in the phylogenetic reconstruction. Because no fossils are available for this group, we used a rate of evolution of 1.05% ($\pm$ 0.05) per lineage per million years for cytochrome b (Weir & Schluter 2008), under a normal distributed prior, to obtain absolute dates. We performed two independent runs with 80 million generations each, with parameters sampled every 10 000 steps and a burn-in of 10%. We checked for convergence between runs and analysis performance using TRACER 1.6 and accepted the results if ESS values were >200. The resulting trees were combined in TreeAnnotator

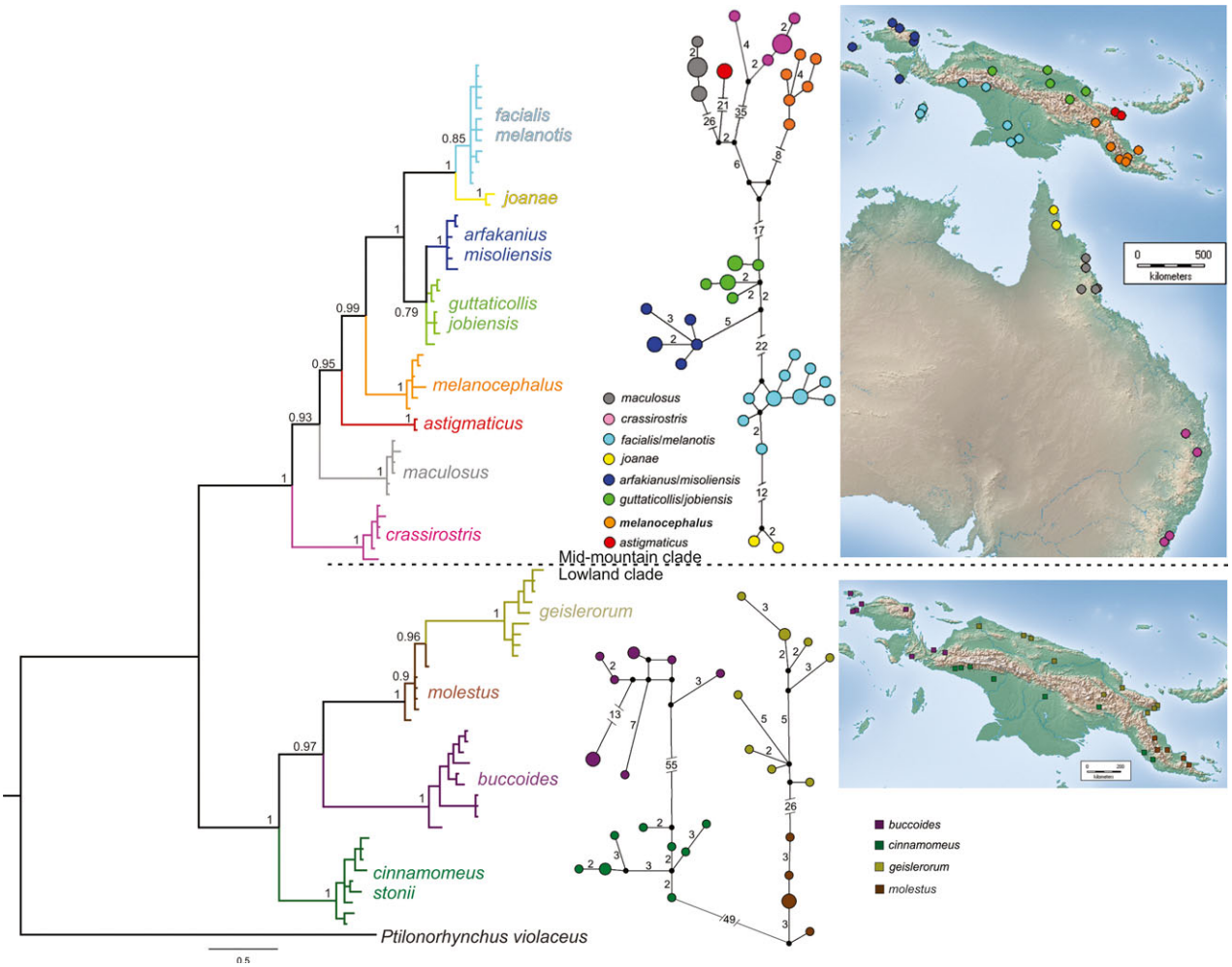

Fig. 1 Estimates of phylogenetic relationships and sampling localities for the molecular analyses. To the left the phylogeny obtained from the MrBayes analysis of the cytochrome b data set with posterior probability support values at the nodes, in the middle median-joining networks for the mid-mountain *Ailuroedus melanotis* and lowland *Ailuroedus buccoides* complexes, respectively, and to the right maps showing sampling localities for these two complexes. In the median-joining networks each coloured circle corresponds to one haplotype and its size is proportional to its frequency; the numbers of mutational steps are indicated by a figure at lines, a line without number refers to one mutational step.

and the consensus species tree with the divergence times was visualized in FIGTREE 1.4 (http://tree.bio.ed.ac.uk/software/figtree/).

Ecological parameters

Using an expanded data set on locality information extracted from museum specimens we obtained altitude, mean annual temperature and annual precipitation the lowland and mid-mountain complexes. We only used locality coordinates that were considered sufficiently detailed and excluded more imprecise localities. Altitude, temperature and precipitation data where then extracted for those localities using layers from the BIOCLIM (Hijmans *et al.* 2005) available at Worldclim (http://www.worldclim.org/). We used DIVA-GIS 7.5 (Hijmans *et al.* 2012) to extract these variables for each georeferenced point. Box plots were generated for each variable in order to see variation between lowland and mid-mountain clades. In addition, we used the Wilcoxon–Mann–Whitney test in software PAST 3.06 (Hammer *et al.* 2001) to investigate whether there were significant differences in these abiotic factors between the lowland and mid-mountain complexes based on the extracted data. We used 10 000 Monte Carlo permutations to obtain significance of this test. As the lowland white-eared catbird complex only occur on New Guinea we implemented these tests with both the Australian populations of the mid-mountain black-eared catbird complex included and excluded.

Morphology

We examined and measured 160 study skins in The Natural History Museum in Tring (UK), Naturalis Biodiversity Center in Leiden (Netherland) and Swedish Museum of Natural History in Stockholm (Sweden) to evaluate previous diagnoses of taxa and to examine whether populations defined by our molecular analyses are morphologically diagnosable. These birds represented all taxa, except *astigmaticus* and *joanae*. For the latter, we had to rely on photographs provided by the Museum für Naturkunde (Berlin, Germany) and the American Museum of Natural History (New York, USA) as well as on descriptions from the literature (Stresemann 1922; Mayr 1931; Rand 1942; Gilliard 1967; Schodde & Mason 1999; Frith & Frith 2004; Higgins *et al.* 2006). Next to skins examined, morphological and mensural data of various forms were obtained from Hartert (1930), Hartert *et al.* (1936), Mayr & Rand (1937), Mayr & Meyer de Schauensee (1939a,b), Ripley (1964) and Mayr & Jennings (1952). Diagnosis as presented here is valid for adults only.

Results

Variation in the molecular data set

We obtained 799 base pairs (bp) from the mitochondrial cytochrome b gene from all 80 catbird samples, 644–638 bp from the myoglobin intron 2 from 44 individuals and 593–598 bp (614 bp in *Ptilonorhynchus violaceus*) from the ornithine decarboxylase (ODC) intron 6 and 7 from 45 individuals. A few indels were observed in the sequenced introns that were either apomorphic or congruent with the phylogenetic results (data not shown), except for a deletion of 6 bp in myoglobin that was randomly distributed in one terminal linage within the mid-mountain *Ailuroedus melanotis* complex (found in two of six *melanocephala*, the only *arfakianus* and all five *melanotis/facialis* individuals sequenced). Authenticity of our sequences obtained from study skin samples is supported by all lines of evidence; all sequences obtained from study skins and fresh tissue samples (10 samples from five taxa) grouped together according to their taxonomic identity, overlapping sequence fragments were identical, the mitochondrial sequences showed no double signal in the electropherograms, the alignment showed no stop codons, insertions or deletions, a vast majority of nucleotide substitutions were found in the 3rd codon and resulted in few amino acid substitutions (of which a majority also was found in sequences obtained from any of the fresh samples). A single study skin sample of *Ailurodelus melanotis guttaticollis* (AMNH679721) grouped with *facialis/melanotis*. Unfortunately, this individual is an immature bird which made a morphological determination inconclusive. However, judging from plumage patterns the sample is more similar to *facialis/melanotis* than to *guttaticollis/jobiensis*, and we conclude that it is likely that this sample has been mislabelled at some point. Due to the uncertain affinity of the sample, it was excluded from the study. Comparison of intraspecific and interspecific genetic variation in cytochrome b between recognized sister species is shown in Table 1.

Phylogeny, biogeography and population structure

The phylogenetic results (Fig. 1) confirm that the catbirds are divided into two major clades, a lowland group consisting of the New Guinean white-eared catbird, and a mid-mountain clade including the black-eared catbird and the Australian Green Catbird.

The BEAST analysis suggests that the genus *Ailuroedus* originated about 20 mya and that the lowland and mid-mountain clades started to diverge from each other about 10 mya (Fig. 2). Within both the lowland and mid-mountain clades, basal divergences are suggested to be of late Miocene or Pliocene age, but the latter clade also has a strong Pleistocene divergence pattern.

Overall, there is good congruence between the nuclear (Appendix S1) and mitochondrial data (Fig. 1, AMOVA Table 2) trees, but the nuclear data are less informative and recent splits are only supported by the mitochondrial data set. The tree topologies obtained from the BEAST and MrBayes analyses are generally similar but disagree in some basal relationships. Within the lowland white-eared catbird clade, *Ailuroedus b. buccoides* forms the sister clade to the other linages in the BEAST tree (Fig. 2), while *Ailuroedus b. cinnamomeus/stonii* is sister to other lineages in the MrBayes tree (Fig. 1). In the mid-mountain clade, the Green Catbird (*Ailuroedus crassirostris*) is nested within the Black-eared Catbird (*Ailuroedus melanotis*) in the BEAST tree but not in the MrBayes tree.

Table 1 Intraspecific and interspecific genetic divergence for taxa that are proposed species herein. Divergences that are highlighted in grey indicate populations where intraspecific divergence overlap with interspecific divergence

Subspecies	Intraspecific divergence	Interspecific divergence
A m joanae/melanotis/facialis	0–0.038	0.033–0.045
A m arfakianus/misoliensis	0–0.006	0.011–0.016
A m jobiensis/guttaticollis	0–0.013	0.011–0.016
Ailuroedus melanocephalus	0.001–0.008	0.033–0.060
Ailuroedus astigmaticus	0	0.048–0066
Ailuroedus maculosus	0–0.004	0.054–0.076
Ailuroedus crassirostris	0–0.009	0.061–0.081
A b stonii/cinnamomeus	0–0.014	0.063–0.085
Ailuroedus buccoides	0–0.021	0.073–0.103
A b geislerorum/molestus	0–0.045	0.063–0.085
A b geislerorum	0–0.020	0.034–0.045
A b molestus	0–0.006	0.034–0.045

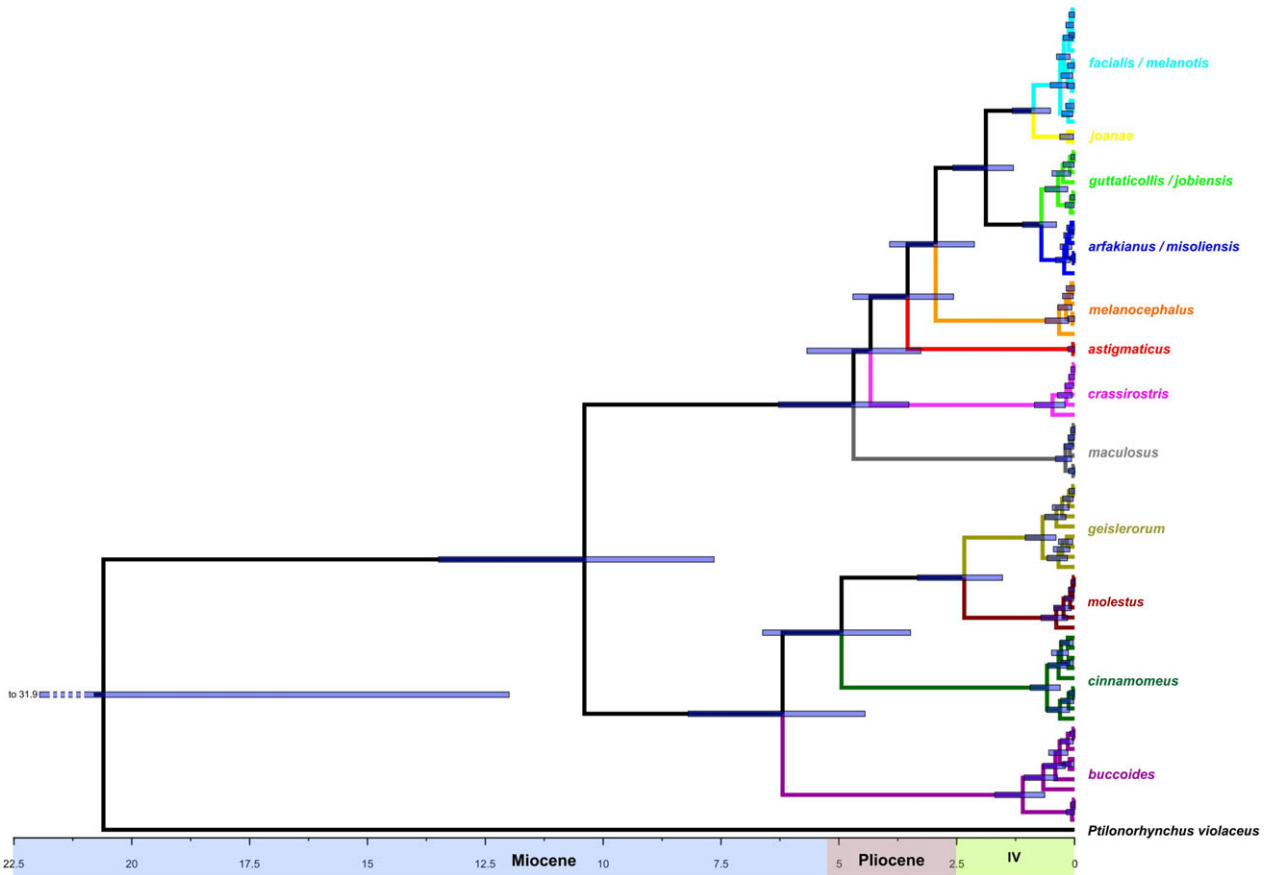

Fig. 2 Estimates of divergence times. The tree is a chronogram based on a BEAST Markov chain Monte Carlo (MCMC) analysis of the cytochrome b dataset. Confidence intervals are indicated by the lilac bars at the nodes.

Table 2 Analysis of molecular variance (AMOVA) in the mid-mountain *Ailuroedus melanotis* complex and the lowland *Ailuroedus buccoides* complex, for cytochrome b (a), ODC (b), and MYO2 (c) genes

	Mid-moutain complex				Lowland complex			
Gene	SV	d.f.	PV	FI	SV	d.f.	PV	FI
(a)	Among groups	7	93.57	PhiCT = 0.9357	Among groups	3	87.37	PhiCT = 0.8737
	Among localities within groups	28	4.81	$P < 0.00001$	Among localities within groups	23	6.93	$P < 0.00001$
	Within localities	11	1.62		Within localities	7	5.70	
	Total	46			Total	33		
(b)	Among groups	5	89.72	PhiCT = 0.8972	Among groups	3	74.86	PhiCT = 0.7486
	Among localities within groups	17	1.08	$P < 0.00001$	Among localities within groups	8	12.09	$P < 0.00001$
	Within localities	31	9.19		Within localities	20	13.05	
	Total	53			Total	31		
(c)	Among groups	5	54.76	PhiCT = 0.5476	Among groups	3	49.48	PhiCT = 0.4948
	Among localities within groups	14	34.74	$P < 0.001$	Among localities within groups	7	17.78	$P < 0.001$
	Within localities	28	10.50		Within localities	19	32.74	
	Total	47			Total	29		

SV, source of variation; d.f., degrees of freedom; PV, percentage of variance; FI, fixation index. All components of variance were significant at $P < 0.05$.

The AMOVA (Table 2) and Mantel tests ($r_{\text{mid-mountain}} = 0.7028$, $P < 0.0001$; $r_{\text{lowland}} = 0.4758$, $P < 0.0001$; Fig. 3) revealed that the mid-mountain Black-eared Catbird (*Ailuroedus melanotis*) complex exhibits higher levels of genetic structure and isolation by distance when compared to lowland White-eared Catbird (*Ailuroedus buccoides*) complex.

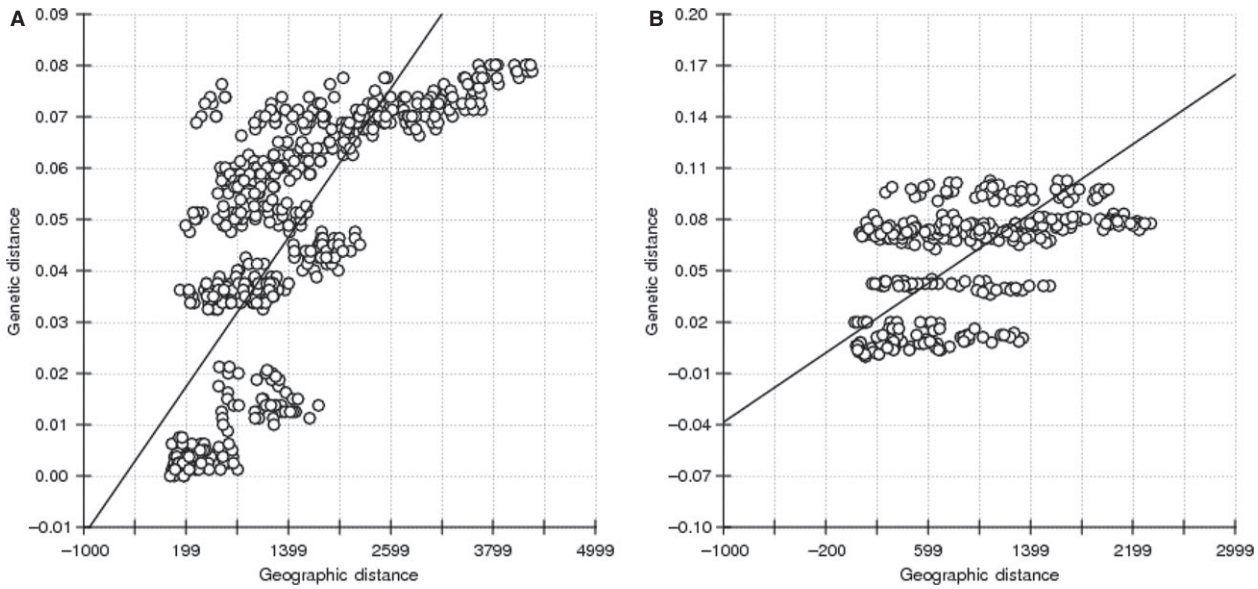

Fig. 3 Relationship between geographical distance (in km) and genetic (uncorrected p) distance in (A) the mid-mountain *Ailuroedus melanotis* complex and (B) the lowland *Ailuroedus buccoides* complex. The line represents the fitted linear regression. The Mantel test revealed a higher correlation between geographical distance and genetic distance in the mid-mountain *Ailuroedus melanotis* complex ($r = 0.7028$, $P < 0.0001$) than in the lowland *Ailuroedus buccoides* complex ($r = 0.4758$, $P < 0.0001$).

Ecological variation

There were no significant differences in the results whether the Australian populations of the mid-mountain black-eared catbird complex were included or excluded, and we thus only show the results for the analyses with all populations included. The variation in abiotic factors within and between mid-mountain and lowland clades obtained from the expanded locality data set is shown in the box plots in Fig. 4. Wilcoxon–Mann–Whitney test revealed significant difference in temperature ($Z = -6.3736$; $P = 0.0001$) and precipitation ($Z = -10.409$; $P = 0.0001$), but not in altitude ($Z = -0.63113$; $P = 0.5266$) between the two catbird complexes. These results show that mid-mountain and lowland complexes exhibit distinct habitat requirements with respect to climatic variables (temperature and precipitation).

Morphological variation

Within the *buccoides* complex, marked variation was found in colour of cap (black-brown to black vs. cinnamon to rufous-brown), in colour of hindneck and underparts (white to cream-yellow vs. cinnamon to rufous) and in size of black spots on hindneck and underparts (Table 3). In the *melanotis* complex, marked variation was found in colour of

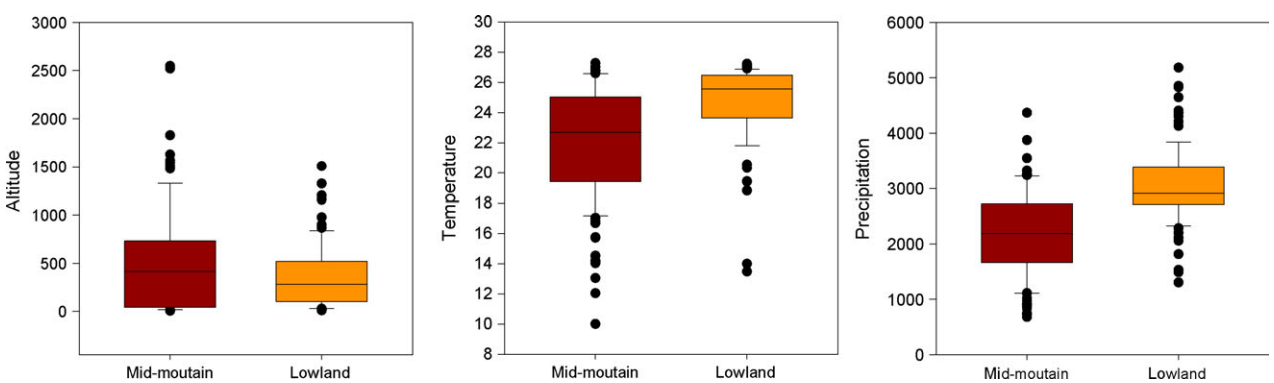

Fig. 4 Box plots showing the variation in abiotic factors within and between mid-mountain *Ailuroedus melanotis* and lowland *Ailuroedus buccoides* complexes obtained from the expanded locality dataset. Wilcoxon–Mann–Whitney test revealed significant difference in temperature ($P = 0.0001$) and precipitation ($P = 0.0001$), but not in altitude ($P = 0.5266$) between the two catbird complexes.

Table 3 Key plumage characters that separates taxa within the lowland *Ailuroedus buccoides* complex

	Cap	Hindneck	Ground-colour breast to vent	Size of spots in underparts
buccoides	Fuscous to black-brown	White or pale cream with bold black spots, black predominating	White to cream-yellow	Large, (4-) 5–6 wide, 5–8 long on breast, gradually smaller towards vent
geislerorum	Rufous	White or pale cream with bold black spots, black predominating	White to cream-yellow	Large, (3-) 4–6 wide, 4–7 long on breast, gradually smaller towards vent
molestus	Liver-brown to fuscous	White or pale cream with bold black spots, black predominating	Cream-white to buff-yellow	Large, (4-) 5–6 wide, 5–8 long on breast, suddenly smaller on belly
cinnamomeus	Fuscous to black-brown	Cinnamon with bold black spots, black predominating	Cinnamon, slight green cast flanks	Large, (4-) 5–6 wide, 5–8 long on breast, gradually smaller towards vent
stonii	Fuscous to black-brown	Cinnamon with black spots, black not predominating	Uniform deep cinnnamon	Small, 1.5–2.5 (-3) wide, 3–4 long; on belly horseshoe-shaped, reduced or absent towards rear

cap and hindneck as well as size and colour of pale spots on cap and hindneck; in size and contrast of dark ear-patch (darker birds also showing black patches near base of lower mandible and on chin), in colour of throat (white, sometimes with some dark barring, vs. black, often marked with pale spots of varying size), in colour of breast (green or black), in shape, size and colour of pale spots on breast, and in colour of belly varying from yellowish-green to rufous (Table 4). See Appendix S1 for morphological species diagnostics.

Discussion

The early history of catbirds

Our phylogenetic analyses of the molecular data recovered the lowland (white-eared) and mid-mountain (black-eared/green) catbird taxa as two monophyletic clades (Fig. 1). These two clades diverged from each other ~10 mya (Fig. 2) during the Late Miocene, while the primary lineage itself originated ~20 mya corresponding to the Early Miocene. The origin of, and major divergence in, *Ailuroedus* corresponds to the period when complex tectonic activity was leading to the establishment of the New Guinean land mass (Dow 1977; Charlton 2000; Hall 2002; Schellart *et al.* 2006). Although there has been a view that the montane regions of New Guinea were a source of diversification in the Late Oligocene to Early Miocene (Jønsson *et al.* 2011a; Aggerbeck *et al.* 2014), Schodde & Christidis (2014) argue that tectonic data, instead is more consistent with earlier views whereby the rainforest-inhabiting flora and fauna took refuge in montane New Guinea in response to increased aridification of Australia during the past 25 million years (Zachos *et al.* 2001; Martin 2006). Although some studies have found deep Miocene divergences between New Guinean and Australian taxa (e.g. Georges *et al.* 2014; Joseph *et al.* 2014), studies of Australo-Papuan marsupials (e.g. Malekian *et al.* 2010; Mitchell *et al.* 2014) suggests that it was not until substantial part of New Guinea had emerged, in the second half of Miocene, that the New Guinean and Australian biotas began to diverge significantly. Whether Australia or proto-New Guinea was the ancestral area of origin for the genus *Ailuroedus* cannot be determined from the current data.

Our results show that the lowland and mid-mountain catbird clades display largely contrasting phylogeographical histories (Figs 1 and 2), the mid-mountain black-eared catbird group having a more complex pattern continuing into the Pleistocene. This is also reflected by the lower genetic divergences within taxa (Table 1) and the higher correlation between genetic and geographical distances (Fig. 3) in the more recently diverged mid-mountain black-eared catbird clade. These results suggest that current phylogeographic signatures in the lowland catbird clade are most likely explained by vicariant events where widely distributed populations have become fragmented into smaller isolated populations, whereas the phylogeographic signatures in the mid-mountain catbird suggest a role for dispersal as well.

In understanding the diversification of the genus *Ailuroedus*, it is thus best to consider the lowland and mid-mountain clades separately.

Phylogeography of the lowland white-eared catbird complex

The results (Fig. 1) recover three major clades within the lowland white-eared catbird complex, *buccoides* in the Vogelkop peninsula, *stonii* and *cinnamomeus* in the southern lowlands and *geislerorum* in the northern lowlands. The northern lowland clade is further divided into two genetically differentiated populations; the first distributed in northern New Guinea from Geelvink Bay to just east of the Huon Peninsula, and the second along the northern lowlands of the south-eastern peninsula. The name *molestus* Rothschild and Hartert, 1929is applicable to the latter population, and this issue is explored further below in the section dealing with taxonomy. The divergence estimates of ~ 6–4.5 mya indicate that the three major clades became isolated from each other during the Pliocene, a period with

Table 4 Key plumage characters that separates taxa within the mid-mountain *Ailuroedus melanotis* complex

	Cap	Hindneck	Throat	Breast	Belly	Ear-patch
crassirostris	Green, no drops	Green with fine olive streaks	Green, traces of fine white streaks and grey feather-bases	Green, narrow white spots	Green, rather short and narrow light green to whitish streaks	Green, no white outlining, not contrasting with remaining side of head
maculosus	Black, large buff-grey drops	Green, feather-centres ill-defined pale grey and with traces of darker olive to black crescents	Light grey with ill-defined olive-grey or grey-olive crescents, narrow chin-patch uniform black	Light grey with green cast and with darker olive-green to dusky olive crescents	Light green with extensive darker olive green crescents	Black with mottled surround
melanocephalus	Black, narrow pale cinnamon to whitish drops	Black, rather small rounded cinnamon to whitish spots	Pink-cinnamon with narrow black crescents	Pale cream to cinnamon, marked with sharply contrasting bold black crescents	Rufous-cinnamon with ill-defined pale green feather-bases	Black with mottled surround
astigmaticus	Black, small lanceolate cream to white marks	Black, rather small rounded cream to white spots	Black, small diamond-shaped pale spots	Pale cream to cinnamon, marked with sharply contrasting bold black crescents	Green-yellow with ill-defined rufous crescents	Black with mottled surround
arfakianus & misoliensis	Black, narrow cream-buff to whitish drops	Black, rather small oval cream-buff to whitish spots	Black, rather small diamond-shaped pale spots	(greenish-) black, feather-centres with narrow white spikes	Light green with buff cast and pale green to whitish streaks	Black with white surround
jobiensis & gutttaticollis	Black, large cinnamon drops	Black, large cinnamon drops	Black, small diamond-shaped cinnamon spots	Rufous-cinnamon with sharply contrasting bold black crescents	Rufous-cinnamon with restricted pale green on feather-bases	Black with mottled surround
melanotis	Black, large pale cinnamon to white drops	Black, large cinnamon to cream feather-centres	Pale cream-buff to white with narrow black feather-tips; black patch on chin reduced or absent	Pale grey-green, feathers washed with buff subterminally and tipped with sharply contrasting bold black crescents	Pale green with ill-defined rufous-buff feather-tips and traces of olive-green crescents, latter sometimes partly black on upper belly	Black with white surround
joanae	Black, large cream to white drops	Black, large pale cinnamon to cream-white feather-centres	Pale cream-buff to white with narrow black feather-tips; black patch on chin reduced or absent	Cream to white, feathers tipped with sharply contrasting bold black crescents	Green-yellow with ill-defined buff feather-tips and olive-green crescents	Black with white surround
facialis	Black, narrow rufous drops	Black, large cinnamon feather-centres	Pale cream-buff to white with narrow black feather-tips; black patch on chin reduced or absent	Pale grey-green, marked with sharply contrasting bold black crescents	Pale green with ill-defined rufous-buff feather-tips and traces of olive-green crescents, latter sometimes partly black on upper belly	Black with mottled surround

considerable geological activity in New Guinea (Hall 2002; Cloos *et al.* 2005). Geological data suggest that the uplift of the central mountain range occurred since at least the Miocene ~12 mya, and that the uplift of the eastern section of the mountain range began ~3 mya later than the western section (Cloos *et al.* 2005). The estimated date of ~4.5 mya for the divergence of the northern and southern populations (Fig. 2) is a pattern found in many other New Guinean taxa (e.g. Dumbacher & Fleischer 2001; Rawlings & Donnellan 2003; Westerman *et al.* 2006; Zwiers *et al.* 2008; Meredith *et al.* 2010; Deiner *et al.* 2011) and congruent with the central mountain range being a major barrier for Papuan lowland organisms.

Apart from the central mountain range, there are few obvious barriers in the contemporary New Guinea lowlands. However, there are numerous examples of distributional breaks at species or subspecies level co-occurring at the same geographic location in the lowlands (Mack & Dumbacher 2007). Several of these are consistent with suggested Pliocene and early Pleistocene lowland barriers (summarized in Deiner *et al.* 2011), while others are less well documented. When comparing the phylogeographical

signature found in the white-eared catbird complex (Figs 1 and 2) with other lowland organisms, both congruent and incongruent patterns emerge. For example, in some lowland taxa, the Vogelkop populations represent an old isolated lineage (e.g. Joseph *et al.* 2001; Georges *et al.* 2014), whereas in other cases the populations there are not differentiated from others along the southern coast (Dumbacher *et al.* 2003; Deiner *et al.* 2011), or the northern coast (Dumbacher & Fleischer 2001).

The genetic signature in the lowland white-eared catbird complex is similar to that found in the New Guinea snapping turtle *Elseya novaeguinea* (Georges *et al.* 2014). In both these complexes, the populations from Vogelkop are genetically divergent from other populations (and possibly the sister taxon to the other populations in New Guinea although the result in the present study is inconclusive). Georges *et al.* (2014) suggested two scenarios for this pattern which they named the 'docking' and '*in situ*' hypotheses. In the former, plate tectonic hitch-hiking during the Early Miocene is implied, while in the latter, a widespread population becomes fragmented by vicariance during the Late Miocene to Early Pliocene, associated with the development of the Central mountain Range, the Langguru Fold Belt and the opening of Cenderawasih Bay (Bailly *et al.* 2009). Our divergence estimates of ~6 mya within the white-eared catbird complex fit much better with the '*in situ*' hypothesis.

The geographical location and the estimated divergence of ~2 mya for the divergence between *geislerorum* and *molestus* in the northern lowlands together indicate that it may be associated with the mountain uplift of Huon peninsula (Cloos *et al.* 2005).

Phylogeography of the mid-mountain black-eared catbird complex

Within the black-eared catbird complex, up to 11 taxa have been described (Dickinson & Christidis 2014) and the form *crassirostris* is often accorded species rank (e.g. Frith & Frith 2004; Christidis & Boles 2008). Other treatments have suggested that the complex comprises four (Schodde & Mason 1999) or three subspecies groups (Dickinson & Christidis 2014). Our result reveals an even more complex pattern of lineages that diverged during Pliocene, as well as more recent divergences during the Pleistocene (Figs 1 and 2). The Pliocene isolated groups include *crassirostris* (central coast of eastern Australia), *maculosus* (north-eastern Australia), *melanocephalus* (south-eastern peninsula, New Guinea) and *astigmaticus* (Huon Peninsula, New Guinea). At present, mesic forests occur as patches along the east coast of mainland Australia within dryer and more open forest communities (mainly in mountains, but there are patches of lowland rainforests on Cape York). Both fossil and phylogenetic data are consistent with fragmentation of mesic habitats in Australia during the Miocene and Pliocene due to climatic changes as the Australian continent drifted north (Byrne *et al.* 2011). The trend from closed wet forests to dryer and more open vegetation is suggested to have accelerated during the Pliocene climatic oscillation (Hill 2004). The dates around 4 mya for the split between the Australian taxa *crassirostris* and *maculosus* from each other, as well as from the New Guinean taxa is consistent with this scenario. The taxa *crassirostris* and *maculosus* could thus be assumed to have survived as isolated lineages within mesic refugia.

In New Guinea, the mid-mountain black-eared catbird complex is divided into three main linages: *astigmaticus* on the Huon Peninsula; *melanocephalus* in the Owen Stanley Range; and a polytypic clade that comprises the remaining New Guinean montane subspecies (*facialis*, *arfakianus*, *misoliensis*, *guttaticollis*, *jobiensis*) along with *melanotis* (Aru Is., Fly-river basin) and *joanae* (Cape York peninsula, Australia). Both *astigmaticus* and *melanocephalus* occur in mountain regions that hold several other endemic bird taxa (Beehler *et al.* 1986; Heads 2002). As these mountain regions consist of distinct and old terranes (Hall 2002; Cloos *et al.* 2005; Baldwin *et al.* 2012), these two black-eared catbird taxa have most likely become isolated as a result of tectonic events.

The polytypic black-eared catbird clade has a patchy distribution in mid-mountain habitats throughout most of New Guinea (except the most eastern parts that are inhabited by *astigmaticus* and *melanocephalus*). In New Guinean mountain birds, a replacement of populations from west to east has been suggested as a general pattern (Beehler *et al.* 2007) and has also been supported by genetic data from logrunners (Joseph *et al.* 2001) and robins (Christidis *et al.* 2011). However, logrunners occur at slightly higher altitudes than black-eared catbirds, and for several mid-mountain taxa, the central mountain range has, as for lowland birds, been found to divide northern and southern populations (McGuigan *et al.* 2000; Dumbacher & Fleischer 2001; Rawlings & Donnellan 2003; Zwiers *et al.* 2008). This pattern is also found in the black-eared catbirds, but our dates are of Pleistocene origin and thus younger than in most other studied taxa.

In our case, the division of populations distributed north of the central mountain range (*guttaticollis/jobiensis*), including the Vogelkop (*arfakianus*) and the Island of Misool (*misoliensis*), from those distributed south of the central mountain range (*facialis/melanotis*) and Cape York peninsula (*joanae*) are best explained by habitat changes due to Pleistocene climate oscillation. While the central mountain range may not have constituted a barrier for gene flow in the black-eared catbird during the Pliocene, the lowering

of the tree line by more than 1000 m during the Pleistocene glacial maxima (Hope *et al.* 1983; Flenley & King 1984) could have prevented exchange between populations across this mountain range. Pleistocene climatic oscillation may also have expanded suitable habitats for the black-eared catbird into the lowlands during certain periods and could explain the disjunct distribution of the black-eared catbird in the lowlands of the Trans-Fly and Aru Islands (*melanotis*) and Cape York peninsula (*joanae*). This is also supported by the observation that the Trans-Fly hosts other avian taxa which are otherwise restricted to mountain habitats, such as *Cinclosoma ajax*, implying that this region has been a Pleistocene refuge for mountain birds (Beehler *et al.* 1986).

Abiotic factors and phylogeographical signatures

Although the variation in abiotic factors between mid-mountain and lowland clades suggests that the mid-mountain black-eared catbird complex has a broader altitude range than the lowland white-eared catbird complex and more frequently occurs at higher altitudes, we found no significant difference in altitudinal distribution between these two complexes. On the other hand, our results suggest that these two complexes occur in habitats with significant difference in temperature and precipitation, where the lowland white-eared catbird complex occupies comparably wetter and warmer forests than the mid-mountain black-eared catbird (Fig. 4). That the mid-mountain black-eared catbird complex has a broad altitudinal distribution is best explained by the occurrence of certain populations in lowland forests (e.g. Frith & Frith 2004). This in turn may be explained by that some lowland regions may be climatic distinct from other lowland areas (see e.g. Foster 2001) and host habitats that are advantageous for the mid-mountain black-eared catbird complex and less favourable for the lowland white-eared catbird complex. An example of one such area is Trans-Fly, which is a refuge also for other mountain birds (Beehler *et al.* 1986). These results highlight the importance of considering habitat requirements when studying phylogeographical patterns and that classification into broad categories such as lowland or mid-mountain organisms might be too general when comparing phylogeographical signatures in many cases. That the lowland white-eared catbird complex lack representatives in Australia might be explained by that mesic forests in Australia are too dry for members in this clade (Byrne *et al.* 2011).

Together, the phylogeographic and abiotic data may also help to explain some of the observed population structures in catbirds. It is, for example, possible that the higher population structure and Pleistocene divergences in the mid-mountain clade (Fig. 1; Table 2) are a result of that this clade was able to maintain more and often isolated populations during glacial cycles from the Pleistocene (or even the Pliocene), as it is able to tolerate colder and drier habitats (Fig. 4). In contrast, the lowland clade shows less population structure and magnitudes of divergence consistent with pre-Pleistocene divergences. These indicate that this clade may have experienced more serious population decline and even extinction of certain populations during glacial ages, as it may only have been able survive in a few humid and warm forest refuges.

Taxonomy of Australo-Papuan catbirds

Estimates of species richness are essential components in macroecological assessments of biodiversity (e.g. Wilson 2003) as well as in formulating conservation and management strategies (e.g. Myers *et al.* 2000). It is consequently important that taxonomy is as objective and standardized as possible across the globe (Mace 2004; Avise & Mitchell 2007). It has been suggested that genetic divergence among sister species is higher in tropical birds than in temperate regions (Weir & Schluter 2007). However, this pattern may simply represent an artefact caused by incomplete studies of species limits in tropical groups (Tobias *et al.* 2008).

The observed genetic differentiation between catbird subspecies (Table 1) often exceeds those commonly observed for sister species in other parts of the world (Johnson & Cicero 2004; Kerr *et al.* 2007, 2009; Johnsen *et al.* 2010; Lohman *et al.* 2010). The examination of plumage variation within catbirds also confirm that genetically distinct taxa also are morphological diagnosable (Tables 3 and 4; Appendix S1). We use an integrative approach to recognize species and recognize species level status when both DNA and morphological assessments reveal strong differentiation (where there is only morphological differentiation we retain subspecies status).

Within the white-eared catbird complex, three deeply divergent DNA clades were apparent and these are supported by significant plumage differentiation. Consequently, we divide the complex into three species: Vogelkop White-eared Catbird *Ailuroedus buccoides*, Southern White-eared Catbird *A. stonii* and Northern White-eared Catbird *A. geislerorum*. Within *A. stonii*, two geographically separated populations are morphologically well-defined but very close genetically and are treated here as subspecies *A. s. stonii* and *A. s. cinnamomeus*. The two genetic clades within *A. geislerorum* are also geographically separate (western and eastern) but are not that morphologically distinct from one another. Although the eastern group has been separated under the name *molestus* Rothschild and Hartert, 1929, recent treatments have kept it in synonomy within *geislerorum* (Frith & Frith 2004; Dickinson & Christidis 2014). Here, the western and eastern populations are

treated as two subspecies *A. g. geislerorum* and *A. g. molestus*. Given the degree of genetic divergence (2 mya separation) between the two, further morphological re-assessment may reveal that *A. g. geislerorum* and *A. g. molestus* are better treated as separate species.

The morphologically distinctive Green Catbird *A. crassirostris* was also highly divergent genetically, thereby confirming its species status.

Within the black-eared catbird complex, six deep clades were recovered in the DNA trees and each of these was defined by significant plumage differentiation. These six clades are here treated as species: Grey-throated Catbird *A. maculosus*, Back-capped Catbird *A. melanocephalus*, Huon Catbird *A. astigmaticus*, Arfak Catbird *A. arfakianus*, Northern Catbird *A. jobiensis* and Spotted Catbird *A.melanotis*. The latter species is polytypic with three geographically isolated and morphologically distinct populations that are genetically very close. These are treated as three subspecies here as follows: *A. m. melanotis*, *A. m. facialis* (New Guinea) and *A. m. joanae* (Australia). Within *A. arfakianus*, two geographically isolated populations are very similar genetically and in plumage patterns but are separable on size. The form *misoliensis* is tentatively retained here as a subspecies within *A. arfakianus*. Conversely, no appreciable genetic, plumage or size differences were found between *A. jobiensis* and the form *guttaticollis*, so the latter is treated as a synonym of *jobiensis*.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Plumage diagnosis of *Ailuroedus* 7.

Table S1. Specimen data and GenBank accession numbers for samples used in the study

Fig. S1. The median-joining networks for the mid-mountain Ailuroedus melanotis and lowland Ailuroedus buccoides complexes based on the nuclear data.

Fig. S2. Estimates of phylogenetic relationships obtained from the MrBayes analysis of the nuclear data set with posterior probability support values at the nodes.