


Title	Pilot biodiversity assessment of the Hkakabo Razi passerine avifauna in northern Myanmar – implications for conservation from molecular genetics
All Authors	Martin Packert, Christopher M. Milensky, Jochen Martens, Myint Kyaw, Marcela Suarez- Rubio, Win Naing Thaw, Sai Sein Lin Oo, Hannes Wolfgramm, Swen C. Renner
Publication Type	International Publication
Publisher (Journal name, issue no., page no etc.)	Bird Conservation International, page 1 of 22
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Keywords	Hkakabo Razi, Bird Area, Myanmar
Citation	
Issue Date	2019

Pilot biodiversity assessment of the Hkakabo Razi passerine avifauna in northern Myanmar – implications for conservation from molecular genetics

MARTIN PÄCKERT, CHRISTOPHER M. MILENSKY, JOCHEN MARTENS,
MYINT KYAW, MARCELA SUAREZ-RUBIO, WIN NAING THAW,
SAI SEIN LIN OO, HANNES WOLFGRAMM and SWEN C. RENNER 

Summary

The Hkakabo Razi region located in northern Myanmar is an Important Bird Area and part of the Eastern Himalayan Biodiversity Hotspot. Within the framework of the World Heritage Convention to enlist the site under criterion (ix) and (x), we conducted a biodiversity assessment for passerine birds using DNA barcoding and other molecular markers. Of the 441 bird species recorded, we chose 16 target species for a comparative phylogeographic study. Genetic analysis was performed for a larger number of species and helped identifying misidentified species. We found phylogeographic structure in all but one of the 16 study species. In 13 species, populations from northern Myanmar were genetically distinctive and local mitochondrial lineages differed from those found in adjacent regions by 3.9–9.9% uncorrected genetic distances (cytochrome-*b*). Since the genetic distinctiveness of study populations will be corroborated by further differences in morphology and song as in other South-East Asian passerines, many of them will be candidates for taxonomic splits, or in case an older taxon name is not available, for the scientific description of new taxa. Considering the short time frame of our study we predict that a great part of undetected faunal diversity in the Hkakabo Razi region will be discovered.

Introduction

Located at the south-eastern margin of the Qinghai-Tibet Plateau the Northern Mountain Forests of Myanmar are located at the crossroads of three major biodiversity hotspots: the Himalayan hotspot, the Indo-Burma hotspot and the Southwestern Chinese Mountain hotspot (Marchese 2015). Therefore, the Northern Mountain Forests of Myanmar harbour highly diverse assemblages of faunal elements from two larger zoogeographic regions, the Palearctic and the Oriental (Indo-Malayan) region. Along the elevational gradient, local species assemblages occupy different ecological niches in a great number of different terrestrial ecoregions (Wikramanayake *et al.* 2002). At 5,881 m above sea level, Myanmar's highest mountain Hkakabo Razi is located in the centre of the third largest of 55 important bird areas (IBA) in Myanmar (country profile of Myanmar; Chan 2004). At a larger spatial scale, the Hkakabo Razi region is part of the Eastern Himalaya Endemic Bird Area (EBA 130) (Stattersfield *et al.* 2005). A first assessment of avian species richness at Hkakabo Razi was conducted by Rappole *et al.* (2011): A long-term study over five expeditions listed no less than 431 bird species in this region. In the course of long-term monitoring this number has been raised to 441 bird species observed at Hkakabo

Razi (Renner *et al.* 2015). An independent study covering four annual surveys (2015–2017) in the Putao region (Zhang *et al.* 2017) recorded a total number of 319 bird species and confirmed a mid-domain effect of species richness with highest diversity at average elevations (Stevens 1992, Acharya *et al.* 2011).

The Northern Mountain Forests of Myanmar are also home to a number of globally threatened vertebrate species; mammals: the recently described Myanmar snub-nosed monkey *Rhinopithecus strykeri* (Geissmann *et al.* 2011) and two endemic deer species of the genus *Muntiacus* (Rabinowitz *et al.* 1999); birds: the critically endangered White-billed Heron *Ardea insignis* (Renner *et al.* 2015), or the Rusty-bellied Shortwing (*Brachypteryx hyperythra*; compare species factsheet BirdLife International (2018). *Brachypteryx hyperythra* is fairly common at Hkakabo Razi, thus except for some fragmented and small populations in Nepal and north-east India, the Northern Mountain Forests of Myanmar are among the last refuges for this species. Among Myanmar's endemic birds (see list at <http://Intreasures.com/burma.html>) most are typical low-land species and distributed farther south, such as the recently rediscovered Jerdon's Babbler *Chrysomma altirostre* (Rheindt *et al.* 2014), or even restricted to single sites farther south such as Nat Ma Taung, also known as Mount Victoria (e.g. the White-browed Nuthatch, *Sitta victoriae*, or the endemic subspecies of Black-throated Tit, *Aegithalos concinnus sharpei*). Other Myanmar endemics such as the endangered Hooded Treepie *Crypsirina cucullata* or the Burmese Bushlark *Mirafra microptera* have not yet been recorded at Hkakabo Razi, though the habitat in theory could fit for both species. However, one narrow-range endemic of the northern mountain forests is the Naung Mung Wren-babbler *Rimator naungmungensis*. Though subject to lively debate since its scientific description by Rappole *et al.* (2005) its species status is well justified based on the results of genetic analyses (Renner *et al.* 2018).

Previous field explorations to Hkakabo Razi resulted in several new bird taxa including the Ashy-headed Babbler *Alcippe cinereiceps hkakaboraziensis* and Abbott's Babbler *Malacocincla abbotti kachinensis* (Renner *et al.* 2015). Furthermore, preliminary data from comparative integrative analyses using morphological, bioacoustic and genetic characters showed that cryptic diversity is still underestimated for the Hkakabo Razi region, in other groups such as babblers (Moyle *et al.* 2012), cupwings *Pnoepyga* spp. (Päckert *et al.* 2013) and leaf-warblers (Päckert *et al.* 2016).

For several passerine target species of our study, we provide evidence of genetic distinctiveness of local populations in the Hkakabo Razi region. Some of these newly discovered genetic lineages are candidates for future study as possible new taxa. This information is relevant for conservation genetics and will be used in the currently ongoing nomination process for a UNESCO World Natural Heritage Site, the "Hkakabo Razi Landscape".

Material and methods

Study region and study sites

The study region is located in the northernmost tip of Myanmar and covers the Hkakabo Razi National Park, the Hponkan Razi Wildlife Sanctuary and the tentative Southern Extension of the Hkakabo Razi National Park (proposed boundaries as of August 2016 which are subject to changes (Figure 1). All three protected areas together are currently under consideration as a UNESCO World Heritage Site, tentatively suggested to be listed under criteria (ix) and (x) of the convention.

The study area within the region covered five major sites: (i) Ziyadam/Wanglaimdam in Hponkan Razi Wildlife Sanctuary, (ii) the Mali Raing and (iii) the Htanga-Shinsanku area in the Southern Extension, (iv) the higher elevations in the Hkakabo Razi National Park, and (v) the Babulontan Range in the Namti-Naung Mung area (Figures 1 and 2). Except for the very high elevations (> 3,000 m) all areas were covered by two field trips (see map in Figure 1). The study region has a unique constellation of land cover and land use types which are mainly stacked by elevational bands and form a diverse set of habitats for birds (Renner *et al.* 2007).

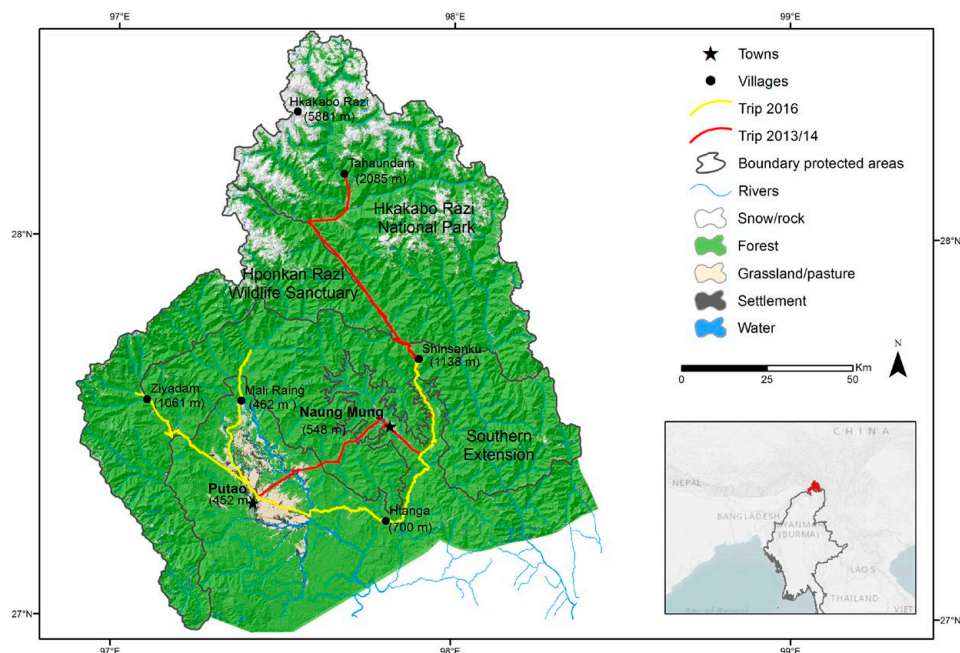


Figure 1. Map of the study region and the protected areas in the Northern Mountain Forests of Myanmar including itineraries during expeditions in 2013/2014 and 2016; elevations (in meters ASL) of study sites and highest summits given in brackets.

Sampling

For a pilot genetic assessment, we chose 16 passerine species locally recorded at Hkakabo Razi (Rappole *et al.* 2005, Renner *et al.* 2015). The basic material for this study consisted of blood samples collected during a field trip from 31 January to 27 March 2016. During this trip we visited three sites; the Ziyadam area within Hponkan Razi Wildlife Sanctuary (six capture days), the Mali Raing area (nine capture days) and the Htanga-Shinsanku area (11 capture days). Further material (blood samples) were collected during another field trip to Hkakabo Razi (15 December 2013 to 30 January 2014, all in Hkakabo Razi National Park from Naung Mung to Tahaundam, with 28 capture days, 10 nets for six consecutive hours per day) and from museum collections (Senckenberg Natural History Collections Dresden [SNSD]; Smithsonian National Museum of Natural History [USNM]).

For a pilot screening of intraspecific genetic differentiation, we focussed on species (taxon pairs) with considerable subspecific variation between populations from Myanmar and those from adjacent Himalayan and Chinese mountain ranges (based on current systematics and morphology). For some of our target species, intraspecific genetic diversification was already suspected from analysis of very few samples ($n < 5$ per species; e.g. core babblers studied by Moyle *et al.* 2012). Furthermore, we used DNA barcoding as a control for correct identification of cryptic species in the field with a broader choice of target species from our total sampling (143 samples from 45 species). Due to their subtle phenotypic distinctiveness, cryptic species are not easily distinguished from their closest relatives without additional data from vocalisations or genetics (Irwin *et al.* 2001, Bickford *et al.* 2007), such as in the case of golden-spectacled warblers of the former *Seicercus burkii* complex (Alström and Olsson 1999, Martens *et al.* 1999, Päckert *et al.* 2004, Olsson *et al.* 2005), today *Phylloscopus burkii* and allies (del Hoyo and Collar 2016). For the eight species-level taxa of this group, DNA barcode reference sequences were recently published



Figure 2. Study sites in the Northern Mountain Forests of Myanmar; a) view at Hkakabo Razi; b) grassland and subtropical forest edge at Mali Raing; c) riverside near Ziyadam; d) Ziyadam, local village (Photos by Marcela Suarez-Rubio and Swen C. Renner).

(Päckert *et al.* 2016). To date, five of these species have been listed for our study site at Hkakabo Razi, however species identification according to phenotypes is highly problematic and these records needed confirmation from molecular markers. We also aimed at verifying species identification in case of a few doubtful records from the field lists, such as Indomalayan species like the Mountain Warbler *Phylloscopus trivirgatus*, or South-East Asian species like the Grey-cheeked Fulvetta *Alcippe morrisonia* (Renner *et al.* 2015). The latter species has a widespread distribution across South-East Asia, however, the northern Myanmar mountain forests are located at the extreme northern edge of the species' range. If the species was present in the northern mountain forests of Myanmar, the local population at Hkakabo Razi would be expected to belong to subspecies *A. m. yunnanensis*, which represents two closely related lineages so far known only from Yunnan and south-west Sichuan (Song *et al.* 2009).

With several competing bird species lists of the world (Dickinson and Christidis 2014, del Hoyo and Collar 2016, Gill & Donsker 2019), avian taxonomy and systematics has become increasingly confusing in certain groups. We follow the taxonomy used by BirdLife International, based on del Hoyo and Collar (2016) for passerines. However, due to recent taxonomic changes particularly in the speciose families of babblers, the taxonomy in published species lists for the study region (Renner *et al.* 2015) might strongly differ from the taxonomic standard applied for this study. To avoid misunderstandings and confusion we provide synonymies for all our target species in Table S1 in the online supplementary material. Our target groups were babbler species from the families Pelloroneidae, Leiотrichidae, Timaliidae (*Alcippe*, *Napothera*, *Pellorneum*, *Pomatorhinus*, *Rimator*, *Schoeniparus*, *Turdinus*, *Trichastoma*), cupwings (Pnoepygidae: *Pnoepyga*), leaf-warblers (Phylloscopidae: *Phylloscopus*), bush warblers (Scotocercidae: *Abroscopus*, *Tesia*) and bulbuls

(Pycnonotidae: *Alophoixus*). A full list of sampled material and sequence data inferred from GenBank for comparison can be found in supplementary Tables S2 and S3.

All samples were taken in accordance with national Myanmar law and the animal protection laws of the European Union. All experimental protocols follow the national laws of Myanmar and have been approved by following the rules for the Nagoya Protocol, represented by the Ministry of Natural Resources and Environmental Conservation (MONREC; details in Acknowledgements). Access to the protected areas was granted by the Forest Department of MONREC under the contract with UNESCO ("Safeguarding Natural Heritage in Myanmar within the World Heritage Framework – Phase II 504MYA4001") for all fieldwork.

Marker choice

In conservation genetics, DNA barcoding using the standard marker cytochrome-oxidase I (COI) is often the method of choice for a first pilot screening of undiscovered genetic variation. The barcode marker COI has been proven to be a useful tool for species identification in birds (Hebert *et al.* 2004, Kerr *et al.* 2009, Barreira *et al.* 2016). Furthermore, DNA barcoding helped uncover intraspecific phylogeographic structure of some Asian bird species (Song *et al.* 2009, Tritsch *et al.* 2017). However, barcode records of the Asian avifauna are still rather scarce, with the exception of the well-screened Japanese avifauna (Saitoh *et al.* 2015). Further sequence data input to the Barcode of Life Database (BOLD) came from a limited number of studies from Korea (Park *et al.* 2011), South-East Asia (Lohman *et al.* 2009) and China (Huang and Ke 2014). Therefore, for several Asian species or even whole genera few COI sequences from previous studies are available for comparison. Our study provides the first COI sequences for several species and even a first complete barcode inventory for some avian genera, such as *Pnoepyga* cupwings.

Because of the general scarcity of barcode sequences for Asian bird species, we also sequenced the mitochondrial cytochrome-*b* and/or ND2 for some study groups depending on the number of sequences available at GenBank for comparison. For the White-throated Bulbul *Alophoixus flaveolus* we amplified and sequenced ATP synthase membrane subunit 6 (ATP6) for selected samples for comparison with sequence data from Fuchs *et al.* (2015).

For a firm inclusion of newly detected genetic lineages in a phylogenetic tree, we performed multi-locus analyses for some groups for which comprehensive multi-locus data sets were already available. We therefore amplified and sequenced further nuclear introns for selected samples of target species. Marker choice depended on sequence data sets available from previous studies and the following combinations of nuclear introns were analysed: 1) ornithine decarboxylase (ODC) introns 6 and 7 and myoglobin (myo) intron 2 for leaf warblers and bush warblers (Alström *et al.* 2011; see their supplementary Table 8); 2) β -fibrinogen intron 5 (fib5), muscle skeletal receptor tyrosine kinase (MUSK) intron 3 and transforming growth factor β 2 (TGFB2) intron 5 for babblers (Moyle *et al.* 2012); for comparison with our sequences from Myanmar we used their complete multi-locus alignment, downloaded from Dryad: doi:10.5061/dryad.100jc764).

Lab protocols

For DNA extraction from blood samples, we used the innuPREP BloodDNA Mini Kit (Analytik Jena AG, Germany). For amplification of the barcoding marker (COI), we used standard primers BirdF1 and BirdR1 (Hebert *et al.* 2004), each one modified with a 5' M13 tail (forward-primer BirdF1-tl: TGTAACACGACGCGCCAGTTTCTCCAACCAC-AAAGACATTGGCAC, reverse-primer BirdR1-tl: CAGGAAACAGCTATGACACGTGG-GAGATAATTCCAAATCCTGG). The PCR protocol for the barcoding marker was 94°C for 5 min followed by 5 cycles of 94°C for 1 min, 50°C for 1:30 min and 72°C for 1:30 min followed by 30 cycles of 94°C for 1 min, 51°C for 1:30 min and 72°C for 1:30 min with a final extension at 72°C for 5 min (modified from Tritsch *et al.* 2017). Along with the barcode marker we amplified the mitochondrial cytochrome-*b* for at least one sample of each taxon investigated with the primer combination O-L14851 (5'-CCT ACC TAG

GAT CAT TCG CCC T-3') and O-H16065 (5'-AGT CTT CAA TCT TTG GCT TAC AAG AC-3' (Weir and Schluter 2008)). The PCR protocol for cytochrome-*b* was 94°C for 10 min followed by 35 cycles of 92°C for 1 min, 53°C for 1 min and 72°C for 2 min with a final extension at 72°C for 10 min. Further information on primer combinations used for PCR and sequencing of further mitochondrial markers and nuclear introns is provided in Table 1.

PCR products were purified using ExoSapit and sequenced on an ABI 3130xl capillary sequencer (Applied Biosystems). Sequencing of the barcoding marker was performed using the non-modified primer pair BirdF1 and BirdR1 (Hebert *et al.* 2004). The sequences were aligned manually using MEGA version 5.10 (Tamura *et al.* 2011) and examined by eye and controlled for possible stop codons or frame shifts in coding sequences.

Sequence analysis

For a first assessment of intraspecific diversification, we reconstructed single-locus phylogenies of mitochondrial markers (COI and/or cytochrome-*b* depending on the number of sequences available for comparison). We included further sequences downloaded from GenBank for comparison into our single-marker analysis, e.g. for scimitar-babblers *Pomatorhinus* from Reddy and Moyle (2011) and from Dong *et al.* (2014); for the Puff-throated Babbler *Pellorneum ruficeps* from Robin *et al.* (2015) (for a full documentation of GenBank sequences used for comparison see Table S3). We reconstructed single-locus trees using Bayesian inference of phylogeny (BI) with MrBAYES vers. 3.2.3 (Ronquist and Huelsenbeck 2003). Data sets were generally partitioned by codon position under the GTR+Gamma+Invariant Sites (GTR + Γ +I) substitution model. We allowed the overall rate to vary between partitions by setting the priors <ratepr = variable> and model parameters such as gamma shape, proportion of invariable sites and the rate matrix were unlinked across partitions. We conducted two runs per analysis with one cold and three heated MCMC chains of 1,000,000 generations with trees sampled every 100 generations and a burn-in of 3,000 trees. In case of intraspecific lineage splits, genetic distances between populations from Myanmar and those from adjacent countries were calculated with MEGA v. 6.06 (Tamura *et al.* 2013). Genetic distances between populations are based on uncorrected p-distances of cytochrome-*b* sequences.

Multi-locus phylogenies were reconstructed with BEAST based on combined datasets of mitochondrial genes and nuclear introns (marker choice depending on the target family, see above). Substitution model choice and partition of the data set were applied according to the original multi-locus studies, compare for babblers (Moyle *et al.* 2012), for bush warblers (Alström *et al.* 2011) and for cupwings (Päckert *et al.* 2013). We ran BEAST for 30,000,000 generations (parameters were logged and trees sampled every 1,000 generations) under the uncorrelated lognormal clock model for all loci with the "auto-optimize" option activated and a birth-death process prior applied to the tree. The log files were examined with Tracer 1.6 (Rambaut *et al.* 2014) in order to ensure effective sample sizes (ESS; which yielded reasonable values for all parameters after 30,000,000 generations) and trees were summarized with TreeAnnotator v1.4.8 (posterior probability limit = 0.5) using a burn-in value of 3,000 trees and the median height annotated to each node.

For a rough estimate of divergence times, we applied a time calibration using an empirical rate estimate for cytochrome-*b* of 0.0105 substitutions per site per lineage per million years (Weir and Schluter 2008). All obtained phylograms were edited in FigTree vers. 1.4.2. For species with adequate intraspecific sampling, we reconstructed haplotype networks of mtDNA markers using TCS version 1.2.1 (Clement *et al.* 2000). Uncorrected genetic distances (p-distances) were calculated with MEGA v. 6.0, all p-distance values refer to pairwise comparisons of cytochrome-*b* sequences.

Newly generated sequences from this project were deposited at GenBank under accession numbers MK547438–MK547510, MK56716–5MK567188, MK598855–MK599135, MK609929–MK609959. The entire sequence data sets for mitochondrial markers (COI, cytochrome-*b*, ND2) have been uploaded to BOLD and are available including all sample metadata under project "UNMYA UNESCO Myanmar".

Table 1. Primer combinations used for amplification and sequencing; *= internal primer used for sequencing only; ann. temp.= annealing temperature.

marker	primer	forward	primer	reverse	ann. temp.	reference
cytb	O-L14851	Sequence (5'-->3') CCTACCTAGGATCATTCGCCCT	O-H16065	Sequence (5'-->3') AGTCTTCAATCTTTGGCTTACAAGAC	52°C	Weir & Schluter (2008)
ND2	L5216	GGCCATACCCCGRAAATG	H6361	ACTCTTRTTTAAGGCTTTGAAGGC	53°C	Fuchs et al. (2015)
ATP6	ATP6_L9245	CCTGAACCTGACCATGAAC	ATP6_H9947	CATGGGCTGGGGTCTACTATGTG	54°C	
myo						
PCR, external	myo2	CGG AAG AGC TCC AGG GCC TT	myo3	GCCACCAAGCACAAGATCCC	60/58/56°C	Alström et al. (2011)
internal*			myo3F	GCAAGGACCTTGATAATGACTT		
ODC						
PCR, external	OD6	GACTCCAAAGCAGTTTGTCTCTCAGTGT	OD8R	TCTTCAGAGCCAGGGAAGCCACCACCAAT	60/58/56°C	Alström et al. (2011)
PCR, external	OD6mod	GGGGCTACACTTAAGACCAG	OD8mod	TCTTCAGAGCCAGGGAAGCCACCACCAAT	60/58/56°C	
internal*	OD6int	GTTCTACTTTCTCTGGAAGTACTGCTC	OD8int	CGCYTWAACAYTCYGCCATCTTACC		
Fib5	Fib5	CGCCATACAGAGTATACTGTGACAT	Fib6	GCCATCCTGGCGATTCTGAA	56/55/54°C	Moyle et al. (2012)
MUSK	MUSK-I3F	CTTCCATGCACTACAATGGGAAA	MUSK-I3R	CTCTGAACATTGTGGATCCTCAA	60/58/56°C	Moyle et al. (2012)
TGFB2	TGFB2-5F	GAAGCGTGCTCTAGATGCTG	TGFB2-6R	AGGCAGCAATTATCCTGCAC	60°C	Moyle et al. (2012)

Results

Intraspecific diversification was remarkable in almost all our target species. We found genetic splits between populations from Myanmar and those from adjacent regions corresponding with p-distance values greater than 3% (cytochrome-*b*) in 13 out of 16 target taxa (Table 2). In two additional species, we found a distinct mitochondrial lineage in Myanmar, though genetic distances ranged at lower values between 1 and 2.5%. Only a single species (the White-throated Bulbul *Alophoixus flaveolus*) did not show any intraspecific differentiation (neither for cytochrome-*b* nor for ATP6; Figure S1). Genetic barcoding found misidentifications in five species that had been confused with a phenotypically very similar relative. We comment on these few cases in the following section.

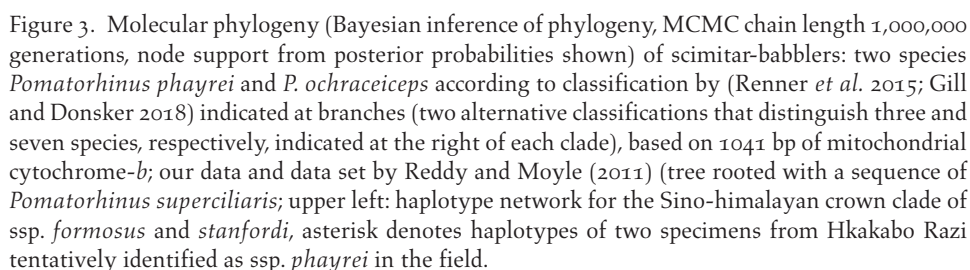
Babblers (*Timaliidae*, *Leiotrichidae*, *Pellorneidae*)

Phylogenetic structure could be found in nearly all our target species (for a phylogeny of the whole babbler data set, see Figure S2). In *Timaliidae*, the Red-billed Scimitar-babbler *Pomatorhinus ochraceiceps* and Brown-crowned Scimitar-babbler *P. phayrei* could be genetically identified in our sampling. Most specimens of the latter species were identified as belonging to subspecies *P. p. stanfordi* in the field, only two individuals were identified as nominate *P. p. phayrei*. Because occurrence of this more southerly distributed subspecies was doubtful, we also genotyped these two specimens. All *P. phayrei* sequences from the study site (ssp. *stanfordi*) formed one haplotype cluster that was separated by 16 substitutions (equalling a p-distance of 2.7%; Table 2) from two haplotypes of the north-east Indian sister taxon *P. p. formosus* (Figure 3).

Genetic distances between *P. phayrei* and its sister species the Coral-billed Scimitar-babbler *P. ferruginosus* from the Himalayas amount to 3.4–4.2%. These two sister species (five clades; Figure 3) differed from their closest relative, the Red-billed Scimitar-babbler by 8.8–9.9%. In the latter species, *P. o. stenorhynchus* from Myanmar differed from populations from Thailand (nominate ssp. *ochraceiceps*) and from Laos (ssp. *alius*) by a p-distance of 1.1% (Figure 3; Table 2). For further details on intraspecific diversification and paraphyly in the Streak-breasted Scimitar-babbler *P. ruficollis* and the White-browed Scimitar-babbler *P. schisticeps*, as evident from the data set by Moyle et al. (2012) see Discussion.

For *Leiotrichidae*, we analysed a larger sample set of one fulvetta species that had been preliminarily identified as the Grey-cheeked Fulvetta *Alcippe morrisonia* in the field. However, all our genotyped samples ($n = 36$) turned out to be individuals of the Nepal Fulvetta *A. nipalensis*. A cluster of 16 different haplotypes from our study site differed from a sequence from the Eastern Himalayas (Arunachal Pradesh, India) by 36 substitutions (equalling a p-distance of 6.7%; Table 2; Figure 4A).

In *Pellorneidae*, we found remarkable intraspecific diversification in four species that appeared as deep splits in the multi-locus tree (Figure 5; the total data set comprised 94 individual sequences of 52 species). Several genotyped individuals identified as the Spot-throated Babbler *Pellorneum albiventris* in the field turned out to be individuals of the Buff-breasted Babbler *Trichastoma tickelli*. In our sampling, we could identify a single sample of *P. albiventris* from Naung Mung (USNM633216) that differed from a Chinese sample of that same species (Guangxi) by a p-distance of 4% (Table 2; Figure 5). The local Myanmar population of the Buff-breasted Babbler belongs to subspecies *T. t. garoense* whose range extends westward to the Eastern Himalayas. Accordingly, samples from Hkakabo Razi formed a clade (haplotype cluster) with samples from north-east India and these were separated from a second clade (cluster) including populations from adjacent Vietnam and southern China (subspecies *T. t. fulvum*) by 26 substitutions (equalling a p-distance of 5.5%; Table 2; Figures 4B, 5). Further intraspecific differentiation was found in the Puff-throated Babbler *Pellorneum ruficeps*: The local subspecies *P. r. pectorale* from the Northern Mountain Forests of Myanmar appeared as one of four deeply separated clades with closest relatives in the Himalayas (ssp. *mandelli*) and in the



Moreover, intraspecific splits were found between Streaked Wren-babbler *Turdinus brevicaudatus* from Hkakabo Razi (Figure 5) and adjacent populations from Vietnam and southern China as well as between Eyebrowed Wren-babbler *Napothera epilepidota* from Hkakabo Razi, Vietnam and Borneo (three different lineages; Figure 5). Finally, the greatest intraspecific p-distance of nearly 10% was found between the local population of the Rufous-throated Fulvetta *Schoeniparus rufogularis collaris* from our study site and adjacent populations from Vietnam (*A. r. kelleyi*; Table 2, Figs 4C, 5).

For a control of correct species identification, we genotyped all samples of Golden-spectacled Warbler. In the field, these were tentatively identified as either Grey-crowned Warbler *Phylloscopus tephrocephalus*, Green-crowned Warbler *P. burkii* or Whistler's Warbler *P. whistleri*. Contrary to our field species lists, all samples are Bianchi's Warbler *Phylloscopus valentini*. The White-spectacled Warbler *Phylloscopus intermedius* is also present in the area; however, some specimens were misidentified as *P. valentini* (for difficulties of species identification, see Discussion). In the haplotype network inferred from a larger sequence set ($n = 41$) the local population at Hkakabo Razi appeared as genetically distinct from the nominate form *P. v. valentini* from south-western China and subspecies *P. v. latouchei* from southern and south-eastern China (Figure 6). Phylogeographic structure in the Grey-cheeked Warbler *Phylloscopus poliogenys*

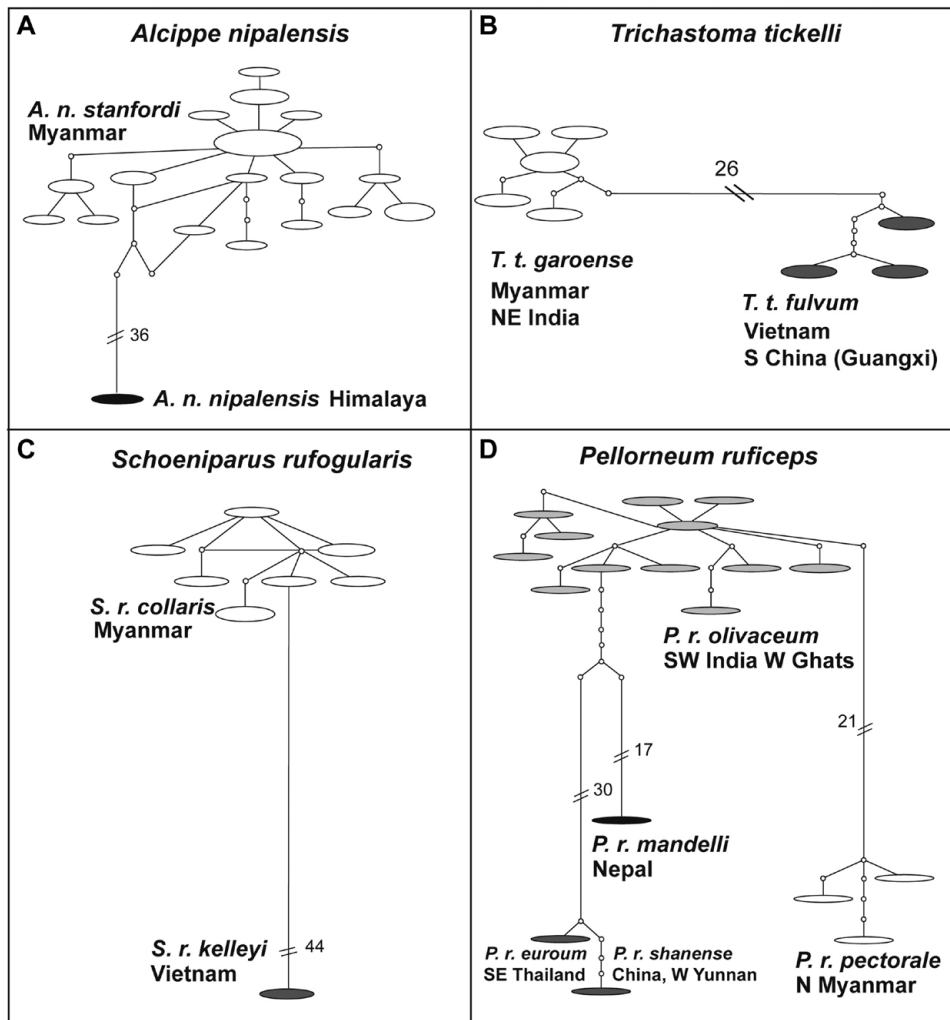


Figure 4. Phylogeographic structure in three South-East Asian babbler species, haplotype networks based on mitochondrial cytochrome-*b*; A) *Alcippe nipalensis*, B) *Trichastoma tickelli*, C) *Schoeniparus rufogularis*; *Pellorneum ruficeps* ($n = 20, 820$ bp).

was less clear, because sequences from Myanmar formed a complex network with samples from southern China and Vietnam and the whole cluster was separated from a sample from the Himalayas (Arunachal Pradesh, India) by a minimum of 24 substitutions (Figure 6). Intraspecific genetic distances in the two leaf warbler species ranged from 1.3 to 4% (Table 2). Furthermore, all samples that were tentatively assigned to the Mountain Warbler *Phylloscopus trivirgatus* turned out to be Yellow-throated Fulvetta *Schoeniparus cinereus*.

Bush warblers (Scotocercidae)

This group attracted our attention when we captured some aberrant individuals of a small warbler species that was preliminarily determined as Yellow-bellied Warbler *Abroscopus superciliaris* – a

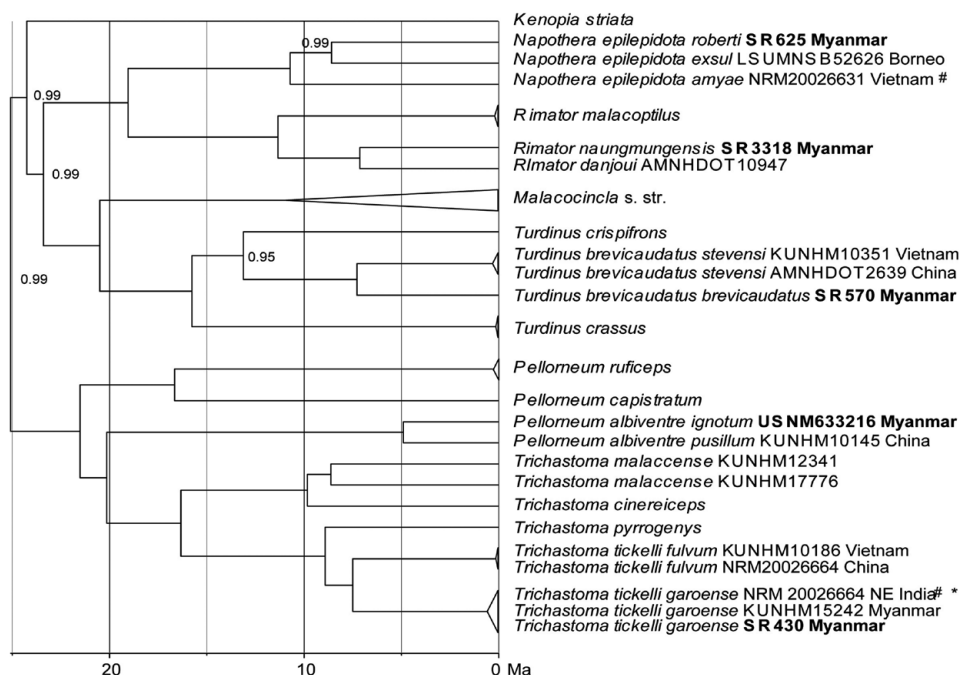


Figure 5. Multi-locus phylogeny of Pellorneidae based on 4009 bp concatenated sequence data of cytochrome-*b* (1134 bp), ND2 (1041bp) *fib5* (586 bp), *MUSK* (638 bp) and *TGFB2* (610 bp); our data set and that of Moyle *et al.* (2012) (total data set: 94 concatenated sequences of 52 species), subclade of their clade B shown; Bayesian inference of phylogeny, MCMC chain length 30,000,000 generations, node support from posterior probabilities shown; our samples from Hkakabo Razi in bold print; # denotes GenBank sequences from Price *et al.* (2014); * = in the original study the specimen had been misidentified as *Pellorneum albiventris*.

species that has not been previously recorded at Hkakabo Razi. However, this local form differed from the nominate form that breeds in eastern and southern Myanmar (and from other subspecies throughout the species' range) by its rather large body size and by a large bright-white belly patch (Figure 7). We tentatively assigned the Hkakabo Razi population to subspecies *A. s. drasticus* that breeds in north-eastern India (Assam) and northern Myanmar. Local samples from our study site differed from nominate subspecies *A. s. supercilialis* from eastern Myanmar by a p-distance of 4.4% (Table 2). Intraspecific differentiation of a similar magnitude was found between local samples of the Rufous-faced Warbler *Abroscopus albobularis albobularis* and samples from southern China and Taiwan (subspecies *A. a. fulvifacies*; Table 2, Figure 7). Within the Black-faced Warbler *A. schisticeps* one sequence differed from a clade of subspecies *A. s. ripponi* from China by a p-distance of 1.6%. However, that sample was taken from a captive individual of unknown origin, so we cannot infer any information on a putative phylogeographic pattern from this shallow split.

Furthermore, the local population of the Chestnut-headed Tesia *Cettia castaneocoronata* belonged to the same genetic lineage as samples from the Himalayas (Arunachal Pradesh, India). The multi-locus tree shows a deep split between this Himalaya-Myanmar lineage and a sample from neighbouring China that equalled a p-distance of 7.8% (Table 2, Figure 7; for the problematic subspecific taxonomy see discussion). That divergence level was similar to between-clade distances among four closely related tesia species (Figure 7; 6.1–7.2%).

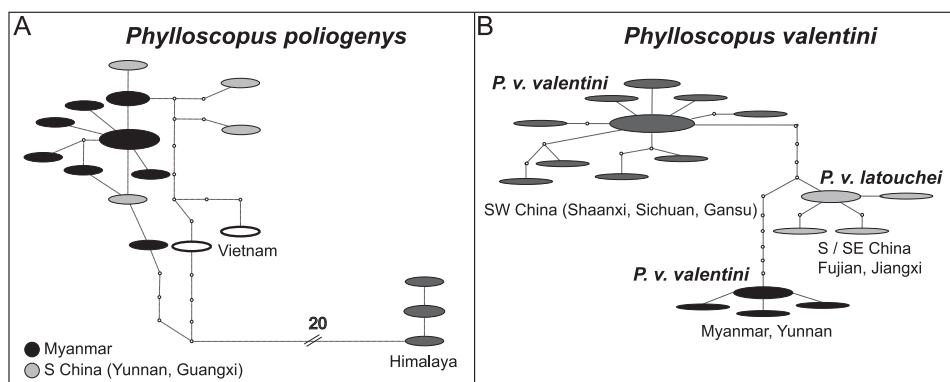


Figure 6. Phylogeographic structure in two Sino-himalayan leaf-warbler species, haplotype networks based on mitochondrial cytochrome-*b*; A) *Phylloscopus poliogenys*, B) *Phylloscopus valentini* ($n = 41$; 595 bp).

Cupwings, Pnoepygidae

So far, only the Pygmy Cupwing *Pnoepyga pusilla* is confirmed for Hkakabo Razi. However, Scaly-breasted Cupwing *P. albiventer* is present at other localities in central and northern Myanmar and represents a separate genetic lineage. The Myanmar populations differ from *P. a. albiventer* and *P. a. pallidior* in the Himalayas, and also from Chinese *P. a. mutica* by genetic p-distances of about 4.0% (Table 2).

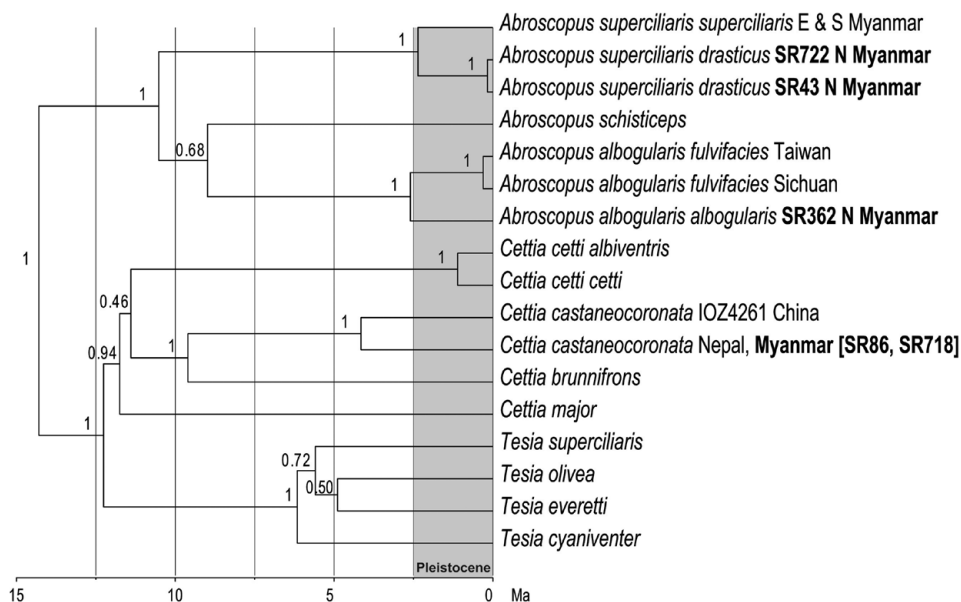


Figure 7. Multi-locus phylogeny of bush warblers (Scotocercidae) based on 2399 bp concatenated sequence data of cytochrome-*b* (1036 bp), myoglobin intron 2 (683 bp) and ODC intron 6 (680 bp); our data set and that of Alström *et al.* (2011), subsample of their basal clades including our target species; Bayesian inference of phylogeny, MCMC chain length 30,000,000 generations, node support from posterior probabilities shown; our samples from Hkakabo Razi in bold print.

Table 2. Intraspecific differentiation between populations of target species from Hkakabo Razi, Myanmar, and those from adjacent regions (mitochondrial DNA, cytochrome-*b*, in %; except *Pellorneum albiventris**= p-dist refers to ND2 due to a lack of *cytb* data); potential candidates for species splits have genetic distances of p-dist > 3 % (see methods).

species	taxon clade 1	country clade 1	taxon clade 2	country clade 2	gen. dist.
subspecific - low differentiation					
<i>Alophoixus flaveolus</i>	<i>flaveolus</i>	Myanmar	<i>flaveolus</i>	Himalayas	0.4%
<i>Phylloscopus valentini</i>	<i>valentini</i>	Myanmar, Yunnan	<i>valentini, latouchi</i>	C + S China	1.3–2.5%
<i>Pomatorhinus ochraceiceps</i>	<i>stenorhynchus</i>	Myanmar	<i>ochraceiceps, alius</i>	Thailand, Laos	1.1%
<i>Pomatorhinus phayrei</i>	<i>stanfordi</i>	Myanmar, Yunnan	<i>formosus</i>	NE India	2.7%
subspecific - high differentiation -potential species-level splits					
<i>Pellorneum ruficeps</i>	<i>pectorale</i>	Myanmar	<i>mandelli, olivaceum</i>	Himalaya, W Ghats	3.1–3.2%
<i>Phylloscopus poliogenys</i>	<i>poliogenys</i>	Myanmar, S China, Vietnam	<i>poliogenys</i>	Himalayas	4.0%
<i>Pnoepyga albiventer</i>	<i>albiventer</i>	Myanmar	<i>albiventer, pallidior, mutica</i>	Himalayas, China	4.0%
<i>Abroscopus superciliaris</i>	<i>drasticus</i>	Myanmar	<i>superciliaris</i>	Myanmar	4.4%
<i>Pomatorhinus phayrei</i>	<i>stanfordi, formosus</i>	Myanmar, Eastern Himalayas	<i>albogularis, dickinsoni, orientalis</i>	Thailand, Vietnam	4.4–4.6%
<i>Abroscopus albogularis</i>	<i>albogularis</i>	Myanmar	<i>fulvifacies</i>	S China, Taiwan	5.6%
<i>Trichastoma tickelli</i>	<i>garoense</i>	Myanmar	<i>fulvum</i>	S China, Vietnam	5.5%
<i>Pellorneum ruficeps</i>	<i>pectorale</i>	Myanmar	<i>shanense, euroum</i>	China, Thailand	6.2%
<i>Alcippe nipalensis</i>	<i>stanfordi</i>	Myanmar	<i>nipalensis</i>	Himalayas	6.7%
<i>Turdinus brevicaudatus</i>	<i>striatus</i>	Myanmar	<i>proximus, rufiventer, stevensi</i>	China, Vietnam	6.7–7.1%
<i>Rimator naungmungensis</i>	<i>naungmungensis</i>	Myanmar	<i>R. danjoui</i>	Vietnam	7.0–7.7%
<i>Pellorneum albiventris</i>	<i>albiventris, ignotum</i>	Myanmar, NE India	<i>cinnamomeum, pusillum</i>	China, SE Asia	7.8%*
<i>Cettia castaneocoronata</i>	<i>castaneocoronata</i>	Myanmar, Nepal	<i>cf. ripleyi</i>	China	7.8%
<i>Napothera epilepidota</i>	<i>roberti</i>	Myanmar	<i>amyae, clara, exsul</i>	Vietnam, Borneo	7.3–8.2%
<i>Schoeniparus rufogularis</i>	<i>collaris</i>	Myanmar	<i>kelleyi</i>	Vietnam	9.9%

Discussion

Species concepts and species limits

Species inventories of living organisms are the basics of all conservation effort. The combined use of different independent analytical approaches for species diagnosis (using phenotypical and bio-acoustic traits as well as molecular markers) including their taxonomy and systematic classification has recently been discussed under the flagship term ‘integrative taxonomy’ (Padial *et al.* 2010, Schlick-Steiner *et al.* 2010). This multi-dimensional approach has been applied to a number of South-East Asian and Indomalayan bird species (Irestedt *et al.* 2013, Päckert *et al.* 2014) some of them new to science (Alström *et al.* 2015, 2016) including a re-evaluation of the species status of the endemic *Rimator naungmungensis* from northern Myanmar (Renner *et al.* 2018).

In contrast to integrative taxonomy, the value of genetic sequence data, in particular that of mitochondrial DNA as a sole indicator of species limits, is restricted (Dávalos and Russell 2014, Mutanen *et al.* 2016, Yu *et al.* 2017). Any taxonomic recommendation inferred from phylogenies will inevitably rely on two criteria of the phylogenetic species concept, i.e. diagnosability and reciprocal monophyly (Sangster 2009, 2014). Distance-based approaches using genetic distances as a threshold can be a useful tool for detection of intraspecific diversification (Tavares and Baker 2008, Aliabadian *et al.* 2009, Johnsen *et al.* 2010, Bergmann *et al.* 2013), however their general application for species delimitation remains problematic (Moritz and Cicero 2004, del Hoyo *et al.* 2014: Figure 12). Typically, good songbird species pairs differ by genetic distances higher than 3% (Dietzen *et al.* 2003) but this can only be regarded as an approximate value. Many sister species of birds differ by genetic distances lower than 2% (Johns and Avise 1998), e.g. in bulbuls (Light-vented Bulbul *Pycnonotus sinensis* and Styan’s Bulbul *P. taiwanus*; Dejaradol *et al.* 2016) and in leaf-warblers (Chestnut-crowned Warbler *Phylloscopus castaniceps* and Javan Warbler *P. grammiceps*; Päckert *et al.* 2004). The practical use of a mere DNA-based taxonomy is even more limited in the case of cryptic species pairs that despite high genetic distances lack distinctive phenotypical or behavioural distinctiveness, such as in some leaf warblers (e.g. *P. affinis*/*P. occisinsensis*; Martens *et al.* 2008). Thus, a genetic survey including the identification of previously unknown genetic lineages from a study region can only be the first step towards a choice of candidate species for more comprehensive follow-up studies based on a broad sampling and analysis of multiple traits.

Additions or corrections to species lists

Cryptic species (lacking clear phenotypic diagnosability against congeners) can be rather difficult to identify in the field, in particular females or juveniles. Based on our genetic analyses, some misidentifications were detected in our sample lists that likely apply to previously published species lists for the study site (Rappole *et al.* 2005, Renner *et al.* 2015, Zhang *et al.* 2017). Our genetic analysis identified two species that have not been previously recorded at Hkakabo Razi: the Yellow-bellied Warbler *Abroscopus superciliaris* and Bianchi’s Warbler *Phylloscopus valentini*. So far, the latter seems to be the only species of the golden-spectacled warbler complex at the study site, because the presence of *P. tephrocephalus*, *P. whistleri* and *P. burkii* (previously listed by Renner *et al.* 2015) could not be confirmed by our genetic analysis.

It is very likely the Grey-cheeked Fulvetta *Alcippe morrisonia* does not occur at our study site, because all individuals in our large sampling set turned out to be a genetically distinct lineage of the Nepal Fulvetta *A. nipalensis*. In fact, the Northern Mountain Forests of Myanmar are located near the far north-western border of the wide breeding range of *A. morrisonia*, thus the species might just not be native to Hkakabo Razi.

Taxonomic confusion

As zoological taxonomy and systematics are in steady flux, nomenclatorial changes can have an impact on species lists (Hazevoet 1996, Isaac *et al.* 2004, Knapp *et al.* 2005, Padial *et al.* 2010).

In the Northern Mountain Forests of Myanmar, scimitar-babblers of the genus *Pomatorhinus* are a striking example. *Pomatorhinus ferruginosus* is listed as one of two species occurring at Hkakabo Razi (Renner *et al.* 2015). This classification is in accordance with Gill and Donsker (2019) who do not distinguish *P. phayrei* at the species level but subsumed all subspecific taxa under *P. ferruginosus* s.l. (compare Figure 3). In contrast, Reddy and Moyle (2011) restricted the range of *P. ferruginosus* to the Eastern Himalayas of Nepal, Bhutan and India and distinguished populations of Northern Myanmar as one of five diagnosable species-level taxa (*P. stanfordi* in Myanmar; Figure 3) (Collar and Inskipp 2012, Nyári and Reddy 2013). For a lack of genetic distinctiveness, Reddy and Moyle (2011) furthermore synonymized the form *phayrei* from the northern Chin Hills with *P. formosus* from Assam. According to current taxonomy in the "Handbook of the Birds of the World" and BirdLife International, *P. ferruginosus* would be the incorrect taxon name for Hkakabo Razi, because the nominate Himalayan form is treated as a separate species and all other taxa are subsumed under *P. phayrei* (Brown-crowned Scimitar-babbler; del Hoyo and Collar 2016). This striking example shows that three different species-level taxon names can be applied to the same genetic lineage of scimitar babblers from Hkakabo Razi depending on the taxonomic authority referred to (Figure 3).

For other *Pomatorhinus* species, previously recommended taxonomic changes have not yet been accepted by any taxonomic authority despite strong evidence of species-level polyphyly from phylogenetic data, such as in the White-browed Scimitar-babbler *P. schisticeps* (Figure S4; Moyle *et al.* (2012). In a phylogenetic study by Reddy and Moyle (2011) nine out of 12 subspecies currently distinguished by del Hoyo and Collar (2016) grouped as three distinct clades with one of them firmly nested in the Streak-breasted Scimitar-babbler *P. ruficollis*. This grouping received further support from a phylogeographic study by Dong *et al.* (2014) who recommended a transfer of five taxa from the *olivaceus* group (including three subspecies that occur in Myanmar) from *P. schisticeps* to *P. ruficollis* (Inskipp *et al.* 2010). Though most taxonomic authorities have not followed this recommendation yet (del Hoyo and Collar 2016, Gill and Donsker 2019), any future taxonomic rearrangement will certainly affect species lists for Myanmar.

Cryptic diversity and its relevance for conservation strategies

A recent study on global avian biodiversity estimated the total number of bird species to be twice as high as the currently accepted 9,000 to 10,000 species-level taxa (Barrowclough *et al.* 2016). However, these high numbers did not result from scientific descriptions of potentially new species but from genetically distinctive subspecies that might deserve full species status. Opponents of this approach reasoned that the putative increase in mammal and bird species numbers is mainly due to oversplitting and taxonomic inflation because of a growing popularity of the phylogenetic species concept over the biospecies concept (Isaac *et al.* 2004, Zachos 2013, Zachos *et al.* 2013). This critique has been greatly challenged by an empirical revision of more than 700 taxonomic papers over almost six decades (Sangster 2009). His conclusion was that the recent increase of accepted bird species numbers is based on robust taxonomic progress using an integrative taxonomic approach that combined results from phenotypic, genetic, ecological and bioacoustic analyses. This statement is important for our study because in case of cryptic phenotypic variation the assessment of genetic diversity can be the first step towards the definition of distinctiveness and diagnosability of a given taxon. In fact, the greatest part of cryptic genetic lineages discovered from our data set could already be assigned to a named taxon, i.e. to a valid subspecies in most cases. Thus, given the support from further morphological and bioacoustic analyses (as in the case of *Rimator naungmungensis*; Renner *et al.* 2018) our results could justify up-ranking of 13 subspecies that are at least partly endemic to the Northern Mountain Forests of Myanmar to full species-level taxa.

Furthermore, it has often been stated that conservation strategies might also consider subspecies particularly when they are endemic for the region under protection (Phillimore and Owens 2006). As taxonomy and systematics are in steady flux and some of the global bird species lists are

updated even annually, opinions on taxonomic rank of endemics might change over time. The Naung Mung Wren-babbler is a good example. Described as a species, some authors have argued against its species status for a long time (Collar and Pilgrim 2007, Collar 2011), until that species-level split was finally recognized in the recent *Illustrated Checklist of Birds of the World* (del Hoyo and Collar 2016). This decision was taken without knowing the strongest argument for this split, i.e. the strikingly high genetic distances of almost 10% between *Rimator naungmungensis* and *R. danjoui* (Renner *et al.* 2018). Because recognition of species-level taxa predominantly depends on the species concept and the criteria of species delimitation applied (Sangster 2009), local and regional species richness and the number of endemics are also affected by these conceptual aspects (Peterson and Navarro-Sigüenza 1999). For instance, in some cases lumping of many taxa into a single widely distributed polytypic species has promoted extinction of island endemics of the Macaronesian archipelago (Hazevoet 1996).

Others have argued against a prominent role of subspecies for conservation policies because the greater part of distinct genetic lineages within species would not represent single subspecies but previously unnamed taxonomic units (Zink 2004). Thus, conservation strategies should rather focus on these unnamed lineages. There are possible solutions for confronting and solving this problem. Because scientific descriptions of new taxa are a complicated and time-consuming work many scientists have argued in favour of an accelerated taxonomy using "operational taxonomic units" (OTU) to speed up the global biodiversity assessment (Costello *et al.* 2013, He *et al.* 2017). For populations that have not been given a scientific name yet, others have introduced the term of the "evolutionary significant unit" (ESU) (Ryder 1986, Möritz 1994). This term is frequently applied to genetically distinct populations at a low distance level whose taxonomic status is still under debate. In our dataset, we also found some examples of genetic splits within one subspecific taxon, e.g. in *Phylloscopus valentini valentini*, *Phylloscopus poliogenys poliogenys*, *Alcippe nipalensis nipalensis* and *Pnoepyga albiventer albiventer* (Päckert *et al.* 2013). These genetically distinct populations might either be treated as ESUs or as "unconfirmed candidate species" (UCS) (Padial *et al.* 2010). ESU or USC are working hypotheses or placeholders for future taxonomic work (fast track taxonomy) (Riedel *et al.* 2013). If genetic distinctiveness of local populations is documented and substantiated by further data, either i) a new taxon can be described in the near future or ii) scientific names available but not in use can be re-established for locally or regionally endemic forms, such as for Chinese buff-barred warblers, *Phylloscopus pulcher vegetus* (Päckert *et al.* 2014).

Conclusion

Cryptic avian diversity in the Hkakabo Razi Landscape of northern Myanmar covers all levels of genetic divergence and taxonomic rank. Our study groups included subspecies that might merit species rank due to genetic (and partly morphological) distinctiveness as well as intraspecific ESUs that might justify improved conservation efforts. These findings highlight the outstanding bird species richness of the pristine forests at Hkakabo Razi. With a surface area of more than 1,000,000 ha and an elevational gradient from 400 to 5,888 m the tentative World Heritage Site of Hkakabo Razi harbours a great diversity of forest and high alpine ecotones that are home to a remarkable faunal species richness (Renner *et al.* 2015, Zhang *et al.* 2017). It should be emphasised that the genetic results are preliminary and were achieved in a pilot study over a narrow period. Therefore, our assessment of avian biodiversity only scratches the surface and detection of more cryptic genetic lineages can be expected from broader future studies. Moreover, our sampling was biased towards understorey tropical species assemblages of the lower to medium elevations. A more pronounced phylogeographic structure can generally be expected from those species occupying sky island habitats of the upper mountain belt and the mountain summits: birds (McCormack *et al.* 2008, Robin *et al.* 2015, Purushotham and Robin 2016); mammals: He *et al.* (2017). Leaf warbler species of the high-elevation forest belt are typical examples, e.g. Bianchi's Warbler (*Phylloscopus valentini*; our study) or Blyth's Warbler, *Phylloscopus reguloides* with ssp.

assamensis as a distinctive genetic lineage from north-east India and Myanmar (Olsson *et al.* 2005, Päckert *et al.* 2009). The outstanding value for biodiversity research of the Northern Mountain Forests of Myanmar is furthermore highlighted by several recent descriptions of plant species new to science from that region (Zhou and Chen 2005). Several new vertebrate species have also been recently described from this region, e.g. bats (Soisook *et al.* 2017). Even in primates a new species of snub-nosed monkey has been recently described from the mountain ranges of north-eastern Kachin State near the border with China (Geissmann *et al.* 2009). Most of these newly described species from northern Myanmar are presumably rare endemics with a narrow distribution range and are thus generally threatened by any kind of anthropogenic impact. During the last 15 years, severe forest decline has been documented in many parts of Myanmar including large areas of forests in the north, including our study region (Renner *et al.* 2007, Bhagwat *et al.* 2017). Yet even in the north, tree cover of forested areas of the Hukaung Valley has decreased by a mean of 1.7% in a study period of five years and an additional 0.6% in the following five years with highest losses at lower elevations (Papworth *et al.* 2017). Increased conservation efforts are advisable to prevent future biodiversity losses, including loss of genetic diversity and so far undescribed species, in the Northern Mountain Forests of Myanmar. We certainly expect that future intensive field surveys across elevational gradients flanked by genetic monitoring of local populations will uncover more examples of cryptic faunal and floral diversity of the Hkakabo Razi Region.

Supplementary Material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0959270919000273>

Acknowledgements

This study was initiated and funded by UNESCO Bangkok under contract number 4500306550, for the genetic study and 4500291033 for fieldwork. The National Geographic Society provided funding for the 2013/14 trip by S. C. R. (GEFNE48-12). We cordially thank Vanessa Achilles, Angsana Chuamthaisong, and Koen Meyers for constant support during the project. We are grateful to Aung Kyaw (Yangon), Pipat Soisook (Hat Yai), San Sein Oo (Nay Pyi Daw), Sang Nai Dee (Putao), and Uraiporn Pimsai (Hat Yai) for help during the field trips. We also cordially thank Townsend A. Peterson (University of Kansas, KU Biodiversity Institute, USA) and Arpad Nyari (University of Tennessee, USA) for providing unpublished cytochrome-*b* sequence data of spectacled warbler species (*Phylloscopus valentini* and *P. poliogenys*) for comparison. We are most grateful to Director General Hla Maung Thein from MONREC for facilitating the genetic research under the regulations of the Nagoya Protocol (document NR-2/2-2017). J.M. was regularly sponsored for field work in Asia by Feldbausch Foundation and Wagner Foundation at *Fachbereich Biologie* of Mainz University. We thank anonymous reviewers for their comments, which helped to improve the manuscript.

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MARTIN PÄCKERT, HANNES WOLFGRAMM

Senckenberg Natural History Collections, Museum of Zoology, Königsbrücker Landstraße 159, 01109 Dresden, Germany.

CHRISTOPHER M. MILENSKY

Smithsonian Institution, National Museum of Natural History, Department of Vertebrate Zoology, 10th and Constitution Ave, N.W. Box 37012, Washington DC, USA.

JOCHEN MARTENS

Institute of Organismic and Molecular Evolution, Johannes Gutenberg University, 55099 Mainz, Germany.

MYINT KYAW

Hkakabo Razi National Park, Nature and Wildlife Conservation Division, Forest Department, Ministry of Natural Resources and Environmental Conservation, Myanmar.

SWEN C. RENNER*, MARCELA SUAREZ-RUBIO

Institute of Zoology, University of Natural Resources and Life Sciences (BOKU), Gregor-Mendel-Str. 33, 1180 Vienna, Austria.

WIN NAING THAW

Nature and Wildlife Conservation Division Forest Department, Ministry of Natural Resources and Environmental Conservation, Myanmar.

SAI SEIN LIN OO

Department of Zoology, University of Mandalay, 05032 Maha Aung Myay Township, Mandalay, Mandalay Division, Myanmar.

*Author for correspondence; email: swen.renner@gmail.com