Taylor & Francis
Taylor & Francis Group

Emu - Austral Ornithology

ISSN: 0158-4197 (Print) 1448-5540 (Online) Journal homepage: http://www.tandfonline.com/loi/temu20

Resolving a phylogenetic hypothesis for parrots: implications from systematics to conservation

Kaiya L. Provost, Leo Joseph & Brian Tilston Smith

To cite this article: Kaiya L. Provost, Leo Joseph & Brian Tilston Smith (2017): Resolving a phylogenetic hypothesis for parrots: implications from systematics to conservation, Emu - Austral Ornithology

To link to this article: http://dx.doi.org/10.1080/01584197.2017.1387030

View supplementary material

Published online: 01 Nov 2017.

Submit your article to this journal

Article views: 51

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
http://www.tandfonline.com/action/journalInformation?journalCode=temu20

Download by: [73.29.2.54] **Date:** 13 November 2017, At: 17:13

EMU - AUSTRAL ORNITHOLOGY, 2018
https://doi.org/10.1080/01584197.2017.1387030

Taylor & Francis
Taylor & Francis Group

REVIEW ARTICLE

Check for updates

Resolving a phylogenetic hypothesis for parrots: implications from systematics to conservation

Kaiya L. Provost [a,b], Leo Joseph [c] and Brian Tilston Smith[b]

[a]Richard Gilder Graduate School, American Museum of Natural History, New York, USA; [b]Department of Ornithology, American Museum of Natural History, New York, USA; [c]Australian National Wildlife Collection, National Research Collections Australia, CSIRO, Canberra, Australia

ABSTRACT

Advances in sequencing technology and phylogenetics have revolutionised avian biology by providing an evolutionary framework for studying natural groupings. In the parrots (Psittaciformes), DNA-based studies have led to a reclassification of clades, yet substantial gaps remain in the data gleaned from genetic information. Here we provide an overview of published genetic data of parrots, characterise sampling depth across the phylogeny, and evaluate support for existing systematic treatments. We inferred a concatenated tree with 307 species from a 30-gene supermatrix. We recovered well-supported relationships among recently proposed clades. Taxonomic groups were more stable towards the base of the tree and increased sampling will be required to clarify relationships at the tips, particularly below the generic level. Only a third of species have been sampled intraspecifically in population genetic or phylogeographic surveys. Intraspecific sampling has not been geographically or phylogenetically even across Psittaciformes, especially poor in the cockatoos, Southeast Asia, and parts of Australo-Papua. Threatened species are poorly sampled in the Neotropics. We highlight where effort should be focused to improve sampling based on geography and conservation status. In sum, phylogenetic relationships among the major parrot clades are robust, but relationships within and between genera and species provide opportunities for future investigations.

ARTICLE HISTORY
Received 27 April 2017
Accepted 21 September 2017

KEYWORDS
Psittaciformes; supermatrix; biodiversity; phylogeography; conservation genetics; IUCN Red List

Downloaded by [73.29.2.54] at 17:13 13 November 2017

Introduction

Discerning higher-level relationships within the Psittaciformes (parrots) has long been a challenge to avian systematists. Morphological data, especially from comparative anatomy, were central to key early works (e.g. Garrod 1874; Thompson 1899 on carotid arteries and cranial osteology, respectively; see Holyoak 1973; Smith 1975; Sibley and Ahlquist 1990; Schodde and Mason 1997 for later reviews). The advent of molecular data, first with distance-based hybridisation studies (e.g. Sibley and Ahlquist 1990), then allozymes (e.g. Christidis *et al.* 1991), and, later, DNA sequences along with more modern phylogenetic methods (e.g. de Kloet and de Kloet 2005; Wright *et al.* 2008), brought substantial change and clarity to higher-level phylogenetic relationships within Psittaciformes. This momentum in resolving higher-level relationships also helped to revitalise morphological and palaeontological analyses (e.g. Mayr 2010, 2015; Boles 2017).

By 2012, what had become a plethora of phylogenetic studies using DNA sequence data provided the basis for a major reclassification of higher-level parrot taxa (Joseph *et al.* 2012; Schodde *et al.* 2013). These classifications proposed three superfamilies, six families, 11 subfamilies, and 12–14 tribes, differing from previous work that recognised six subfamilies in either one (Sibley and Ahlquist 1990) or three families (Forshaw 1989). Molecular phylogenetic studies have consistently recovered three major clades recognised as superfamilies by Joseph *et al.* (2012): Strigopoidea (the New Zealand kea, kakapo, and kaka), Cacatuoidea (the cockatoos and cockatiel), and Psittacoidea (all other parrots) (de Kloet and de Kloet 2005; Tokita *et al.* 2007; Wright *et al.* 2008; Schweizer *et al.* 2010, 2011; Joseph *et al.* 2011). Within each of these major clades, recognition of families, subfamilies, and tribes should reflect the monophyly and arrangement of taxa into natural evolutionary groupings recovered from phylogenetic analyses.

The data used to estimate phylogenetic relationships within the parrot clade have varied substantially in terms of taxonomic sampling and genetic markers employed. Phylogenetic relationships among major

CONTACT Kaiya L. Provost kprovost@amnh.org

This article was originally published with errors. This version has been corrected. Please see Corrigendum (https://doi.org/10.1080/01584197.2018.1404426).
Supplemental data for this article can be accessed here.

© 2017 BirdLife Australia

Downloaded by [73.29.2.54] at 17:13 13 November 2017

groups have typically been estimated either by sampling a diverse array of species at higher taxonomic levels (e.g. Wright *et al.* 2008; Schweizer *et al.* 2011; Schirtzinger *et al.* 2012), or by sampling within individual genera or species (e.g. Ribas *et al.* 2009; White *et al.* 2011; Smith *et al.* 2013; Schweizer *et al.* 2015). The data have also varied in terms of the number and source of genetic markers (e.g. nuclear vs. mitochondrial DNA). Finally, several studies have compiled existing data to produce more comprehensive phylogenetic hypotheses for the entire parrot clade. One such study assembled a phylogeny of all bird species that included 354 parrot species, building clade-specific trees using available DNA sequences, grafting the trees to a backbone phylogeny, and placing data-deficient species onto the tree using birth–death simulations (Jetz *et al.* 2012). Another focused on all birds for which genetic data were available and used a supermatrix approach (Burleigh *et al.* 2015). Data from different sources were combined into a single matrix for analysis that included 299 parrot species and 29 loci (Burleigh *et al.* 2015). Despite these efforts, the stability of taxonomic groups recovered within the parrot clade remains untested.

A broad aim of this paper is to assess the robustness of the current phylogenetic hypothesis for parrots. A robust parrot phylogeny would have widespread implications for basic and applied research on this order of birds. Such a phylogeny would provide the foundation for understanding the extent, origin, and mode of evolution of parrot diversity and a framework for comparison with other clades. Parrots exhibit advanced cognitive (e.g. problem-solving: Pepperberg 2009), communicative (e.g. learned contact calls: Berg *et al.* 2012) and behavioural abilities (e.g. tool use: Auersperg *et al.* 2012, 2016), and so understanding how these traits evolved within Psittaciformes and relative to other behaviourally advanced groups (e.g. Passeriformes or Primates) is of great interest (Pfenning *et al.* 2014). Moreover, metrics characterising phylogenetic diversity and evolutionary distinctiveness can be summarised to identify biodiversity hotspots that are independent of areas identified using species richness (e.g. Jetz *et al.* 2014; Voskamp *et al.* 2017). For conservation purposes, genetic metrics can be further expanded by understanding the phylogeographic structure, past and present gene flow, historical demography, and genetic diversity within species (e.g. Rocha *et al.* 2014). Parrots harbour more threatened and endangered species than any other avian order (Forshaw 2011, 2017; Toft and Wright 2015). Researchers and species managers will have to utilise the array of existing tools to meet the tremendous challenge of conserving parrot diversity.

Here, we present an overview of how DNA sequence-based data, derived primarily from single-locus sequencing technologies dominant in the last 30 years (i.e. Sanger sequencing), inform phylogenetic relationships within Psittaciformes. This phylogenetic review will provide a basis for later analyses derived from next-generation sequencing tools and genome-wide datasets. By examining the extent of intraspecific genetic studies across the clade, we also provide an overview of the depth and extent of genetic sampling across parrot species. Given the expected high heterogeneity in data sources and missing characters, we use a supermatrix (e.g. Burleigh *et al.* 2015) comprising 30 genes and 307 parrot species to estimate a phylogeny and evaluate support for currently recognised clades (superfamilies to tribes; see Joseph *et al.* 2012; Schodde *et al.* 2013). We also assess the robustness of these classifications to subsampling the data to fewer numbers of loci and species. We visualised the density of species-level sampling by plotting the proportion of species currently sampled for phylogenetic and intraspecific genetic studies on maps showing geographical distributions. Collectively, this suite of analyses provides insight into the stability of phylogenetic relationships, sampling gaps, and areas requiring the most attention for future research.

Materials and methods

We batch downloaded and processed all published DNA sequence data for parrots. We wrote a pipeline in Python v. 3.5.2 to extract, process, and align DNA sequence data from GenBank. Source publications from which these data were derived provide details about how the DNA sequences were generated and originally analysed (see Supplementary TableS 1). A brief summary of the pipeline follows (for more details, see Supplementary Information). GenBank records for all parrots were downloaded in March 2017 (GenBank Release 218) by downloading all records associated with each genus using Biopython 1.68 (Cock *et al.* 2009). We chose to download by genus instead of by order as we discovered that such a large query failed to include all sequences. Individual loci within these GenBank files were parsed out, and any regions that were not of interest (i.e. non-coding regions) were removed from the analysis (e.g. retrotransposons, microsatellites, tRNA, etc.). To account for variation in user-specified locus names, we combined suspected orthologs with different spellings (e.g. 'cytochrome b'

Downloaded by [73.29.2.54] at 17:13 13 November 2017

vs 'cytb'). To be retained in our analysis, a locus must have been sampled in at least four species. Any loci that did not meet this criterion were deemed phylogenetically uninformative and removed. We also removed loci that were less than 100 base pairs (bp) in length. For the remaining loci, we chose one individual of each species per locus, either the individual with the highest number of bp, or, in case of a tie, arbitrarily.

For simplicity, we set up analyses mostly following the species-level taxonomy of Clements (*et al.* 2016; hereafter 'Clements'). We chose to use the Clements taxonomy as it had the most recent updates and thus presumably reflects recent revisions in parrot systematics. However, we followed Podsiadlowski *et al.* (2017) in retaining *Coracopsis* for the Vasa and Black Parrots *C. vasa* and *C. niger*, respectively, and we used the sequences of the extinct Mascarene Parrot *Mascarinus mascarin* in Podsiadlowski *et al.* (2017), not the contaminated sequence from Kundu *et al.* (2012). Synonyms and taxonomic changes were accounted for during this process (e.g. *Neopsephotus bourkii*). We also followed generic changes within Loriini proposed by Schweizer *et al.* (2015). Lastly, we chose to use *Psephotellus* instead of *Psephotus* for *P. varius*, *P. dissimilis*, *P. pulcherrimus*, and *P. chrysopterygius* because these four species are shown to be monophyletic to the exclusion of *P. haematonotus* in multiple phylogenetic studies (see Joseph *et al.* 2011; Schweizer *et al.* 2012). We selected four outgroup taxa that are representatives from clades closely related to parrots (*Falco mexicanus*, *Acanthisitta chloris*, *Tyrannus tyrannus*, and *Passer montanus*; see Hackett *et al.* 2008). Nucleotide sequences were checked for reverse complementarity and paralogy before being aligned using Muscle (Edgar 2004) on default settings. We removed from the dataset genes that had large disparities in the number of bp per species (e.g. the gene TLR7, in which three species had fewer than 900 bp and one species (*Nestor notabilis*) had over 3000). Retaining these genes led to misplaced taxa in downstream analyses, presumably due to large amounts of missing data. Sequences were then concatenated into one locus representing all genes per species. If a species was missing a gene, that gene was coded entirely as missing sequence. We partitioned the alignment by gene using PartitionFinder 2.1.1 (Lanfear *et al.* 2016) to determine the best-fitting substitution model for each gene. We used the rclusterf algorithm to choose between models in the GTR family (Lanfear *et al.* 2014; Stamatakis 2014).

RAxML (Stamatakis 2014), via the portal CIPRES (Miller *et al.* 2010), was used to perform a maximum likelihood search with 100 rapid bootstraps under a GTR-Γ model. We subsampled the partitioned gene alignment post hoc to investigate the effect of gene coverage on higher-level phylogenetic relationships (superfamilies through tribes). We generated subsets of species where each species in the subset met a threshold number of genes. The threshold ranged from all species having at least one gene (the full dataset) through to species having at least 15 genes, with progressively fewer species being retained as the threshold number of genes increased. We independently estimated a tree in RAxML for each of the 14 subsampled alignments using the same settings as above. Then, we assessed stability of higher-level relationships by comparing how support values for clades changed across the trees.

We surveyed the literature for studies that contained intraspecific genetic data (≥ three samples) for parrot species. Intraspecific studies generally focus on phylogeny, phylogeography, conservation genetics, or some combination. Using ggtree (Yu *et al.* 2016), we plotted this information as a binary character on the tree obtained from Jetz *et al.* (2012), as well as the number of subspecies under Clements and IUCN conservation status. Jetz *et al.* (2012) includes representatives of all species within Psittaciformes, so we examined the phylogenetic distribution of unsampled taxa on this tree. This figure illustrates clades where species-level diversity may be underestimated. Subspecies can be poor proxies of evolutionary units (Zink 2004; Joseph and Omland 2009) or represent clinal variation (Remsen 2005), but taxa with high numbers of subspecies not yet assessed with intraspecific genetic data are excellent candidates for further study.

Finally, we produced maps to visualise spatial biases in genetic, within-species, and threatened species sampling. We obtained range maps for all parrot species as shapefiles from BirdLife International (BirdLife International and NatureServe 2015); seven species recognised by Clements are not present in these shapefiles due to recent taxonomic revisions (*Cyanoramphus cookii*, *C. hochstetteri*, *C. saisseti*, *Northiella narethae*, *Loriculus camiguinensis*, *Psittacara maugei*, *P. strenuus*). We excluded 15 extinct species from the range maps (see Fuller 2001; Steadman 2006; Hume 2007) (*Nestor productus*, *Mascarinus mascarin*, *Eclectus infectus*, *Psittacula wardi*, *P. exsul*, *P. bensoni*, *L. mauritianus*, *Necropsittacus rodericanus*, *Cyanoramphus ulietanus*, *C. zealandicus*, *Amazona martinicana*, *A. violacea*, *Conuropsis carolinensis*, *Ara tricolor*, *Psittacara labati*). We used a custom R v. 3.3.1 (R Development Core Team 2008) and Python v. 3.5.2 pipeline to process shapefiles (for more details, see Supplementary Information). Briefly, the script converted the

Downloaded by [73.29.2.54] at 17:13 13 November 2017

shapefiles to raster files, then summed the number of species of interest (with respect to genetic, intraspecific, and threatened species sampling) present in each cell and calculated the proportion of species that were phylogenetically surveyed in each cell. Raster files had a 0.1 × 0.1 lat–long resolution. While BirdLife shapefiles are somewhat inaccurate at that fine-scale resolution (Hurlbert and Jetz 2007), some parrot taxa are extremely range-restricted, particularly on islands, and using a coarser resolution excludes them from maps. Therefore, we chose to use a finer resolution to retain these highly endemic species.

Results

As of March 2017, there were five published whole genomes of parrot species in GenBank: *Nestor notabilis*, *Amazona vittata*, *A. aestiva*, *Ara macao*, and *Melopsittacus undulatus* (Oleksyk *et al.* 2012; Seabury *et al.* 2013; Ganapathy *et al.* 2014; Zhang *et al.* 2014; Teixeira *et al.* 2015). The genomes of *M. undulatus* and *N. notabilis* are annotated. Because of the disparity of genetic data available for these five species, we excluded sequence data from these genomes from our data extraction pipeline; predicted genes from these genomes have their own unique GenBank numbers and were included, however. There were additionally 90 mitochondrial genomes from 49 species and these were included. In total, we downloaded 43 558 DNA sequences from parrot taxa, of which 5472 were tagged as mitochondrial. This represented 1215 uniquely named mitochondrial loci and 35 914 uniquely named nuclear loci for a total of 37 129 unique names. Most of these uniquely named entries were duplicates (53), anonymous loci (24 403), microsatellites (391), non-coding regions (i.e. unnamed introns, promoters, retrotransposons; 14), or tRNA sequences (98); these data were excluded before further processing. This left 221 differentially named mitochondrial and 12 170 putative nuclear loci. Most of the loci (12 100, 97.6%) were excluded because that particular locus was not present in enough ingroup species (at least four). After filtering (see Materials and methods), we retained 2386 unique GenBank accession numbers. We next constructed a supermatrix of 30 genes (12 mitochondrial, 18 nuclear) representing 88 genera and 307 parrot species, plus the four outgroups (Figure 1). That supermatrix comprised 1661 of the original 2386 accession numbers and includes all currently recognised genera except monotypic *Ognorhynchus* (Figure 2). The final alignment was 83 607 bp long, including indels and missing data. Missing data for each species averaged 84.7% (median 85.9%, range 21.1–98.9%; see Supplementary Figure S3). The average number of loci per species was 5.3 (median 5, range 1–22), and the average number of species per locus was 55.4 (median 31.5, range 4–265) (Figure 2).

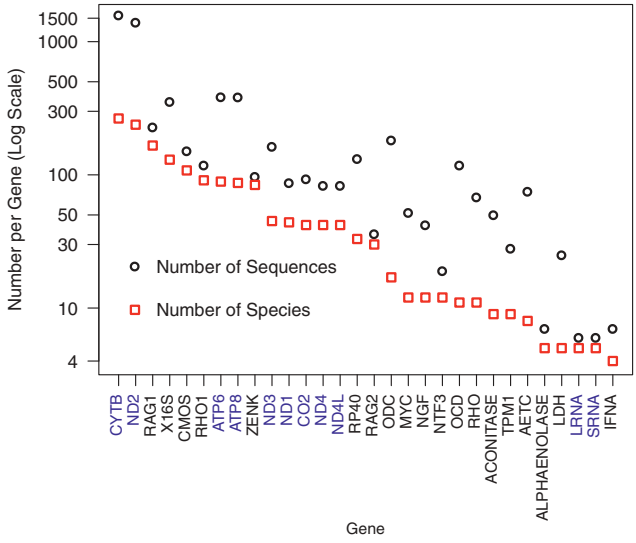

Figure 1. Distribution of number of parrot sequences per locus (black open circle) and species (red open square). The *x*-axis shows locus names with mitochondrial and nuclear DNA loci coloured in blue and black, respectively. The *y*-axis shows the number of sequences per locus (log scale). For reference to color, please see online publication.

Phylogenetic relationships and clade stability

We recovered strongly supported relationships (bootstraps BS = 100%; hereafter, for brevity, given simply as percentages; see Supplementary Figure S1 and Supplementary Figure S2 for phylogeny with support values) showing that Strigopoidea was sister to Cacatuoidea and Psittacoidea (Figure 3). Monophyly of each superfamily was robust (100% for all); however, at the 14-gene cut-off, no Cacatuoidea species met our threshold, and Strigopoidea was reduced to a single species. Here, we highlight sections of the tree that are of particular interest.

Strigopoidea

Strigopoidea (number of species sampled/total number of species, 3/4) comprised two families of New Zealand parrots: monospecific Strigopidae (*Strigops habroptilus*, 1/1) and Nestoridae (*Nestor*, 2/3). *Strigops habroptilus* was sister to *Nestor meridionalis* and *N. notabilis* (100%) (Figure 3).

Cacatuoidea

Cacatuoidea (20/21), the superfamily of the cockatoos and allies, comprises a single family, Cacatuidae. Cacatuidae contains three main groups, which

Downloaded by [73.29.2.54] at 17:13 13 November 2017

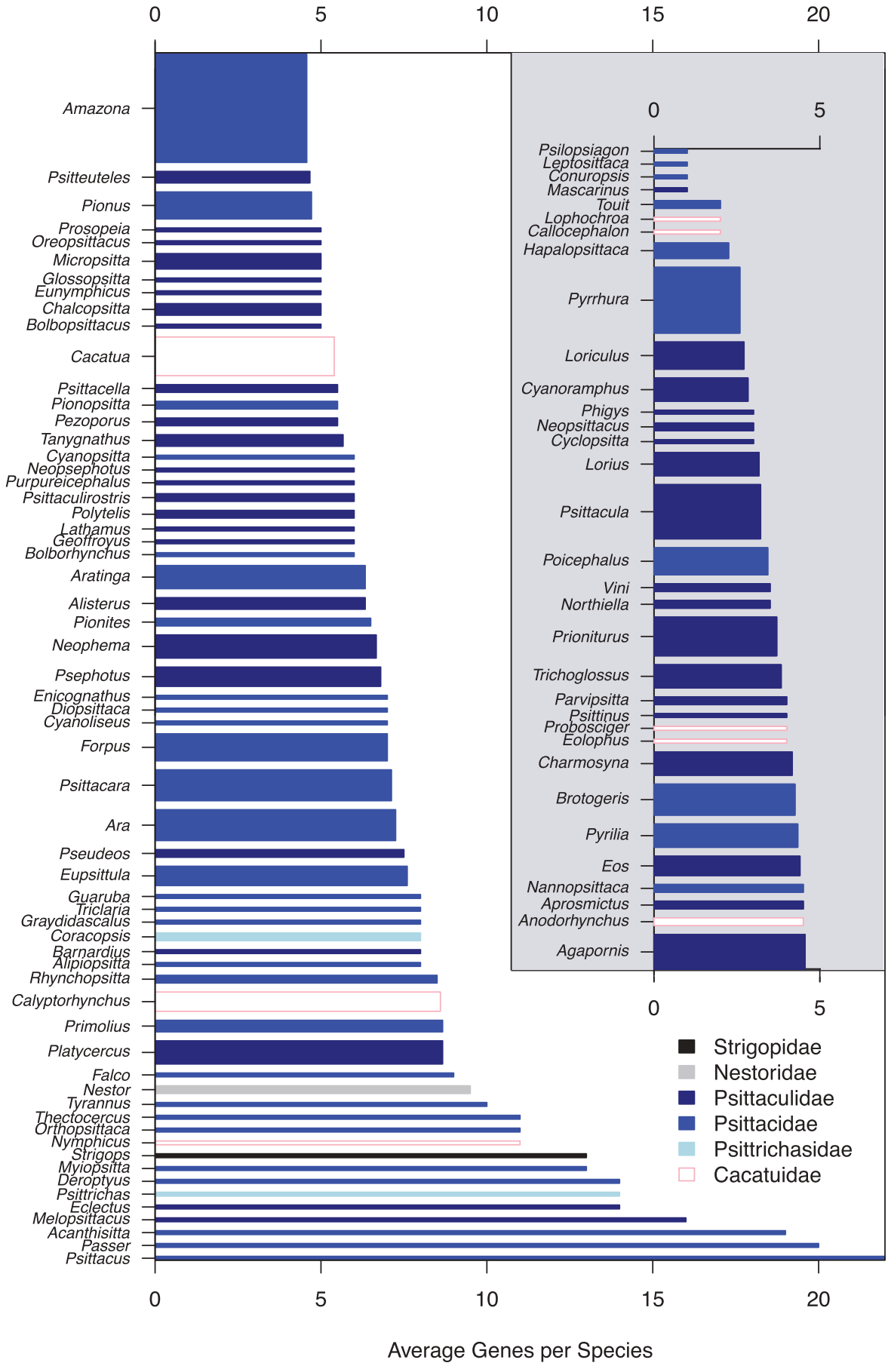

Figure 2. Distribution of genetic sampling of parrots and outgroups per species in each genus. The *y*-axis shows genera ordered by number of genes and coloured by their respective family; the height of the bar is the number of species sampled. The *x*-axis shows the average number of genes per species. The inset displays the 33 genera with the lowest number of species sampled, while the outset displays the remaining 61 genera. For reference to color, please see online publication.

Downloaded by [73.29.2.54] at 17:13 13 November 2017

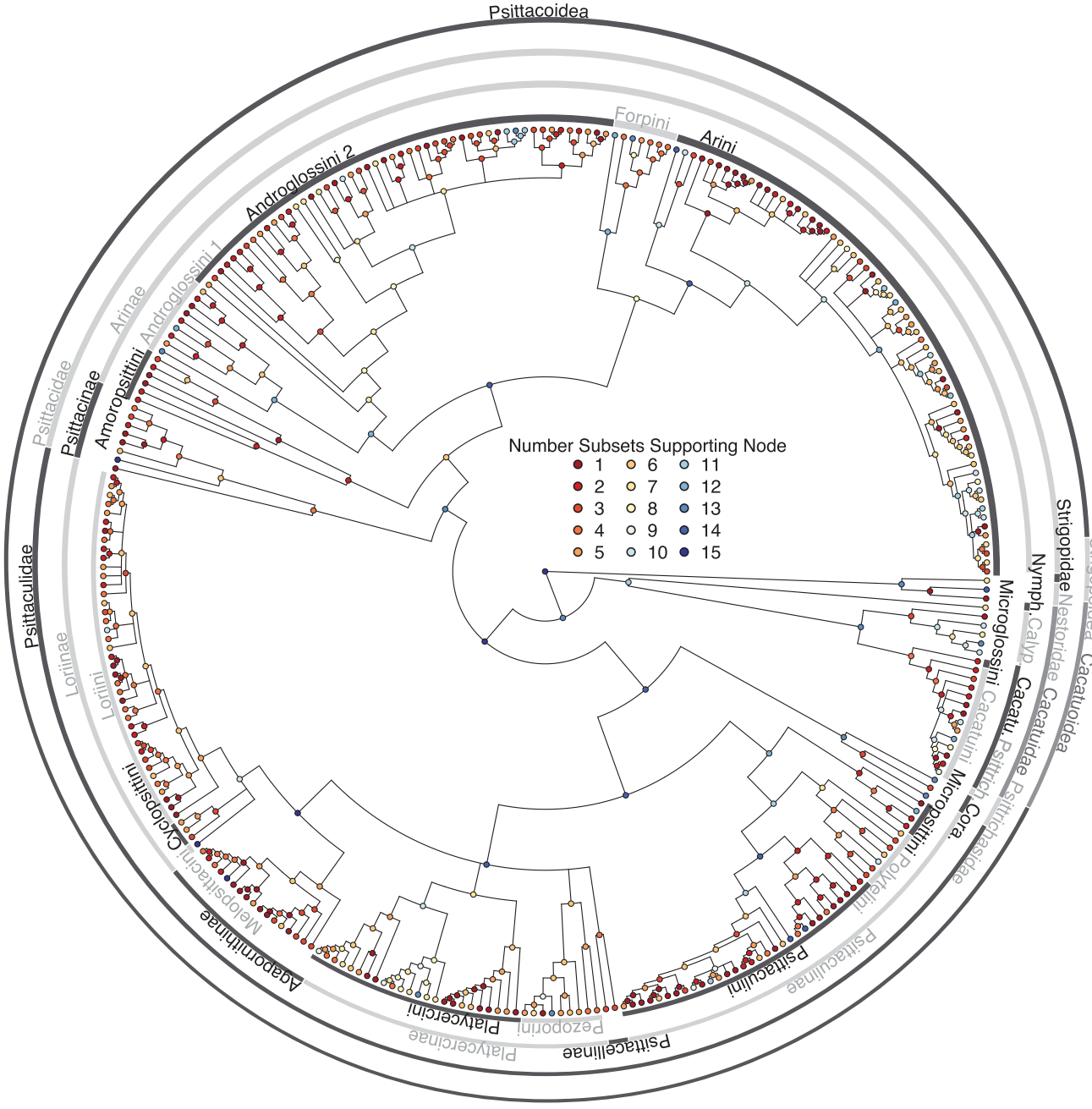

Figure 3. Phylogeny based on full dataset showing threshold values for subsetted data. Only species with enough genes to meet the threshold were retained in each subset. Colours on nodes indicate the strictest subset in which the node still exists, with 15 (dark blue) corresponding to the most reduced 15-gene subset and therefore all subsets. Warmer-coloured nodes denote a more rapid loss of the node. Greyscale rings illustrate, from outermost to innermost, superfamilies, families, subfamilies, and tribes. Changes in grey shades within rings indicate different clades. Text abutting the rings denotes clade names and matches the associated ring shade. Abbreviations indicate the following subfamilies: 'Nymph.' for Nymphicinae, 'Calyp.' for Calyptorhynchinae, 'Cacatu.' for Cacatuinae, 'Psittrich.' for Psittrichasinae, and 'Cora.' for Coracopseinae. For individual species names, see Supplementary Figure S4.

correspond to the subfamilies Nymphicinae, Calyptorhynchinae, and Cacatuinae. Nymphicinae, comprising only *Nymphicus hollandicus*, was sister to the rest of the family (91%). Cacatuinae (14/15) and Calyptorhynchinae were each monophyletic (98% and 93%, respectively). Tribes Microglossini (1/1) and Cacatuini (13/14) were sisters within Cacatuinae (97%) (Figure 3).

Psittacoidea

Psittacoidea (284/347) is represented by the families Psittaculidae (Asian parrots, Australian parrots, and

Downloaded by [73.29.2.54] at 17:13 13 November 2017

lories), Psittacidae (New World and African parrots), and Psittrichasidae (Indian Ocean *Coracopsis* and New Guinean *Psittrichas*). Monophyly of Psittrichasidae and Psittaculidae was robust (99% and 97%, respectively) while that of Psittacidae was weaker (72%) and did not stabilise through the subsets, even becoming paraphyletic in the 14-gene subset. Psittrichasidae was sister to Psittaculidae with weak support (79%; Figure 3).

Psittacidae. Psittacidae (141/168) was present in all subsets, though it was represented by a single species at the 14-gene cut-off. This family included two sister subfamilies (100%), Psittacinae and Arinae. Psittacinae is monophyletic (97%) and contains *Psittacus* (1/1) and *Poicephalus* (6/9). Notably, placement of *Psittacus erithacus* within *Poicephalus* rendered the latter paraphyletic. *Psittacus erithacus*, however, has data from 22 genes, whereas *Poicephalus* species have 1–6 genes each.

Arinae was monophyletic in the full tree (100%) and remains so with full support until it drops out at the 15-gene cut-off (Figure 3). We found five highly supported (100% for all) monophyletic groups representing Arini, Amoropsittini, Forpini, and two clades of Androglossini. In Amoropsittini, we found *Bolborhynchus lineola* nested within *Nannopsittaca* (2/2) with high support (97%). This was supported through all subsets until both genera dropped out at the 7-gene subset. The two well-supported clades within Androglossini consisted of: Clade 1: *Myiopsitta monachus* (1/1) and monophyletic *Brotogeris* (7/8, 100%), and Clade 2: *Pionopsitta pileata*, *Triclaria malachitacea*, *Hapalopsittaca* (4/4), *Pyrilia* (7/7), *Pionus* (7/7), *Graydidascalus brachyurus*, *Alipiopsitta xanthops*, and the species-rich genus *Amazona* (28/30). The non-monotypic genera are monophyletic (100% for all). Support for monophyletic Androglossini was weak (84%) and de-resolves at the 13-gene cut-off.

Within Arini all non-monotypic genera are monophyletic with high support (>93% for all) with the exception of *Aratinga*; the extinct *Conuropsis carolinensis* falls within *Aratinga* (69%), and the clade containing these two genera has moderate support (89%). There are three within-tribe clades with 100% support: Clade 1: *Pionites* (2/2) and *Deroptyus accipitrinus*, Clade 2: *Pyrrhura* (21/23), and Clade 3: the remaining genera. Clade 2 and Clade 3 are sister (100%).

Psittrichasidae. Psittrichasidae (3/4) includes two genera and two subfamilies, *Psittrichas fulgidus* and *Coracopsis* (2/3) in Psittrichasinae and Coracopseinae, respectively. *Psittrichas fulgidus* was sister to *Coracopsis* (100%). No species from this family was retained in the 15-gene subset.

Psittaculidae. Psittaculidae (138/175) had six monophyletic groups corresponding to Psittaculinae (100%), Psittacellinae (100%), Pezoporini (99%), Platycercini (100%), Agapornithinae (100%), and Loriinae (97%). Notably, Platycercinae (Pezoporini, Platycercini) was not monophyletic, perhaps because of a large disparity in genes per species (range 1–14) in that subfamily. There are three tribes within Psittaculinae: Micropsittini was sister to Polytelini and Psittaculini (99%). Within Polytelini, *Polytelis* (2/3) was not monophyletic relative to *Alisterus* (3/3, 100%) and *Aprosmictus* (2/2, 100%), though these relationships are nearly unresolved (52%). Within Psittaculini, many relationships were also poorly resolved. *Tanygnathus* and the extinct *Mascarinus mascarin* rendered *Psittacula* paraphyletic. Within Platycercini, both *Purpureicephalus* (1/1) and *Northiella* (2/2) are embedded within *Psephotus* (5/5) with weak support (63%). Within Loriinae, *Charmosyna* (6/14) is paraphyletic, with *Phigys* (1/1) and *Vini* (2/5) embedded within it. Within the remaining taxa there are many unresolved or weak relationships between *Psittueteles* (3/3), *Glossopsitta* (1/1), *Chalcopsitta* (3/3), *Pseudeos* (2/2), *Lorius* (6/6), *Trichoglossus* (6/7), and *Parvipsitta* (2/2). *Psitteuteles* and *Trichoglossus* are paraphyletic.

Visualisation of sampling

The species richness maps show the known pattern of Neotropical and Australasian regions harbouring higher diversity than the Afrotropical region (Figure 4(A)). Overall, we found no qualitative spatial biases at the continental scale in species-level sampling (Figure 4(B)). The density and proportion of this diversity that was represented by published genetic data was largely uniform, with few exceptions being driven predominantly by species-poor areas. The pattern was more complex for species having intraspecific genetic sampling. Only within the less species-rich areas of New Zealand and Africa was there a high density of species sampled intraspecifically (Figure 4(C)). Areas with a low proportion of species sampled with intraspecific data were not just in species-poor areas; regions such as New Guinea with high diversity have also been largely unsampled at this level (Figure 4(C)).

Species that have not been studied at population genetics or phylogeographic levels are of particular importance for future research and conservation. We thus examined densities of species that are simultaneously not classified as least concern by IUCN and lack within-species genetic

Downloaded by [73.29.2.54] at 17:13 13 November 2017

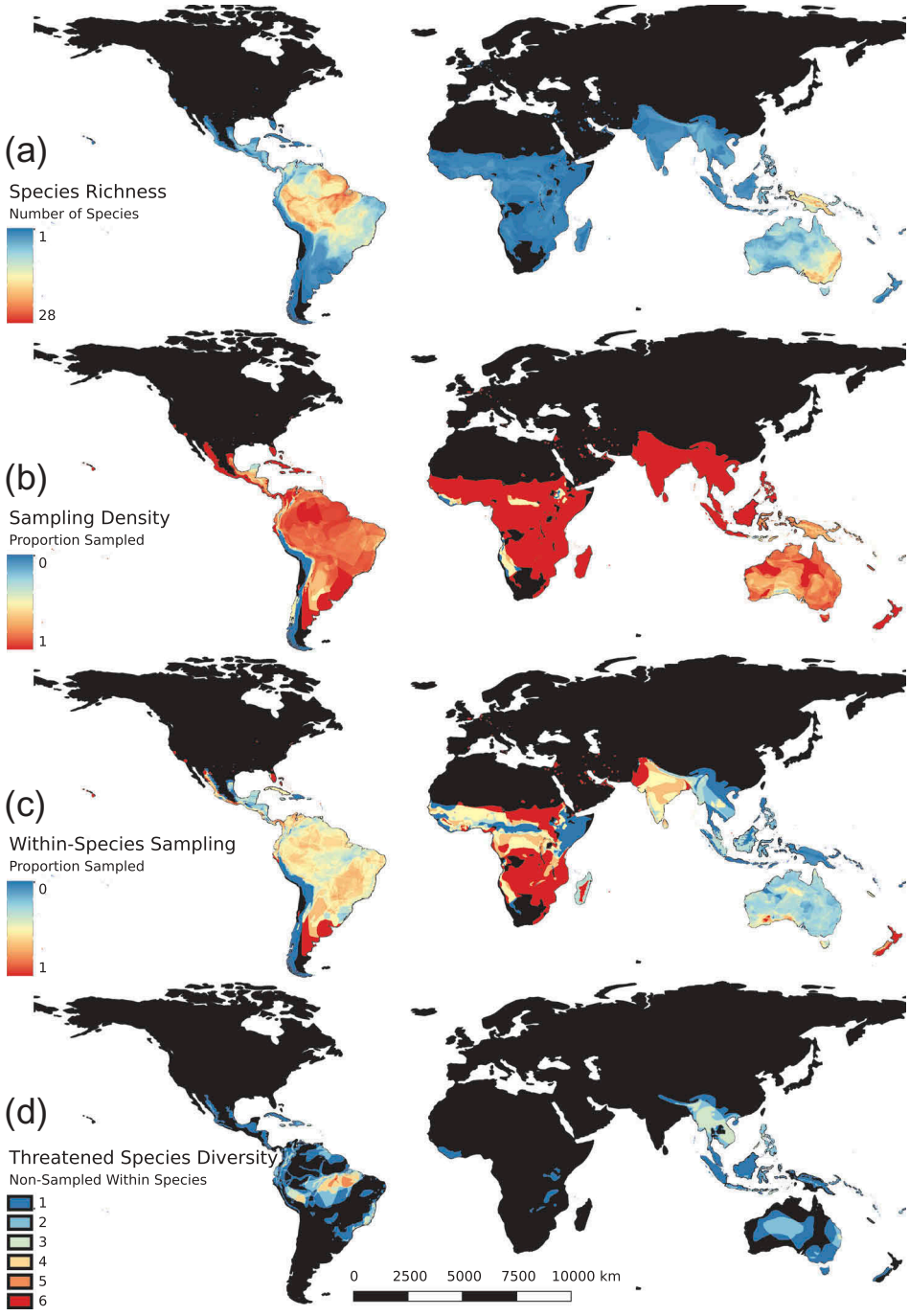

Figure 4. Spatial distributions of parrot species, sampling diversity, and threat level. (A) Species richness map (top panel); (B) proportion of total species sampled with genetic data (second panel); (C) proportion of species sampled with within-species genetic sampling (third panel); and (D) number of near-threatened and threatened species (excluding IUCN status 'least concern') that do not have within-species sampling. Warmer colours indicate a higher number (A, D) or proportion (B, C) of species. Greenland is omitted for visibility. For reference to color, please see online publication.

sampling (Figure 4(D)). For this subset of species, there are relatively few regions of overlap – most of Africa and the Indian subcontinent have no representatives (Figure 4 (D)). The highest density of this subset falls within the middle Amazon, with moderate densities in Southeast Asia, Indonesia, and Eastern Australia. We found that species that were present on GenBank were more likely to be least concern (57.1% vs. 42.3%) than species that were absent (Figure 5). Subspecies number varies widely across taxa (0–16), and taxa with subspecies are more likely to be

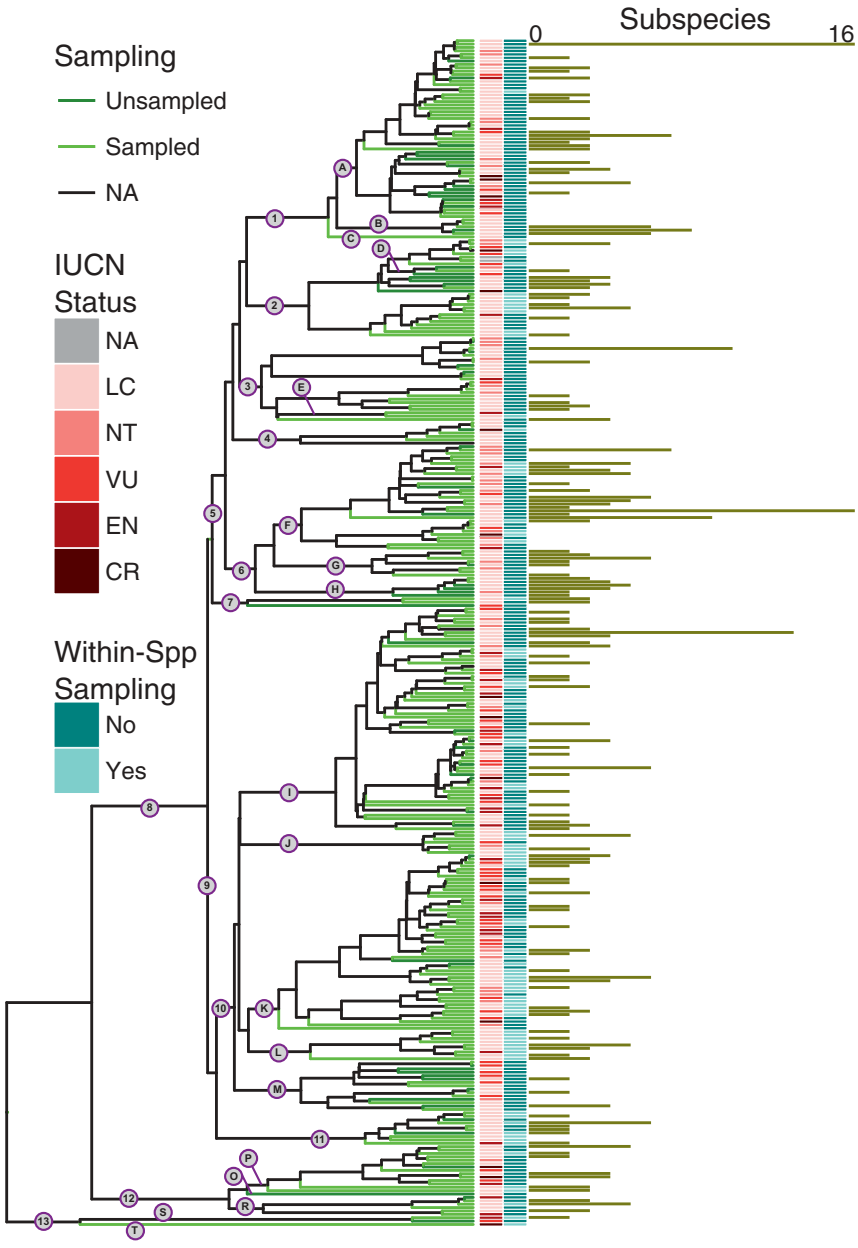

Figure 5. All-parrot tree (from Jetz et al. 2012) with sampled and unsampled species (forest green shades), IUCN Red List status (red shades), intraspecific sampling (blue shades), and number of subspecies (olive green shades). Tip branch colours on the tree indicate whether a species was sampled (bright forest green) or unsampled (dark forest green) in our supermatrix. IUCN status and intraspecific sampling are shown next to the tips. Darker shades of red correspond to more threatened IUCN status. Intraspecifically sampled species are bright blue, whereas non-sampled species are dark blue. Dark olive green beside the tips illustrates the number of subspecies present within a taxon under Clements et al. (2016), ranging from zero subspecies (no bar) to 16 (longest bar). Circles on edges (or pointing to edges, e.g . letters D, E, O, P) denote taxon names, with numbers indicating larger clades such as superfamilies and families, and letters indicating smaller clades such as tribes and genera. Numbers denote the following: (1) Loriinae, (2) Platycercinae (Platycercini), (3) Agapornithinae, (4) Platycercinae (Pezoporini), (5) Psittaculidae, (6) Psittaculinae, (7) Psittrichasidae, (8) Psittacoidea, (9) Psittacidae, (10) Arinae, (11) Psittacinae, (12) Cacatuoidea, (13) Strigopoidea. Letters denote the following: (A) Loriini, (B) Cyclopsittini, (C) Melopsittacus, (D) Psittacellinae, (E) Pezoporus (Pezoporini), (F) Psittaculini, (G) Polytelini, (H) Micropsitta, (I) Arini, (J) Forpus, (K) Androglossini (Amazona clade), (L) Androglossini (Brotogeris clade), (M) Amoropsittini, (O) Nymphicus, (P) Cacatuinae, (R) Calyptorhynchus, (S) Nestor, (T) Strigops. For reference to color, please see online publication.

sampled on GenBank (94.2% vs. 77.0%), have within-species sampling (35.5% vs. 20.3%), and be of least concern (81.9% vs. 40.1%) (Figure 5).

Discussion

We set out to synthesise all available molecular data on parrots to establish a clear roadmap for future areas of

Downloaded by [73.29.2.54] at 17:13 13 November 2017

Downloaded by [73.29.2.54] at 17:13 13 November 2017

study that will require greater resolution from genomic analyses, as well as to highlight areas for intraspecific sampling. Genetic sampling across parrots was diverse in the depth of coverage across species and loci, but a stable backbone to the phylogeny has emerged. The Linnaean classification for parrots (Joseph *et al.* 2012; Schodde *et al.* 2013) from superfamilies to tribes was largely robust to reduced species and genetic sampling. Our study further highlights clear areas where future molecular research should focus. Particular attention is warranted in resolving relationships within tribes and genera, which will require complete species-level sampling. We found that there was no clear spatial bias in sampling of species (e.g. Neotropical vs. Australasian species) and that undersampled areas largely represent species-poor regions. At finer scales, genetic sampling within species was poor to non-existent for most areas. The paucity of phylogeographic studies is a particular issue in the Amazon Basin, northern Andes, and Southeast Asia, where multiple unstudied species are of conservation concern. Sampling gaps at the tips of the parrot tree must be filled to fully harness the power of genetic resources for comparative biology and conservation in this group.

Comparison to existing phylogenies

Comparing our results with earlier studies, especially large-scale bird phylogenies (Jetz *et al.* 2012; Burleigh *et al.* 2015), reaffirms that the relationships at the base of the tree are more stable than those among clades towards the tips. The relationships between subfamilies and tribes of Cacatuidae here agree with Burleigh *et al.* (2015), but relationships among Nymphicinae, Calyptorhynchinae, and Cacatuinae differ in the Jetz *et al.* (2012) tree. Within Psittacidae, relationships among the clades of Arinae are extremely variable. In contrast to our results, Jetz *et al.* (2012) and Burleigh *et al.* (2015) both have completely different sister relationships among the four tribes. Relationships within Psittaculidae are the least consistent of all parrot families. All topologies agree that Psittaculinae is sister to the rest of the family, and none of the phylogenies recover a monophyletic Platycercinae. The apparent and possibly artefactual non-monophyly of Platycercinae centres on clarification of relationships with Agapornithinae, which appears to be sensitive to the dataset being used. Joseph *et al.* (2011) recovered a similar result with 48 taxa and five loci, but when they used 27 taxa and eight loci, Platycercinae and Agapornithinae were not closely related. Similar debate centres on whether *Psittacella* is close to the platycercines (Christidis *et al.* 1991; Schweizer et al. 2012) or at the base of a large radiation in the Australo-Papuan region (Joseph *et al.* 2011). The Jetz *et al.* (2012) tree indicates considerable paraphyly: Psittacellinae is embedded within Platycercini whereas *Pezoporus* (Pezoporini) is embedded within Agapornithinae. In contrast, we found that all of these groups are monophyletic. Relationships between the clades of Psittaculidae are also variable. As with our phylogeny, Burleigh *et al.* (2015) shows sister relationships between Loriinae and Agapornithinae. Jetz *et al.* (2012), instead, has part of Pezoporini sister to a trichotomy of the remaining clades. We point to these discrepancies as a focus for clarification by genomic work.

Our analysis quantifies support for family-group taxa (tribe to superfamily) in parrots. Based on available data, these classifications (Joseph *et al.* 2012; Schodde *et al.* 2013) are generally robust across our subsampling thresholds. However, our subsampling itself did not provide an independent assessment of phylogeny (e.g. Reddy *et al.* 2017), because the same loci were present in the reduced species datasets. Although we were able to provide comparisons to relationships among large-scale avian phylogenies, many of the data used to produce the three phylogenies are the same. In our alignments, loci from the mitochondrial genome were overrepresented and the depth of sampling was also uneven across species. This uneven sampling of loci has presumably biased relationships and rendered groups paraphyletic (e.g. *Psittacus* with *Poicephalus*, and generic relationships within Platycercinae). Comparisons of alternative avian phylogenies show that there is still considerable disagreement in relationships among and within groups (Brown *et al.* 2017). Future studies employing phylogenomic approaches that are more evenly sampled with respect to loci and species will provide independent evidence for the support of current groups.

Implications for generic limits

We discuss three categories of cases where more, rather than fewer, genera are needed to describe phylogenetic hypotheses in parrots, and for which our analyses agree. First are cases in which the relevant species are now confidently understood not to be each other's closest relatives. Three examples follow. Australian *Psephotus* is now monotypic having only the Red-rumped Parrot *Ps. haematonotus*; other species placed in it are now necessarily in *Northiella* and *Psephotellus* (see also Schodde and Mason 1997; Joseph *et al.* 2011; Schweizer *et al.* 2012; Dickinson and Remsen 2013).

Downloaded by [73.29.2.54] at 17:13 13 November 2017

Similarly, *Glossopsitta* now contains only the Musk Lorikeet *G. concinna*; its other two species necessarily are moved to *Parvipsitta* (Schweizer *et al.* 2015). In the Neotropics, the Yellow-faced Amazon had long been known as *Amazona xanthops*. Being sister to similarly monotypic *Graydidasculus*, it necessarily must be moved out of *Amazona* and is now recognised in monotypic *Alipiopsitta*.

Second are genera that have been dismantled in recent literature because of the depth of structure in various character sets within the groups. These taxa are each other's closest relatives, yet are divergent from each other and readily diagnosable groupings can be discerned within them. For example, *Aratinga* and *Ara* in the Neotropics (Kirchman *et al.* 2012; Remsen *et al.* 2013; see also Whitney 1996; Collar 1997; Juniper and Parr 1998) and *Calyptorhynchus* in Australia (Dickinson and Remsen 2013) have all been broken into smaller, component genera. The relevant species are indeed each other's closest relatives, however, and so could continue to be recognised validly with a single genus. Decisions to dismantle the larger genera in each case into component smaller ones have been based on the clear phylogenetic structure revealed by DNA studies coupled with variation in other character sets (e.g. plumage, anatomy, vocalisations). Although this category of generic dismantlement has seen the recognition of many genera with at most a handful of species in recent years, there seems to be consensus that it helps to reflect the topological complexity of the parrot tree.

Third are genera where the member species are not each other's closest relatives but for which some species remain unsampled. Final composition, or circumscription, of the genera to result in such cases is not yet possible. Examples are *Polytelis* and *Trichoglossus* in the Australo-Papuan region, *Psittacula* in the Indo-African area, and *Bolborhynchus* in the Neotropics. Thus, we can affirm the need to dismantle *Polytelis* but note that its type-species, Superb Parrot *P. swainsonii*, remains unsequenced. Further, its other two species, Regent Parrot *P. anthopeplus* and Princess Parrot *P. alexandrae*, appear not to be sisters. How *Polytelis* should be dismantled, then, awaits further work. Similarly, recognition among Afro-Asian species that the extinct Mascarene Parrot *Mascarinus mascarin* and three of the four species of *Tanygnathus* so-far-studied are nested within *Psittacula* argues for the breakup of the latter. Further taxon sampling remains to be done in this case.

Species limits, phylogeography, and conservation genetics

Although our analysis has been a coarse-scale summary of genetic sampling within parrots to date, we can identify several patterns. Most dramatic is that only about a third of the species have been subject to any phylogeographic or population genetics study. If we used more stringent criteria (e.g. having range-wide sampling or multilocus data) the proportion would be even lower. This is particularly problematic when the spatial distribution of sampling is taken into account. For example, Australo-Papua has high parrot diversity, but phylogeographic work there to date poorly represents the region's species- and family-level diversity, especially in New Guinea. We are aware of work in progress that will help remedy this. In the meantime, from Australia, only 4 of 14 cacatuids and 10 of 40 psittacoids have been the focus of phylogeographic study, specifically one lorikeet, all but one rosella *Platycercus*, the ringnecks *Barnardius*, one grass parrot (Mulga Parrot *Psephotellus varius*), and Eastern and Western Ground Parrots (*Pezoporus wallicus*, *P. flaviventris*, respectively) (Joseph and Wilke 2006; Murphy *et al.* 2007, 2011; Joseph *et al.* 2008; White *et al.* 2014; Dolman and Joseph 2015; Engelhard *et al.* 2015; Shipham *et al.* 2017; McElroy *et al.* 2018). Just one New Guinean cacatuid, *Probosciger aterrimus*, has been studied phylogeographically (Murphy *et al.* 2007). Subspecies described on the basis of plumage and size variation may be an inconsistent predictor of evolutionary units, but phenotypic variation can provide target areas for identifying deep genetic breaks or problems with species limits, as shown in the South American genera *Forpus* (Smith *et al.* 2013) and *Pionus* (Ribas *et al.* 2007). Such studies collectively highlight biases in taxonomic knowledge that are not accounted for in threat assessments to parrots (e.g. Berkunsky *et al.* 2017; but see Martin *et al.* 2014).

Parrot genomics onward

The technological advancements that led to major changes in parrot systematics over the last few decades are not slowing down. An array of new genomic resources allows researchers to sample more widely across the genome in a time- and cost-effective manner. Techniques using reduced-genome representation libraries (sequence capture: Faircloth *et al.* 2012; RAD-seq: Baird *et al.* 2008) can yield thousands of loci or single-nucleotide polymorphisms from hundreds of individuals on a single lane of an Illumina DNA sequencer. Even whole genome sequencing is fast becoming a tool for parrot biologists. For example, the B10K initiative proposes to sequence genomes of >10 000 bird species, including all parrots (Zhang 2015). Resources of this magnitude are informative for an array of basic and applied scientific purposes.

Downloaded by [73.29.2.54] at 17:13 13 November 2017

More directly applicable to the conservation of single species, a separate initiative plans to sequence whole genomes from all remaining kakapos (*Strigops habroptilus*), which could provide detailed information on pedigree, inbreeding depression, and other factors relevant for species management. We are technologically well positioned to build increasingly powerful genomic toolkits to study all aspects of parrot biology.

A major hurdle that the research community faces, however, is obtaining high-quality genetic resources from wild birds. Many of the published DNA sequences used here were extracted from captive birds or old museum skins. Often these sources for genetic material are adequate, but captive birds may be of direct hybrid origin, descended from distant hybridisation events in captivity, or simply be of unknown geographical provenance. Material from museum skins brings increased costs and bioinformatic challenges due to degraded DNA. As questions turn to more fine-scale processes dealing with species delimitation, phylogeographic structure, and gene flow, existing genetic resources will require urgent and systematic expansion. Greater coordination among field biologists who work directly with parrots in the wild and those who study genetics in the lab will help ameliorate the paucity of archived population-level sampling. As shown here, phylogenetic relationships among higher taxa of Psittaciformes are mostly resolved, but there remains a wide-open frontier for research at the tips of the tree to investigate species and generic limits, phylogeography, and population-level processes.

Acknowledgements

We thank R. Heinsohn for inviting our contribution to this issue. We acknowledge our great debt to all workers who originally produced the data used in this study. We thank R. DeSalle, A. Paasch, A. Buczek, M. Ingala, D. DeCarle, J. Tejada, and A. DeRenzis for support during this work. We also thank K. Buchanan and T. Wright for reviews, as well as L. R. Moreira, L. Musher, W. M. Mauck III, L. A. Coelho, A. V. Rocha, M. Andersen, J. Cracraft, and J. Klicka for comments and suggestions.

ORCID

Kaiya L. Provost http://orcid.org/0000-0002-5865-7238
Leo Joseph http://orcid.org/0000-0001-7564-1978

References

Auersperg, A. M. I., Borasinski, S., Laumer, I., and Kacelnik, A. (2016). Goffin's cockatoos make the same tool type from different materials. *Biology Letters* **12**, 20160689. doi:10.1098/rsbl.2016.0689

Auersperg, A. M. I., Szabo, B., von Bayern, A. M. P., and Kacelnik, A. (2012). Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo. *Current Biology* **22**, R903–R904. doi:10.1016/j.cub.2012.09.002

Baird, N. A., Etter, P. D., Atwood, T. S., Currey, M. C., Shiver, A. L., Lewis, Z. A., Selker, E. U., Cresko, W. A., Johnson, E. A., and Fay, J. C. (2008). Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS One* **3**, e3376. doi:10.1371/journal.pone.0003376

Berg, K. S., Delgado, S., Cortopassi, K. A., Beissinger, S. R., and Bradbury, J. W. (2012). Vertical transmission of learned signatures in a wild parrot. *Proceedings of the Royal Society B: Biological Sciences* **279**, 585–591.

Berkunsky, I., Quillfeldt, P., Brightsmith, D. J., Abbud, M. C., Aguilar, J. M. R. E., Alemán-Zelaya, U., Aramburú, R. M., Arce Arias, A., Balas McNab, R., Balsby, T. J. S., Barredo Barberena, J. M., Beissinger, S. R., Rosales, M., Berg, K. S., Bianchi, C. A., Blanco, E., Bodrati, A., Bonilla-Ruz, C., Botero-Delgadillo, E., Canavelli, S. B., Caparroz, R., Cepeda, R. E., Chassot, O., Cinta-Magallón, C., Cockle, K. L., Daniele, G., De Araujo, C. B., De Barbosa, A. E., De Moura, L. N., Del Castillo, H., Díaz, S., Díaz-Luque, J. A., Douglas, L., Figueroa Rodríguez, A., García-Anleu, R. A., Gilardi, J. D., Grilli, P. G., Guix, J. C., Hernández, M., Hernández-Muñoz, A., Hiraldo, F., Horstman, E., Ibarra Portillo, R., Isacch, J. P., Jiménez, J. E., Joyner, L., Juarez, M., Kacoliris, F. P., Kanaan, V. T., Klemann-Júnior, L., Latta, S. C., Lee, A. T. K., Lesterhuis, A., Lezama-López, M., Lugarini, C., Marateo, G., Marinelli, C. B., Martínez, J., McReynolds, M. S., Mejia Urbina, C. R., Monge-Arias, G., Monterrubio-Rico, T. C., Nunes, A. P., Nunes, F., Olaciregui, C., Ortega-Arguelles, J., Pacifico, E., Pagano, L., Politi, N., Ponce-Santizo, G., Portillo Reyes, H. O., Prestes, N. P., Presti, F., Renton, K., Reyes-Macedo, G., Ringler, E., Rivera, L., Rodríguez-Ferraro, A., Rojas-Valverde, A. M., Rojas-Llanos, R. E., Rubio-Rocha, Y. G., Saidenberg, A. B. S., Salinas-Melgoza, A., Sanz, V., Schaefer, H. M., Scherer-Neto, P., Seixas, G. H. F., Serafini, P., Silveira, L. F., Sipinski, E. A. B., Somenzari, M., Susanibar, D., Tella, J. L., Torres-Sovero, C., Trofino-Falasco, C., Vargas-Rodríguez, R., Vázquez-Reyes, L. D., White, T. H., Williams, S., Zarza, R., and Masello, J. F. (2017). Current threats faced by Neotropical parrot populations. *Biological Conservation* **214**, 278–287. doi:10.1016/j.biocon.2017.08.016

BirdLife International and NatureServe (2015). 'Bird Species Distribution Maps of the World.' (BirdLife International: Cambridge, UK.)

Boles, W. E. (2017). Fossil history of parrots. In 'Vanished and Vanishing Parrots'. (Eds J. M. Forshaw.) pp. 1–12. (CSIRO Publishing: Melbourne.)

Brown, J., Wang, N., and Smith, S. (2017). The development of scientific consensus: Analyzing conflict and concordance among avian phylogenies. Molecular Phylogenetics and Evolution **116**, 69-77. doi:10.1016/j.ympev.2017.08.002.

Burleigh, J. G., Kimball, R. T., and Braun, E. L. (2015). Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution* **84**, 53–63. doi:10.1016/j.ympev.2014.12.003

Downloaded by [73.29.2.54] at 17:13 13 November 2017

Christidis, L., Schodde, R., Shaw, D., and Maynes, S. (1991). Relationships among the Australo-Papuan parrots, lorikeets and cockatoos (Aves: Psittaciformes): protein evidence. *The Condor* **93**, 302–317. doi:10.2307/1368946

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Roberson, D., Fredericks, T. A., Sullivan, B. L., and Wood, C. L. (2016). The eBird/Clements checklist of birds of the world: V2016. Available at http://www.birds.cornell.edu/clementschecklist/download/

Cock, P. J., Antao, T., Chang, J. T., Chapman, B. A., Cox, C. J., Dalke, A., Friedberg, I., Hamelryck, T., Kauff, F., Wilczynski, B., and De Hoon, M. J. (2009). Biopython: freely available python tools for computational molecular biology and bioinformatics. *Bioinformatics* **25**, 1422-1423. doi: 10.1093/bioinformatics/btp163

Collar, N. J. (1997). Family Psittacidae (Parrots). In 'Handbook of the Birds of the World. Vol. 4'. (Eds J. del Hoyo, A. Elliott, and J. Sargatal.) pp. 280–479. (Lynx Edicions: Barcelona.)

de Kloet, R. S., and de Kloet, S. R. (2005). The evolution of the spindlin gene in birds: Sequence analysis of an intron of the spindlin W and Z gene reveals four major divisions of the Psittaciformes. *Molecular Phylogenetics and Evolution* **36**, 706–721. doi:10.1016/j.ympev.2005.03.013

Dickinson, E. C., and Remsen, J. V. (2013). 'The Howard & Moore Complete Check-list of the Birds of the World. 4th Edition. Volume 1. Non-passerines.' (Aves Press: Eastbourne, UK.)

Dolman, G., and Joseph, L. (2015). Evolutionary history of birds across southern Australia: Structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species. *Emu* **115**, 35–48.

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**, 1792–1797. doi:10.1093/nar/gkh340

Engelhard, D., Joseph, L., Toon, A., Pedler, L., and Wilke, T. (2015). Rise (and demise?) of subspecies in the Galah (*Eolophus roseicapilla)*, a widespread and abundant Australian cockatoo. *Emu* **115**, 289–301. doi:10.1071/MU15018

Faircloth, B. C., McCormack, J. E., Crawford, N. G., Harvey, M. G., Brumfield, R. T., and Glenn, T. C. (2012). Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology* **61**, 717–726. doi:10.1093/sysbio/sys004

Forshaw, J. M. (1989). 'Parrots of the World,' 2nd edn. (Lansdowne Editions: Melbourne.)

Forshaw, J. M. (2011). 'Parrots of the World. Illustrated by Frank Knight.' (CSIRO Publishing: Melbourne.)

Forshaw, J. M. (2017). 'Vanished and Vanishing Parrots. Illustrated by Frank Knight.' (CSIRO Publishing: Melbourne.)

Fuller, E. (2001). 'Extinct Birds.' (Comstock Publishing Associates: Ithaca, NY.)

Ganapathy, G., Howard, J. T., Ward, J. M., Li, J., Li, B., Li, Y., Xiong, Y., Zhang, Y., Zhou, S., Schwartz, D. C., Schatz, M., Aboukhalil, R., Fedrigo, O., Bukovnik, L., Wang, T., Wray, G., Rasolonjatovo, I., Winer, R., Knight, J. R., Koren, S., Warren, W. C., Zhang, G., Phillippy, A. M., and Jarvis, E. D. (2014). High-coverage sequencing and annotated assemblies of the budgerigar genome. *GigaScience* **3**, 11. doi:10.1186/2047-217X-3-11

Garrod, A. H. (1874). On some Points in the Anatomy of the Parrots which bear on the Classification of the Suborder. *Proceedings of the Zoological Society of London* **42**, 586–598. doi:10.1111/j.1096-3642.1874.tb02515.x

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K.-L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C., and Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763–1768. doi:10.1126/science.1157704

Holyoak, D. T. (1973). Comments on taxonomy and relationships in the parrot subfamilies Nestorinae, Loriinae and Platycercinae. *Emu* **73**, 157–176. doi:10.1071/MU973157

Hume, J. P. (2007). Reappraisal of the parrots (Aves: Psittacidae) from the Mascarene Islands, with comments on their ecology, morphology, and affinities. *Zootaxa* **1513**, 1–76.

Hurlbert, A. H., and Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences, USA* **104**, 13384–13389. doi:10.1073/pnas.0704469104

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., and Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* **491**, 444–448. doi:10.1038/nature11631

Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K., and Mooers, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology* **24**, 919–930. doi:10.1016/j.cub.2014.03.011

Joseph, L., Dolman, G., Donnellan, S., Saint, K. M., Berg, M. L., and Bennett, A. T. (2008). Where and when does a ring start and end? Testing the ring-species hypothesis in a species complex of Australian parrots. *Proceedings of the Royal Society of London B: Biological Sciences* **275**, 2431–2440. doi:10.1098/rspb.2008.0765

Joseph, L., and Omland, K. (2009). Phylogeography: Its development and impact in Australo-Papuan ornithology with special reference to paraphyly in Australian birds. *Emu* **109**, 1–23. doi:10.1071/MU08024

Joseph, L., Toon, A., Schirtzinger, E. E., and Wright, T. F. (2011). Molecular systematics of two enigmatic genera *Psittacella* and *Pezoporus* illuminate the ecological radiation of Australo-Papuan parrots (Aves: Psittaciformes). *Molecular Phylogenetics and Evolution* **59**, 675–684. doi:10.1016/j.ympev.2011.03.017

Joseph, L., Toon, A., Schirtzinger, E. E., Wright, T. F., and Schodde, R. (2012). A revised nomenclature and classification for family-group taxa of parrots (Psittaciformes). *Zootaxa* **3205**, 26–40.

Joseph, L., and Wilke, T. (2006). Molecular resolution to the population history, systematics, biogeography and of the Australian ringneck parrots *Barnardius*: Are we there yet? *Emu* **106**, 49–62. doi:10.1071/MU05035

Juniper, T., and Parr, M. (1998). 'Parrots: A Guide to the Parrots of the World.' (Pica Press: Sussex.)

Kirchman, J. J., Schirtzinger, E. E., and Wright, T. F. (2012). Phylogenetic relationships of the extinct Carolina Parakeet

Downloaded by [73.29.2.54] at 17:13 13 November 2017

(*Conuropsis carolinensis*) inferred from DNA sequence data. *The Auk* **129**, 197–204. doi:10.1525/auk.2012.11259

Kundu, S., Jones, C. G., Prys-Jones, R. P., and Groombridge, J. J. (2012). The evolution of the Indian Ocean parrots (Psittaciformes): extinction, adaptive radiation and eustacy. *Molecular Phylogenetics and Evolution* **62**, 296–305. doi:10.1016/j.ympev.2011.09.025

Lanfear, R., Calcott, B., Kainer, D., Mayer, C., and Stamatakis, A. (2014). Selecting optimal partitioning schemes for phylogenomic datasets. *BMC Evolutionary Biology* **14,** 82.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., and Calcott, B. (2016). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* **34**, 772–773.

Martin, R. O., Perrin, M. R., Boyes, R. S., Abebe, Y. D., Annorbah, N. D., Asamoah, A., Bizimana, D., Bobo, K. S., Bunbury, N., Brouwer, J., Diop, M. S., Ewnetu, M., Fotso, R. C., Garteh, J., Hall, P., Holbech, L. H., Madindou, I. R., Maisels, F., Mokoko, J., Mulwa, R., Reuleaux, A., Symes, C., Tamungang, S., Taylor, S., Valle, S., Waltert, M., and Wondafrash, M. (2014). Research and conservation of the larger parrots of Africa and Madagascar: a review of knowledge gaps and opportunities. *Ostrich* **85**, 205–233. doi:10.2989/00306525.2014.948943

Mayr, G. (2010). Parrot interrelationships – morphology and the new molecular phylogenies. *Emu* **110**, 348–357. doi:10.1071/MU10035

Mayr, G. (2015). A reassessment of Eocene parrotlike fossils indicates a previously undetected radiation of zygodactyl stem group representatives of passerines (Passeriformes). *Zoologica Scripta* **44**, 587–602. doi:10.1111/zsc.2015.44.issue-6

McElroy, K., Symonds, M., Beattie, K., and Joseph, L. (2018). Mitogenomic and nuclear diversity in the Mulga Parrot of the Australian arid-zone: cryptic subspecies and tests for selection. *Emu* **118**. this issue.

Miller, M. A., Pfeiffer, W., and Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Gateway Computing Environments Workshop (GCE)*, 14 November **2010**, 1–8.

Murphy, S., Joseph, L., Burbidge, A., and Austin, J. (2011). A cryptic and critically endangered species revealed by mitochondrial DNA analyses – The Western Ground Parrot. *Conservation Genetics* **12**, 595–600. doi:10.1007/s10592-010-0161-1

Murphy, S. A., Double, M. C., and Legge, S. M. (2007). The phylogeography of palm cockatoos, *Probosciger aterrimus*, in the dynamic Australo-Papuan region. *Journal of Biogeography* **34**, 1534–1545. doi:10.1111/jbi.2007.34.issue-9

Oleksyk, T. K., Pombert, J.-F., Siu, D., Mazo-Vargas, A., Ramos, B., Guiblet, W., Afanador, Y., Ruiz-Rodriguez, C. T., Nickerson, M. L., Logue, D. M., Dean, M., Figueroa, L., Valentin, R., and Martinez-Cruzado, J.-C. (2012). A locally funded Puerto Rican parrot (*Amazona vittata*) genome sequencing project increases avian data and advances young researcher education. *GigaScience* **1**, 14. doi:10.1186/2047-217X-1-14

Pepperberg, I. M. (2009). 'The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots.' (Harvard University Press: Cambridge.)

Pfenning, A. R., Hara, E., Whitney, O., Rivas, M. V., Wang, R., Roulhac, P. L., Howard, J. T., Wirthlin, M., Lovell, P. V., Ganapathy, G., Mountcastle, J., Moseley, M. A., Thompson, J. W., Soderblom, E. J., Iriki, A., Kato, M., Gilbert, M. T. P., Zhang, G., Bakken, T., Bongaarts, A., Bernard, A., Lein, E., Mello, C. V., Hartemink, A. J., and Jarvis, E. D. (2014). Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science* **346**, 1256846. doi:10.1126/science.1256846

Podsiadlowski, L., Gamauf, A., and Töpfer, T. (2017). Revising the phylogenetic position of the extinct Mascarene Parrot *Mascarinus mascarin* (Linnaeus 1771) (Aves: Psittaciformes: Psittacidae). *Molecular Phylogenetics and Evolution* **107**, 499–502. doi:10.1016/j.ympev.2016.12.022

R Development Core Team (2008). 'R: A Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna.) Available at http://www.R-project.org.

Reddy, S., Kimball, R. T., Pandey, A., Hosner, P. A., Braun, M. J., Hackett, S. J., Han, K.-L., Harshman, J., Huddleston, C. J., Kingston, S., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Witt, C. C., Yuri, T., and Braun, E. L. (2017). Why do phylogenomic data sets yield conflicting trees? Data type influences the avian tree of life more than taxon sampling. *Systematic Biology* **66**, 857–879. doi:10.1093/sysbio/syx041

Remsen, J. Jr (2005). Pattern, process, and rigor meet classification. *Auk* **122**, 403–441. doi:10.1642/0004-8038(2005)122[0403:PPARMC]2.0.CO;2

Remsen, J. V. Jr, Schirtzinger, E. E., Ferraroni, A., Silveira, L. F., and Wright, T. F. (2013). DNA-sequence data require revision of the parrot genus *Aratinga* (Aves: Psittacidae). *Zootaxa* **641**, 296–300. doi:10.11646/zootaxa.3641.3.9

Ribas, C. C., Miyaki, C. Y., and Cracraft, J. (2009). Phylogenetic relationships, diversification and biogeography in Neotropical *Brotogeris* parakeets. *Journal of Biogeography* **36**, 1712–1729. doi:10.1111/jbi.2009.36.issue-9

Ribas, C. C., Moyle, R. G., Miyaki, C. Y., and Cracraft, J. (2007). The assembly of montane biotas: Linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of the Royal Society B: Biological Sciences* **274**, 2399–2408. doi:10.1098/rspb.2007.0613

Rocha, A. V., Rivera, L. O., Martinez, J., Prestes, N. P., and Caparroz, R. (2014). Biogeography of speciation of two sister species of Neotropical *Amazona* (Aves, Psittaciformes) based on mitochondrial sequence data. *PLoS One* **9**, e108096. doi:10.1371/journal.pone.0108096

Schirtzinger, E. E., Tavares, E. S., Gonzales, L. A., Eberhard, J. R., Miyaki, C. Y., Sanchez, J. J., Hernandez, A., Müeller, H., Graves, G. R., Fleischer, R. C., and Wright, T. F. (2012). Multiple independent origins of mitochondrial control region duplications in the order Psittaciformes. *Molecular Phylogenetics and Evolution* **64**, 342–356. doi:10.1016/j.ympev.2012.04.009

Downloaded by [73.29.2.54] at 17:13 13 November 2017

Schodde, R., and Mason, I. J. (1997). 'Zoological Catalogue of Australia. Vol. 37.2: Aves (Columbidae to Coraciidae).' (CSIRO Publishing: Melbourne.)

Schodde, R., Remsen, J. V. Jr, Schirtzinger, E. E., Joseph., L., and Wright, T. F. (2013). Higher classification of New World parrots (Psittaciformes; Arinae), with diagnoses of tribes. *Zootaxa* **3691**, 591–596. doi:10.11646/zootaxa.3691.5.5

Schweizer, M., Güntert, M., and Hertwig, S. T. (2012). Out of the Bassian province: Historical biogeography of the Australasian platycercine parrots (Aves, Psittaciformes). *Zoologica Scripta* **42**, 13–27. doi:10.1111/zsc.2012.42.issue-1

Schweizer, M., Seehausen, O., Güntert, M., and Hertwig, S. T. (2010). The evolutionary diversification of parrots supports a taxon pulse model with multiple trans-oceanic dispersal events and local radiations. *Molecular Phylogenetics and Evolution* **54**, 984–994. doi:10.1016/j.ympev.2009.08.021

Schweizer, M., Seehausen, O., and Hertwig, S. T. (2011). Macroevolutionary patterns in the diversification of parrots: Effects of climate change, geological events and key innovations. *Journal of Biogeography* **38**, 2176–2194. doi:10.1111/jbi.2011.38.issue-11

Schweizer, M., Wright, T. F., Peñalba, J. V., Schirtzinger, E. E., and Joseph, L. (2015). Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes). *Molecular Phylogenetics and Evolution* **90**, 34–48. doi:10.1016/j.ympev.2015.04.021

Seabury, C. M., Dowd, S. E., Seabury, P. M., Raudsepp, T., Brightsmith, D. J., Liboriussen, P., Halley, Y., Fisher, C. A., Owens, E., Viswanathan, G., Tizard, I. R., and Janke, A. (2013). A multi-platform draft de novo genome assembly and comparative analysis for the Scarlet Macaw (*Ara macao*). *PLoS ONE* **8**, e62415. doi:10.1371/journal.pone.0062415

Shipham, A., Joseph, L., Schmidt, D., and Hughes, J. H. (2017). A genomic approach reinforces a hypothesis of mitochondrial capture in eastern Australian rosellas. *The Auk* **134**, 181–192. doi:10.1642/AUK-16-31.1

Sibley, C. G., and Ahlquist, J. E. (1990). 'Phylogeny and Classification of Birds.' (Yale University Press: New Haven.)

Smith, B. T., Ribas, C. C., Whitney, B. M., Hernández-Baños, B. E., and Klicka, J. (2013). Identifying biases at different spatial and temporal scales of diversification: A case study in the Neotropical parrotlet genus *Forpus*. *Molecular Ecology* **22**, 483–494. doi:10.1111/mec.12118

Smith, G. A. (1975). Systematics of parrots. *Ibis* **117**, 18–68. doi:10.1111/j.1474-919X.1975.tb04187.x

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**, 1312–1313. doi:10.1093/bioinformatics/btu033

Steadman, D. W. (2006). A new species of extinct parrot (Psittacidae: *Eclectus*) from Tonga and Vanuatu, South Pacific. *Pacific Science* **60**, 137–145. doi:10.1353/psc.2005.0061

Teixeira, M. M., Souza, R. C., Almeida, L. G., Vicente, V. A., de Hoog, S., Bocca, A. L., et al. (2015). Laboratório Nacional de Computação Científica. Unpublished data.

Thompson, D. A. (1899). On characteristic points in the cranial osteology of the parrots. *Proceedings of the Zoological Society of London* **1899**, 9–46.

Toft, C. A., and Wright, T. F. (2015). 'Parrots of the Wild. A Natural History of the World's Most Captivating Birds.' (University of California Press: Oakland, CA.)

Tokita, M., Kiyoshi, T., and Armstrong, K. N. (2007). Evolution of craniofacial novelty in parrots through developmental modularity and heterochrony. *Evolution & Development* **9**, 590–601. doi:10.1111/ede.2007.9.issue-6

Voskamp, A., Baker, D. J., Stephens, P. A., Valdes, P. J., and Willis, S. G. (2017). Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. *Journal of Biogeography* **44**, 709–721. doi:10.1111/jbi.12916

White, N. E., Bunce, M., Mawson, P. R., Dawson, R., Saunders, D. A., Allentoft, M. E., and Austin, J. (2014). Identifying conservation units after large-scale land clearing: A spatio-temporal molecular survey of endangered white-tailed black cockatoos (*Calyptorhynchus* spp.). *Diversity and Distributions* **20**, 1208–1220. doi:10.1111/ddi.2014.20.issue-10

White, N. E., Phillips, M. J., Gilbert, T., Alfaro-Núñez, A., Willerslev, E., Mawson, P. R., Spencer, P.B.S, and Bunce, M. (2011). The evolutionary history of cockatoos (Aves: Psittaciformes: Cacatuidae). *Molecular Phylogenetics and Evolution* **59**, 615–622. doi:10.1016/j.ympev.2011.03.011

Whitney, B. M. (1996). Flight behavior and other field characteristics of the genera of Neotropical parrots. *Cotinga* **5**, 32–42.

Wright, T. F., Schirtzinger, E. E., Matsumoto, T., Eberhard, J. R., Graves, G. R., Sanchez, J. J., Capelli, S., Müller, H., Scharpegge, J., Chambers, G. K., and Fleischer, R. C. (2008). A multilocus molecular phylogeny of the parrots (Psittaciformes): Support for a Gondwanan origin during the Cretaceous. *Molecular Biology and Evolution* **25**, 2141–2156. doi:10.1093/molbev/msn160

Yu, G., Smith, D. K., Zhu, H., Guan, Y., and Lam, T. T. Y. (2016). ggtree: An r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* **8**, 28–36. doi:10.1111/2041-210X.12628

Zhang, G. (2015). Genomics: Bird sequencing project takes off. *Nature* **522**, 34–34. doi:10.1038/522034d

Zhang, G., Li, B., Li, C., Gilbert, M. T. P., Jarvis, E. D., and Wang, J. (2014). Comparative genomic data of the Avian Phylogenomics Project. *GigaScience* **3**, 26. doi:10.1186/2047-217X-3-26

Zink, R. M. (2004). The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society B: Biological Sciences* **271**, 561–564. doi:10.1098/rspb.2003.2617