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Micro-evolutionary diversification among Indian Ocean parrots: temporal and spatial changes in phylogenetic diversity as a consequence of extinction and invasion

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Almost 90% of global bird extinctions have occurred on islands. The loss of endemic species from island systems can dramatically alter evolutionary trajectories of insular species biodiversity, resulting in a loss of evolutionary diversity important for species adaptation to changing environments. The Western Indian Ocean islands have been the scene of evolution for a large number of endemic parrots. Since their discovery in the 16th century, many of these parrots have become extinct or have declined in numbers. Alongside the extinction of species, a number of the Indian Ocean islands have experienced colonization by highly invasive parrots, such as the Ring-necked Parakeet *Psittacula krameri*. Such extinctions and invasions can, on an evolutionary timescale, drive changes in species composition, genetic diversity and turnover in phylogenetic diversity, all of which can have important impacts on species potential for adaptation to changing environmental and climatic conditions. Using mtDNA cytochrome *b* data, we resolve the taxonomic placement of three extinct Indian Ocean parrots: the Rodrigues *Psittacula exsul*, Seychelles *Psittacula wardi* and Reunion Parakeets *Psittacula eques*. This case study quantifies how the extinction of these species has resulted in lost historical endemic phylogenetic diversity and reduced levels of species richness, and illustrates how it is being replaced by non-endemic invasive forms such as the Ring-necked Parakeet. Finally, we use our phylogenetic framework to identify and recommend a number of phylogenetically appropriate ecological replacements for the extinct parrots. Such replacements may be introduced once invasive forms have been cleared, to rejuvenate ecosystem function and restore lost phylogenetic diversity.

Keywords: ecological replacements, evolution, invasive alien species, *Psittacula*.

Elevated rates of extinctions and invasions by non-native species as a result of human activities continue to affect biodiversity on a global scale (McKinney 2006, Cassey *et al.* 2007). As a consequence of these dual processes, biotic homogeniza-

tion (the increase in the taxonomic similarity of biotas over time; Olden 2006) can disrupt the net biological distinctiveness and diversity of a region by replacing unique endemic species with already widespread non-indigenous species (McKinney & Lockwood 1999). In particular, extinctions and invasions can have detrimental consequences on

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endemic taxa in oceanic island ecosystems, which are a rich source of evolutionary diversity (Whittaker & Fernández-Palacios 2007). The isolated nature of these environments means that endemic species are acutely vulnerable to extinction as a consequence of habitat loss, predation by introduced mammals, introduced disease and other human impacts on islands (Steadman 1995, Blackburn *et al.* 2004, Frankham 2005). Indeed, human activities have resulted in the extinction of as many as 2000 bird species across the Pacific islands (Steadman & Martin 2003, Boyer 2008, Duncan *et al.* 2013), and these extinctions are resulting in significant losses of ecological function and functional diversity (Boyer & Jetz 2014). The loss of such endemic island species can dramatically alter evolutionary trajectories of species assemblages as a result of reduced species interactions (Mooney & Cleland 2001, Rosenzweig 2001). In this way, extinctions and invasions can disrupt species diversity, affecting their composition, genetic and phylogenetic diversity (Olden & Poff 2003, Cassey *et al.* 2006). For example, high levels of endemic population genetic and phylogenetic diversity are important to allow adaptation to changing environmental and climatic conditions on an ecological and evolutionary timescale (Maherali & Klironomos 2007, Jump *et al.* 2009). In contrast, a disruption in the level of species diversity may result in a decreased capacity to adapt to environmental change (Olden & Poff 2003, Olden 2006). Fundamentally, extinctions and invasions may compromise the potential for future evolutionary diversification and persistence of endemic species (Day & Young 2004).

Phylogenetic diversity (Faith 1992, Crozier 1997) is a measure of biodiversity and a good predictor of ecological function (Flynn *et al.* 2011, Cadotte 2013, Jetz *et al.* 2014), which can be used to quantify these changes in evolutionary diversification. Based on phylogenetic species assemblages, they are a measure of the evolutionary history of a group of taxa (Vane-Wright *et al.* 1991) and prioritize species or environments of high conservation value (Rodrigues & Gaston 2002, Jetz *et al.* 2014). Phylogenetic diversity can be used as a biodiversity measure and can be applied to a variety of conservation situations (Winter *et al.* 2013, Fenker *et al.* 2014, Pio *et al.* 2014). For example, phylogenetic diversity has been used to assess conservation value based on how much of the encompassing phylogeny of a species is preserved (Crozier 1997, Crozier *et al.* 2005) by describing the evolutionary distinct-

tiveness of a group of taxa (Faith 1992, Helmus *et al.* 2007, Cadotte *et al.* 2010, Jetz *et al.* 2014). Conservation approaches that embrace such changes in evolutionary processes are also valuable because they can help to identify and preserve species biodiversity, important for higher productivity and ecosystem function (Crozier *et al.* 2005, Thomassen *et al.* 2011, Rolland *et al.* 2012). Phylogenetic diversity has recently been applied to conservation strategies such as the Evolutionary Distinct and Globally Endangered (EDGE) programme (Isaac *et al.* 2007, Jetz *et al.* 2014), the evolutionary framework for biodiversity science, bioGENESIS (<http://www.diversitas-international.org/activities/research/biogenesis>), and the Intergovernmental Platform on Biodiversity and Ecosystem Services, IPBES (www.IPBES.net). Phylogenetic diversity is also important in conservation management for assessing biodiversity change. The loss of phylogenetic diversity following human-mediated extinctions is often much greater than from natural random extinctions, as the entire network of unique evolutionary branches from which extinct species descend are lost (Purvis *et al.* 2000). Island systems such as the Pacific and Indian Ocean islands are often subjected to human-induced extinctions and invasions, and as these events are often well documented (Steadman & Martin 2003, Cheke & Hume 2008), they provide an ideal framework for quantifying non-random changes in phylogenetic diversity over the past few hundred years.

The parrots (Psittaciformes) are one of the most endangered groups of birds in the world, with 95 (26.8%) of the 354 known parrot species currently threatened with extinction, accounting for 2.4 billion years of global avian phylogenetic diversity (of 82.1 billion years total avian phylogenetic diversity: Jetz *et al.* 2014). Over the past 500 years approximately 163 avian extinctions have occurred across the globe, including some 20 parrot species (12%), half of which were island endemics (Collar 2000, Butchart *et al.* 2006). In this study, we examine the Western Indian Ocean islands of Mauritius, Seychelles, Madagascar, Reunion, Rodrigues and Grand Comoros, which have been the evolutionary source for at least 14 endemic parrot species (Hume 2007). These islands remained largely pristine until the 16th century (Hume 2007, Fig. 1), followed by extinctions and invasions, driven predominately by human impacts such as habitat destruction (Cheke & Hume 2008). Subsequently, intense hunting and the introduc-

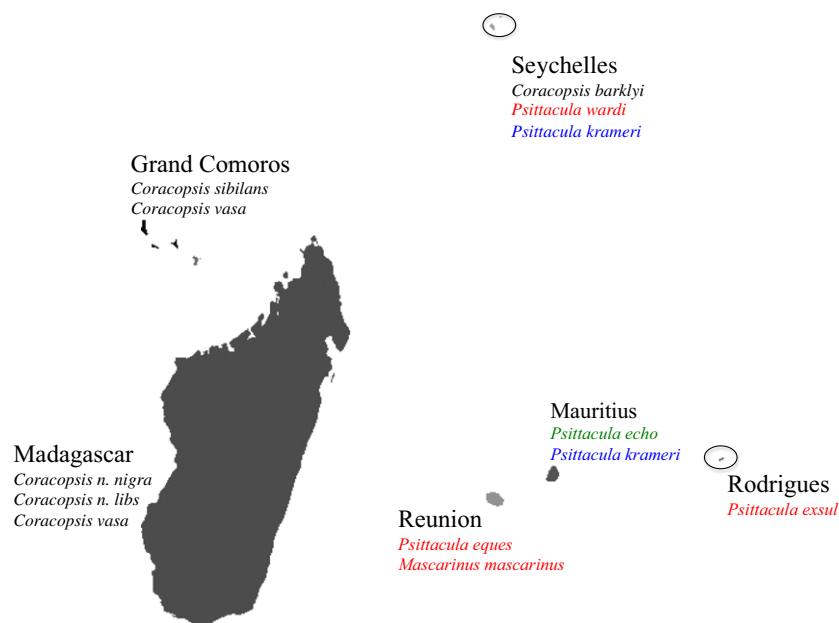


Figure 1. Distribution of extinct (red; *P. wardi*, *P. eques*, *M. mascarinus* and *P. exsul*), endangered endemic (green; *P. echo*), other endemic (black; *C. barklyi*, *C. sibilans*, *C. vasa*, *C. n. nigra* and *C. n. libs*) and invasive (blue; *P. krameri*) parrots across the Indian Ocean Islands.

tion of predatory exotic mammals have led to the extinction of nine endemic parrots, including the Reunion Parakeet *Psittacula eques*, which was last recorded in 1732, the Rodrigues Parakeet *Psittacula exsul*, extinct by 1875, the Seychelles Parakeet *Psittacula wardi*, lost between 1881 and 1906, and the Mascarene Parrot *Mascarinus mascarinus*, lost from Reunion by the end of the 19th century (Hume 2007, Hume & Walters 2012).

Alongside these extinctions, the islands have been colonized by invasive parrots. Invasive species are of global concern as they have detrimental impacts upon native species, ecosystems and communities (Sakai *et al.* 2001, Allendorf & Lundquist 2003, Gurevitch & Padilla 2004). In particular, the invasive Ring-necked Parakeet *Psittacula krameri* is recognized as one of the top 100 worst invasive alien species in Europe (DAISIE 2008, *Handbook of Alien Species in Europe*, Springer Netherlands). Native to Asia and sub-Saharan Africa, these birds are a major agro-economic and environmental concern, they are a severe crop pest in their native range, decimating maize and fruit crops (Ramzan & Toor 1973, Forshaw 2010, Ahmad *et al.* 2012) and they also act as secondary cavity-nesters and compete with native species for nesting holes (Strubbe & Matthysen 2007, 2009). Breeding populations of *P. krameri* have established in over 35

countries across five continents, where the species has become widespread with evidence of rapid population growth (Butler 2003, Butler *et al.* 2013). *Psittacula krameri* has invaded some of the Western Indian Ocean islands, including Mauritius, where they compete with the endangered Mauritius Parakeet *Psittacula echo* for nest-sites and food resources (Tatayah *et al.* 2007, Jones *et al.* 2013). On Mauritius, *P. krameri* are a suspected source of Psittacine beak and feather disease (Pbfd), caused by the highly infectious Beak and Feather Disease Virus, which threatens the population of the endangered endemic *P. echo* (Kundu *et al.* 2012a). *Psittacula krameri* also occur on the Seychelles where their recent establishment (Jones *et al.* 2013) presents a potential disease threat to the endemic Seychelles Black Parrot *Coracopsis barklyi* (Seychelles Islands Foundation, 2012).

As a consequence of the small number of museum specimens of the extinct endemic parrots from the Western Indian Ocean, there is taxonomic uncertainty surrounding their evolutionary affinities. For example, the taxonomic placement of *P. exsul* and *P. eques* within the Indian Ocean parrots has remained unresolved. *Psittacula exsul* was hunted to extinction by the mid-19th century and only two museum specimens remain, a female collected in 1871 and a male collected in August

1874 (Cheke & Hume 2008). Osteological characteristics suggest it shares a close relationship with other Mascarene species of *Psittacula* (Hume 2007). *Psittacula eques* had become extinct by 1770 and only one specimen is held, at the National Museums, Scotland, collected in 1750 (Hume & Walters 2012). A number of documents explicitly refer to *Psittacula eques*; however, this specimen is considered to be the only material proof of the existence of the Reunion island form and taxonomists remain unsure whether *P. eques* was a distinct species or conspecific with the endangered *P. echo*.

To date, there have been few attempts to quantify the historical loss of endemic phylogenetic diversity across a region and its insidious replacement by non-endemic invasive forms (Graham & Fine 2008, Winter *et al.* 2009). Here, we describe new molecular phylogenetic data for extinct and invasive *Psittacula* parrots and integrate them with existing data (Kundu *et al.* 2012b) into a detailed phylogenetic framework to quantify changes in phylogenetic diversity over the past 260 years (dating back to 1750, the date of our earliest museum specimen *P. eques*). Specifically, we use mitochondrial (mtDNA) cytochrome *b* sequence to resolve phylogenetic affinities of the extinct *P. exsul*, *P. eques* and *P. wardi*, determine whether *P. eques* warrants distinct species status or can be considered as conspecific with the extant *P. echo*, and examine the effect of these extinctions and invasions of parrots on phylogenetic diversity. We apply our findings to identify potential ecological replacement species for introduction onto appropriate Western Indian Ocean islands where historical extinctions have occurred in order to rebuild lost ecosystem function.

METHODS

Sample collection

Toepad samples for *P. exsul* and *P. wardi* were obtained from the Cambridge Museum of Zoology. A toepad sample was obtained from *P. eques* from the specimen held at the National Museums, Scotland. To establish whether *P. eques* was a distinct species, samples were obtained from three historical *P. echo* museum specimens from the Natural History Museum in Tring and the Muséum National d'Histoire Naturelle in Paris for comparison. For invasive populations of *P. krameri*, contemporary blood specimens were obtained from Seychelles ($n = 2$) and Mauritius ($n = 25$) (Table 1). We combined our data with cytochrome *b* sequences for other Indian Ocean parrots, including the extinct *M. mascarinus*, obtained from GenBank (Kundu *et al.* 2012b).

DNA isolation, amplification and sequencing

Processing of the museum specimens, including DNA extraction and polymerase chain reaction (PCR) amplifications, were carried out in a laboratory dedicated to ancient DNA work, under a UV-irradiated fume hood to prevent contamination. All equipment and surfaces were sterilized before and after each use by irradiation from UV light and with 10% bleach. Negative controls were included during the DNA extraction and PCR process and a selection of negative extractions and PCRs were sequenced to ensure there was no contamination. DNA was extracted from both contemporary blood and historical toepad samples using a Bioline Isolate

Table 1. Museum samples (from which DNA was successfully extracted), along with two contemporary samples representing invasive Ring-necked Parakeet haplotypes. All three sampled individuals of the Mauritius Parakeet produced a single identical haplotype, which was submitted to European Nucleotide Archive (ENA) using sample CG1911 No. 2114, as this individual produced the longest sequence.

Taxon	Common name	Source	Sample	Ref.	ENA accession no.
<i>Psittacula exsul</i>	Rodrigues Parakeet	Cambridge	Toepad	18/PSI./67/h/1	LN614516
<i>Psittacula eques</i>	Reunion Parakeet	Edinburgh	Toepad	N/A	LN614517
<i>Psittacula wardi</i>	Seychelles Parakeet	Cambridge	Toepad	18/PSI/67/g/1869	LN614515
<i>Psittacula echo</i>	Mauritius Parakeet	Paris	Toepad	CG1911 No 2114	LN614518
<i>Psittacula echo</i>	Mauritius Parakeet	Paris	Toepad	CG1936 No 1695	n/a
<i>Psittacula echo</i>	Mauritius Parakeet	Tring	Toepad	90.10.10.7	n/a
<i>Psittacula krameri manillensis</i>	Ring-necked Parakeet	Mauritius	Blood	N/A	LN614520
<i>Psittacula krameri borealis</i>	Ring-necked Parakeet	Seychelles	Blood	N/A	LN614519

Genomic DNA extraction kit (Bioline, London, UK). Samples were suspended in 400 μL lysis buffer plus 25 μL proteinase K and incubated at 55 °C overnight, or until the material had completely digested. DNA was washed through a spin column and blood specimens were suspended in 200 μL of elution buffer, and historical specimens in 40 μL of elution buffer.

Amplification from contemporary blood samples was conducted for cytochrome *b* using PKCBf and PKCBr (Appendix S1). PCR cycling conditions were 94 °C for 1 min followed by 35 cycles of 94 °C for 15 s, 55 °C for 15 s and 72 °C for 10 s, and a final elongation step of 72 °C for 10 min. For historical samples, amplification of cytochrome *b* was conducted using a suite of short overlapping primers (100–200 bp; Appendix S1). PCR cycling conditions were 94 °C for 1 min followed by 35 cycles of 94 °C for 15 s, 52 °C for 15 s and 72 °C for 10 s, and an elongation step of 72 °C for 10 min. All amplicons were examined by agarose gel electrophoresis. Amplification volumes of 25 μL contained 1 μL of template DNA from contemporary samples or 2 μL of template DNA from historical samples, 12.5 μL MyTaq HS Red Mix, containing dNTPs and MgCl_2 (Bioline), 0.5 μL of each primer and 10.5 μL (contemporary PCR) or 9.5 μL (historical PCR) of dH_2O . PCR product was purified and amplified using a 3730xl analyser (Macrogen, Amsterdam, the Netherlands). Sequences were edited in 4PEAKS (Griekspoor & Groothuis 2005) and aligned in CLUSTAL (Larkin *et al.* 2007). Manual edits were made in JALVIEW (Waterhouse *et al.* 2009).

Phylogenetic analysis

Phylogenetic trees were reconstructed using Bayesian and maximum likelihood methods with *Falco* as an outgroup. PARTITIONFINDER (Lanfear *et al.* 2012) was used to identify the best-fit models of nucleotide evolution according to Bayesian information criteria (BIC). Bayesian inference was implemented in MRBAYES v3.2 (Ronquist & Huelsenbeck 2003) on the CIPRES Science Gateway (Miller *et al.* 2010) with 10 million generations over four parallel Monte Carlo Markov chains (MCMC), under an HKY evolutionary model (Felsenstein 1981). TRACER v1.6 (Rambaut & Drummond 2007) was used to assess convergence. After discarding the first 25%, tree topologies were sum-

marized in a 50% consensus tree. A maximum likelihood search was conducted in RAXML (Stamatakis 2006). Ten independent runs were performed with 1000 non-parametric bootstrap replicates to obtain the best likelihood score under a GTRGAMMA model and summarized in a majority rule consensus tree. All trees were visualized in FIGTREE v1.4 (Rambaut 2012). Finally, net between-group mean genetic distances were calculated using MEGA 5.05 (Tamura *et al.* 2011) under the Kimura two-parameter model (Kimura 1980) with gamma distribution of rates among sites.

Molecular dating

Time-calibrated phylogenies were estimated using BEAST v.1.8.0 (Drummond & Rambaut 2007) using cytochrome *b* data. Given that relative to other bird families the fossil record for parrots is poor (Mayr & Göhlich 2004), we combined our data with cytochrome *b* sequences for other Indian Ocean parrots obtained from GenBank and ran phylogenetic analyses by adopting a similar approach to Wright *et al.* (2008) using two alternative calibration dates for the origin of the parrots. The first calibration used was obtained from the oldest known fossil belonging to a crown group of parrots, *Mopsitta tanta*, dated to approximately 54 Mya in the Tertiary period (Waterhouse *et al.* 2008). A second calibration of 80 Mya was obtained from a previous dating analysis of extant bird orders, suggesting a Cretaceous date for the divergence of parrots (Hedges *et al.* 1996). This calibration was given a normal distribution with a standard deviation of 10 Mya to ensure the 95% distribution (60.4 and 99.6 Mya) does not exceed the 100 Mya date for the divergence of bird orders (Hedges *et al.* 1996). An uncorrelated strict molecular clock model was used in preference to a lognormal relaxed molecular clock model as identified by the Akaike information criterion (AIC) through MCMC (AICM) comparison of models (Baele *et al.* 2012) with a uniform distribution under the Yule speciation tree prior (Ho *et al.* 2007). MCMC was performed for 20 million generations with sampling every 1000 iterations. Convergence was confirmed by effective sample sizes (ESS) > 200 for all parameters using TRACER v1.6 (Drummond & Rambaut 2007). Trees from the first 1000 generations were discarded as burn-in. A maximum clade credibility tree was summarized using

TREEANNOTATER v1.7.5 (Drummond & Rambaut 2007), visualized in FIGTREE v1.4 (Rambaut 2012), and edited in INKSCAPE (www.inkscape.org).

Phylogenetic diversity

Phylogenetic diversity is a distance-based method that measures the phylogenetic information of a species assemblage by summing up the branch lengths of the subtree that includes the communities' species (Faith 1992). Branch lengths are indicative of molecular characteristics accumulated over evolutionary time (Schweiger *et al.* 2008), and hence phylogenetic diversity was calculated using our time-calibrated phylogeny and is reported in millions of years (Myr). Phylogenetic diversity was calculated using the 'Picante' package in R (Kembel *et al.* 2010) for 1000 replications to obtain standard errors. Diversity metrics were calculated for the following three scenarios involving the inclusion of all (endemic) Indian Ocean island parrots, extinct and extant (referred to as 'historical PD'), the historical taxa less the four extinct species, i.e. *P. exsul*, *P. eques*, *P. wardi* and *M. mascarinus* (referred to as 'post-extinction PD'), and the extant *P. echo* and invasive *P. krameri* (referred to as 'current PD'). Additionally, species richness was counted for each of our scenarios. For species richness on a spatial scale, Ring-necked Parakeets on Seychelles and Mauritius were counted as separate island populations.

RESULTS

DNA was amplified from one specimen of *P. exsul*, *P. wardi* and *P. eques* and three *P. echo* specimens. The DNA sequences obtained from the three Mauritius *P. echo* samples were identical and condensed into a single haplotype. The sequence data from invasive *P. krameri* on the Seychelles were identical and condensed into a single haplotype, but the sequence data derived from *P. krameri* sampled from Mauritius were collapsed into five different haplotypes. For the purpose of this study, the most common haplotype was chosen to capture prevalent levels of phylogenetic diversity within Mauritius *P. krameri*.

Phylogenetic reconstruction and molecular dating

A total of 1000 bp of cytochrome *b* was used for phylogenetic reconstruction, taxonomic placement

and molecular dating of the extinct Indian Ocean parakeets. Although this study is based on a single gene, the cytochrome *b* gene has been shown to produce phylogenies that are congruent at major nodes when compared with phylogenies built with other mitochondrial and nuclear genes (Faulkes *et al.* 2004), suggesting it is a robust choice of marker. Furthermore, we chose cytochrome *b* based on the availability of a large number of cytochrome *b* sequences for other Indian Ocean Parrots (Kundu *et al.* 2012b). As the museum specimens were up to 260 years old, for some specimens only partial sequences (503–760 bp) of the cytochrome *b* gene could be amplified (European Nucleotide Archive accession numbers LN614515–LN614520). Topologies reconstructed from Bayesian and maximum likelihood trees were largely congruent at all major nodes, inferring a distinct and well-supported phylogenetic structure of the Indian Ocean parrots (Fig. 2; for details of geographical localities of each taxa see Appendix S2).

Assuming a calibration of 54 Mya, *P. wardi* clustered deep within the Alexandrine Parakeet *P. eupatria* clade and diverged 2.2 Mya. *Psittacula exsul* clusters were ancestral to *P. eques* and *P. echo*, which all fall within the *P. krameri* clade. *Psittacula exsul* diverged 3.82 Mya, whereas *P. eques* and *P. echo* split from each other just 0.61 Mya. The invasive Seychelles and Mauritius *P. krameri* both cluster with their native counterparts from southern Asia (*Psittacula krameri manillensis* and *Psittacula krameri borealis*, Fig. 2). When the calibration age is extended to 80 Mya, the divergence dates also move further back in time. The *P. wardi* divergence increases to 3.54 Mya and *P. exsul* is estimated to have diverged 6.15 Mya, whereas *P. eques* and *P. echo* diverged 0.99 Mya (Appendix S3).

Genetic divergences

Table 2 gives the uncorrected nucleotide distances between Indian Ocean endemic parrots (extinct and extant) and invasive *P. krameri*. The highest observed divergences were between the *Psittacula* parakeets and Vasa *Coracopsis* parrots, for which divergences ranged between 9.6 and 14.8%. The extinct *P. exsul* and *P. wardi* differ by 5.4%, whereas *P. exsul* and *P. echo* are closely related, with only 2.9% difference. The extinct *P. eques* differs by 0.2% from historical *P. echo*. The inva-

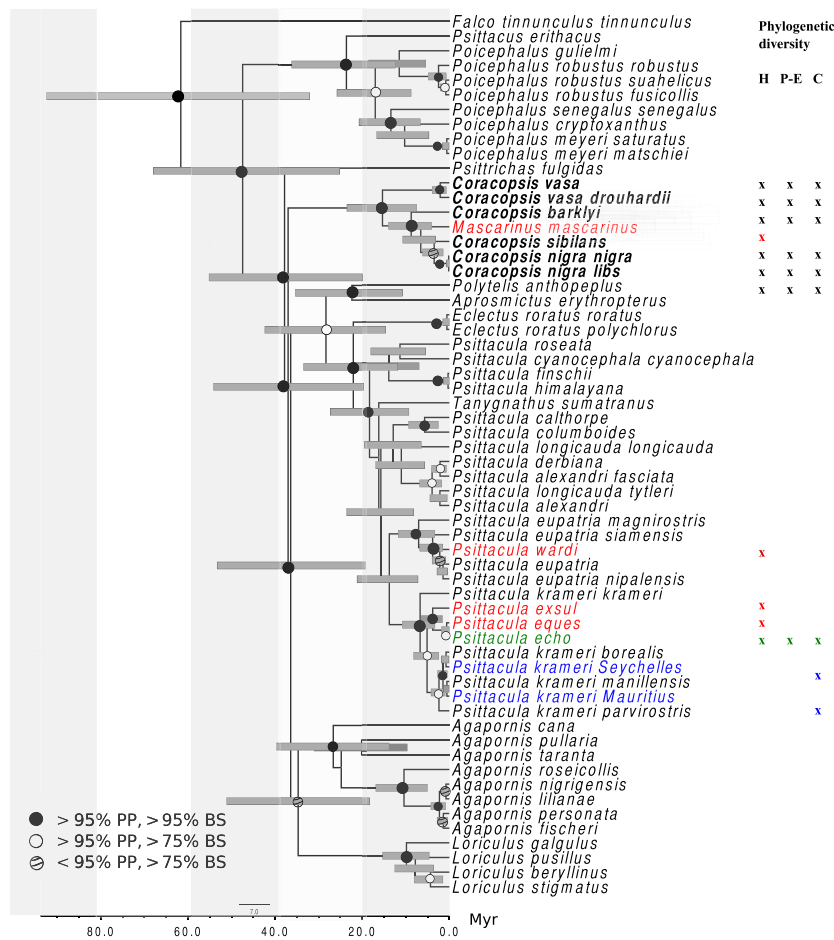


Figure 2. Phylogenetic placement of extinct Indian Ocean parrots. Estimated divergence times resolved using BEAST with a specified time to most recent common ancestor of 54 Mya. Error bars display the 95% highest posterior density, and the axis is given in millions of years (Myr) before present. Black dots indicate nodes with Bayesian posterior probability (PP) > 95% and maximum likelihood bootstrap support (BS) > 95%, white dots indicate > 95% PP and > 75% BS, striped dots indicate < 95% PP and > 75% BS. Node values lower than both 95% PP and 75% BS respectively are not given. Colours identify the extinct parrots (red; *P. wardi*, *P. exsul*, *M. mascarinus* and *P. eques*), endangered parrots (green; *P. echo*) and invasive parrots (blue; *P. krameri*) included in the phylogenetic diversity calculations. Crosses indicate which species are included within the different phylogenetic diversity scenarios: historical (H), post-extinction (P-E) and current (C).

sive *P. krameri* found on Mauritius and the Seychelles differ by only 2.2–2.6% with *P. eques* and *P. echo*, and 3.5–3.6% with *P. exsul*.

Phylogenetic diversity

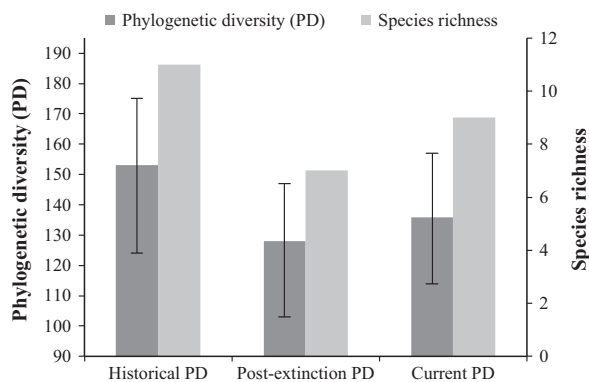
Prior to the extinction of the four parrot species from these Indian Ocean islands, phylogenetic diversity was 153.0 million years (Myr) with a species richness value of 11. Following the extinction events, species richness was reduced to seven, with a concomitant reduced level of phylogenetic diversity by 17% to 128.00 Myr. The establishment of invasive *P. krameri* on Mauritius and Seychelles

and their introduction of non-endemic phylogenetic diversity resulted in a net increase of 5% to 135.90 Myr. Species richness increased to nine (Fig. 3).

When comparing changes over time on a spatial scale, the extinction of endemic parrots from Rodrigues and Reunion has resulted in a complete loss of phylogenetic diversity and species richness. On Rodrigues phylogenetic diversity has been reduced from 61.64 Myr to 0 Myr, and species richness from one to zero. Similarly on Reunion, phylogenetic diversity has decreased from 98.66 Myr to 0 Myr, and species richness from two to zero. The Seychelles has experienced a 38% reduction of

Table 2. Uncorrected nucleotide distances between Indian Ocean parrot taxa. Extinct (*M. mascarinus*, *P. wardi*, *P. exsul*, and *P. eques*) and invasive (*P. krameri*) parrots are included.

	1	2	3	4	5	6	7	8	9	10	11	12
1. <i>Coracopsis vasa</i>												
2. <i>Coracopsis vasa drouhardii</i>	0.014											
3. <i>Coracopsis barklyi</i>	0.090	0.081										
4. <i>Mascarinus mascarinus</i>	0.085	0.079	0.035									
5. <i>Coracopsis nigra libs</i>	0.086	0.079	0.038	0.036								
6. <i>Coracopsis nigra nigra</i>	0.087	0.084	0.039	0.038	0.000							
7. <i>Coracopsis sibilans</i>	0.090	0.084	0.041	0.045	0.022	0.023						
8. <i>Psittacula wardi</i>	0.148	0.136	0.124	0.111	0.141	0.145	0.148					
9. <i>Psittacula exsul</i>	0.131	0.118	0.100	0.096	0.119	0.123	0.116	0.054				
10. <i>Psittacula echo</i>	0.139	0.136	0.103	0.099	0.128	0.134	0.126	0.052	0.020			
11. <i>Psittacula eques</i>	0.133	0.127	0.096	0.097	0.129	0.129	0.127	0.051	0.029	0.002		
12. <i>Psittacula krameri</i> (Seychelles)	0.143	0.137	0.128	0.117	0.139	0.142	0.133	0.064	0.036	0.022	0.022	
13. <i>Psittacula krameri</i> (Mauritius)	0.144	0.134	0.117	0.111	0.135	0.139	0.131	0.065	0.035	0.024	0.026	0.007

**Figure 3.** Phylogenetic diversity (PD; dark grey columns) and species richness (light grey columns) for Indian Ocean parrots, under each of the three temporal grouping scenarios.

phylogenetic diversity from 98.66 to 61.64 Myr and species richness from two to one following extinctions. The introduction of Ring-necked Parakeets to Seychelles has increased phylogenetic diversity to 98.66 Myr and species richness to two. Following the invasion of *P. krameri* on Mauritius, phylogenetic diversity increased from 61.64 to 66.75 Myr and species richness from one to two (Fig. 4).

DISCUSSION

This study has provided a resolution for the phylogenetic placement of the extinct *P. exsul*, *P. eques* and *P. wardi* within the Indian Ocean *Psittacula* parrot radiation. It has also quantified the temporal and spatial effects on phylogenetic diversity due to

historical extinctions and the insidious introduction of invasive parrots across the Western Indian Ocean islands.

Evolution of the Indian Ocean parrots

The molecular phylogenetic analysis suggests the extinct island parrots experienced recent divergences within their clades, implying the Indian Ocean islands have played a key role in the evolutionary radiation of *Psittacula* parakeets. *Psittacula wardi* groups within the Alexandrine parakeets (which originate from Asia) and diverged 3.83 Mya, whereas *P. exsul* and *P. eques* group with *P. krameri* (native to Asia and Africa). *Psittacula exsul* diverged from the *P. echo* and *P. eques* lineage 3.82 Mya, with *P. echo* subsequently differentiating from *P. eques* 0.61 Mya. This recent divergence of *P. echo* and *P. eques* is consistent with previous findings that *P. echo* diverged between 0.7 and 2.0 Mya (Groombridge *et al.* 2004); however, the inclusion of newly acquired DNA sequence data from the extinct *P. exsul*, and its resolved taxonomic placement as ancestral to *P. echo*, has resulted in a more recent date of divergence for *P. echo* than that of 4.5 Mya estimated by Kundu *et al.* (2012b).

Although islands are usually colonized from their nearest mainland source, a high proportion of biota found across the Western Indian Ocean islands show affinities with Asia rather than Africa (Warren *et al.* 2010). The low sea levels over the previous 10 Myr may have facilitated radiations by 'island-hopping' from Asia towards Madagascar,

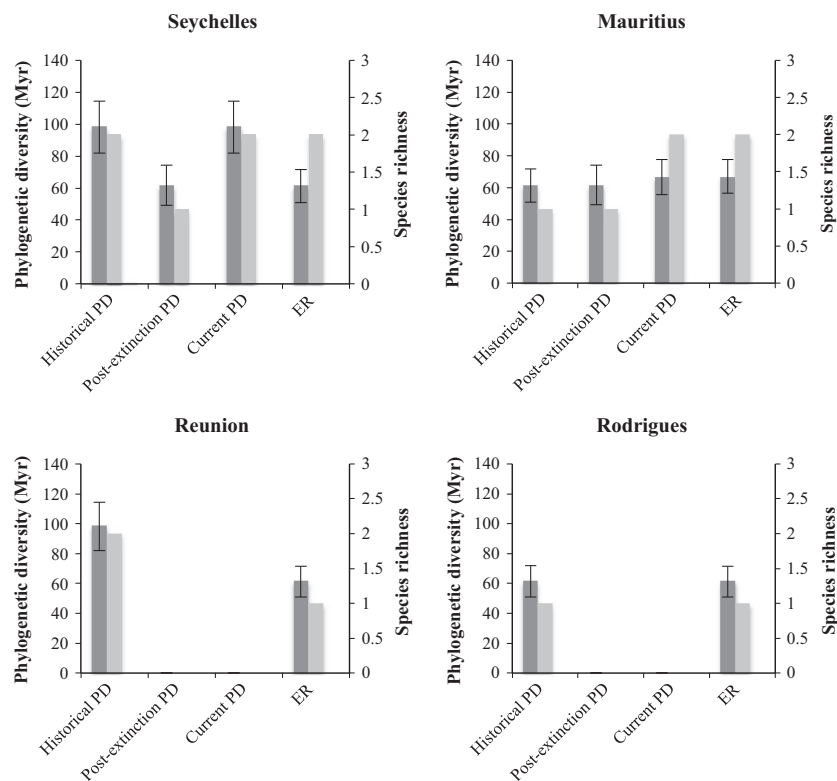


Figure 4. Phylogenetic diversity (PD; dark grey columns) in Myr and species richness (light grey columns), under each of the three grouping scenarios for four Indian Ocean islands that have experienced extinction/invasion events (Seychelles, Mauritius, Rodrigues and Reunion). An additional fourth scenario for the inclusion of ecological replacements, 'ER', gives predicted levels of phylogenetic diversity and species richness as a result of the use of the Mauritius Parakeet *Psittacula echo* as an analogue on Rodrigues and Reunion, the use of the Alexandrine Parakeet *Psittacula echo magnirostris* as an analogue on the Seychelles, and the removal of invasive Ring-necked Parakeets *Psittacula krameri* from the Seychelles.

allowing colonization of the Indian Ocean islands (Cheke & Hume 2008, Warren *et al.* 2010).

The close phylogenetic relationship and low but detectable nucleotide divergence between the single specimen of the extinct *P. eques* and the extant *P. echo* (0.2%) suggest that these island populations had evolutionarily diverged, but the low level of divergence suggests it is likely the populations on Reunion and Mauritius were only divergent at a sub-specific level. Comparable levels of nucleotide divergence are seen between some of the species of *Coracopsis* black parrots of the Indian Ocean; within this genus, values range from 0.28% between the sympatric *Coracopsis nigra libis* and *Coracopsis nigra nigra* found on Madagascar, to 1.79–4.29% between them and *Coracopsis sibilans* on Grand Comoros and *C. barklyi* on Seychelles, although recent accounts describe the Madagascan subspecies as a single species and the Grand Comoros and Seychelles forms as separate species

(del Hoyo *et al.* 2014, H. Jackson, N. Bunbury, N. Przelomska & J. Groombridge unpubl. data).

Historical and spatial changes in phylogenetic diversity

Losing evolutionarily divergent taxa can result in phylogenetic homogenization of species assemblages. Such losses of unique phylogenetic and taxonomic information may have detrimental impacts upon the capability of species' assemblages to respond to changing environments, leaving an impoverished and more homogeneous global biota (Webb *et al.* 2001, Winter *et al.* 2009). Our study has demonstrated how the extinction of four endemic parrot species and establishment of the invasive *P. krameri* has resulted in biotic homogenization across the Indian Ocean islands, reflected by the overall decrease of parrot species assemblage. In the last 500 years, a majority (> 89.3%) of the

163 documented avian extinctions have occurred on islands, with large numbers of recent avian extinctions occurring on Mauritius ($n = 18$) and Reunion ($n = 11$). Such islands have recently been highlighted as effective priority areas for the conservation of evolutionary distinctiveness and phylogenetic diversity (Jetz *et al.* 2014). Parrots have suffered a high number of extinctions (Butchart *et al.* 2006), of which half were endemic parrots from islands (Collar 2000). Our study demonstrates that the extinction of just four island forms of parrot across the Western Indian Ocean islands has resulted in a 17% loss (25 Myr) in phylogenetic diversity, with a complete loss of phylogenetic diversity in this group on the islands of Reunion and Rodrigues. With current extinction rates 1000 times faster than natural background rates of extinction (approximately 0.1 extinctions per million species per year; Pimm *et al.* 2014), our observed losses in phylogenetic diversity are much greater than would be expected, suggesting that global parrot assemblages may have experienced substantial reduction in phylogenetic diversity from the documented extinction of 20 species of parrot, many of them from island systems.

Our phylogenetic analysis suggests invasive *P. krameri* found on Mauritius and Seychelles originate from southern Asia and comprise two subspecies, *P. k. borealis* (introduced on Seychelles) and *P. k. manillensis* (introduced on Mauritius). This establishment of invasive *P. krameri* on Mauritius and Seychelles has replaced lost endemic phylogenetic diversity with non-endemic forms, which are representatives of a globally widespread continental form (Frankham 1997).

Using ecological replacements to restore lost parrot diversity

More recently, ecologists have begun to embrace evolutionary perspectives based upon the idea that closely related species are ecologically similar (Losos 2008). Our phylogenetic framework provides an opportunity to use evolutionary information to inform long-term conservation efforts. The use of ecological replacements to replace extinct species is a conservation tool for restoring lost ecological function in disrupted ecosystems (Griffiths *et al.* 2013, Hunter *et al.* 2013). This approach involves deliberately introducing a species into an environment to fill an ecological niche formerly occupied by a now extinct species (Donlan *et al.* 2006, Grif-

fiths *et al.* 2010). Ecological replacements are generally considered to be acceptable where the benefits of their expected ecological function outweigh the potential risks of them becoming detrimental to the ecosystem (Parker *et al.* 2010, IUCN/SSC 2013), for example by introducing unintended pathogens or becoming an invasive species. Despite these risks, the use of ecological replacements as a conservation management strategy has proven successful; for example, the Aldabra Giant Tortoise *Aldabrachelys gigantea* has been introduced to a number of offshore islands in Mauritius successfully refilling herbivory and seed-dispersal niches left vacant by the extinction of endemic Mauritian tortoises (Griffiths *et al.* 2010, 2011).

The extinct parrots of the Western Indian Ocean, in particular *P. exsul*, *P. wardi* and *P. eques*, represent phylogenetic diversity within *Psittacula* that is irreplaceable. However, our molecular phylogeny can inform the initial identification of the most closely related extant taxa that might form appropriate candidates. Such phylogenetically close species may exhibit patterns of phylogenetic niche conservatism (the tendency of taxa to retain ancestral niche-related traits over macro-evolutionary time: Wiens *et al.* 2010, Crisp & Cook 2012). Such divergence constraints on ecological traits between closely related species may enable successful introductions of ecological replacements into ecologically similar environments; however, introductions into contrasting environments are likely to be unsuccessful, as species are unable to adapt to their new environments (Losos 2008, Crisp & Cook 2012). The identification of such appropriate candidates for introduction on to these islands as ecological replacements may help restore ecosystem function (Griffiths *et al.* 2013, Hunter *et al.* 2013) and, on an evolutionary timescale, enable endemic phylogenetic diversity to re-evolve *in situ* (potential increases in phylogenetic diversity and species richness for each island are given under our ecological replacements scenario, see Fig. 4).

In this way, our phylogeny identifies the extant *P. echo* as the most evolutionarily appropriate ecological replacement candidate for *P. exsul* and *P. eques*, given that this species is the last remaining island representative of the *P. exsul/P. echo/P. eques* phylogenetic lineage. *Psittacula echo* was the world's rarest parrot in the 1980s when the total population consisted of fewer than 20 indi-

viduals prior to an intensive conservation management programme which restored the species' wild population to over 500 individuals by 2010 (Raisin *et al.* 2012, Tollington *et al.* 2013). Establishment of populations of *P. echo* on Rodrigues and Reunion, by way of a conservation introduction, could therefore help to secure the short-to-medium term future of this recently restored parrot population while at the same time providing phylogenetically appropriate material for longer-term evolutionary forces to act upon to return an endemic parrot form to those islands.

The introduction of endemic *P. echo* from Mauritius to Reunion and Rodrigues would probably reactivate the ecological roles that the extinct parakeets had within their ecosystems. There is accumulating evidence that there has been co-evolution on Mauritius between some of the endemic trees and the endemic parrots that fed on their fruit. Many canopy trees produce fruits that are dispersed by fruit bats (Cheke & Hume 2008) and parrots (Jones *et al.* 2013). *Psittacula echo* feeds on the fruit of canopy trees with a fleshy epicarp and very hard seeds. This parrot eats the epicarp and then discards the seeds, thereby acting as probable dispersal agent. Introducing *P. echo* to Reunion and Rodrigues as an ecological replacement would probably rejuvenate this function (Jones 1987, Jones *et al.* 2013).

Our phylogeny also suggests *P. eupatria*, from Southern Asia, as a phylogenetically appropriate potential ecological replacement for the extinct *P. wardi* on Seychelles. However, in contrast to *P. echo*, which has phylogenetic affinities to the extinct Indian Ocean parrots of Reunion and Rodrigues, and has evolved within an island ecosystem, *P. eupatria* originates from the Asian mainland and may therefore carry risks associated with invasiveness because the worst invasive species tend to be continental forms (Blackburn *et al.* 2009). Ideally, ecological replacements ought to be selected for their ecological and evolutionary similarity to the extinct species they are replacing, in order to reduce the possible unwanted risks that could accompany such introductions (Seddon & Soorae 1999, Parker *et al.* 2010). For example, extinct island species should be replaced by evolutionarily closely existing island forms. Here, our phylogeny indicates that the most suitable candidate may be *Psittacula eupatria magnirostris* from the Andaman Islands, which is basal within the *P. eupatria* clade. Our phylogenetic framework has addressed

the evolutionary component of this issue, but clearly detailed ecological studies would be required to further refine the choice of any ecological replacement.

The invasion of *P. krameri* from Southern Asia across the Indian Ocean presents a concern for conservationists. *Psittacula krameri* pose a serious threat to the surviving endemic parrot species in the Indian Ocean. They are currently being controlled on the Seychelles (Seychelles Islands Foundation, 2012) whereas the populations on Mauritius are more widely established and, as with many invasive bird populations, present a longer-term challenge. Elsewhere, *P. krameri* are known to be a crop pest across large parts of their native and invasive range (Ramzan & Toor 1973, Forshaw 2010, Ahmad *et al.* 2012). Therefore, local communities on Rodrigues who grow subsistence maize crops may be justifiably apprehensive about the purposeful introduction of the endangered *P. echo* as an ecological replacement, given that it looks very similar to *P. krameri* and might be anticipated to behave like *P. krameri* when introduced to a new environment. Our phylogenetic framework, however, lends support from an evolutionary perspective to the idea of using an endangered species from a neighbouring island as an ecological replacement, a concept which is relatively novel but is gaining wider acceptance in modern ecological restoration (Griffiths *et al.* 2010, Hansen 2010).

CONCLUSIONS

The Indian Ocean islands are an important source of endemic species that contribute substantially to global biodiversity (Whittaker & Fernández-Palacios 2007). The extinction of endemic species from islands results in a loss of historical phylogenetic diversity and reduced levels of species richness. The arrival of invasive alien species replaces lost phylogenetic diversity with non-endemic diversity represented by globally widespread continental forms. Phylogenetic frameworks can inform conservation strategies such as the use of ecological replacements to restore island ecosystems. On an evolutionary timescale these conservation initiatives may result, through natural selection, in the evolution of novel island forms and the restoration of lost phylogenetic diversity (Cadotte *et al.* 2009, Gravel *et al.* 2012).

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SUPPORTING INFORMATION

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

Appendix S1. Suite of PCR primers designed to amplify 1000 bp of the cytochrome *b* gene.

Appendix S2. Molecular phylogeny with location information alongside.

Appendix S3. Molecular dated phylogeny using an 80-Mya calibration.