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1 **Genomic erosion across avian lineages in the context of their evolutionary** 2 **history**

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1 **Abstract**

2 Loss of genetic diversity threatens species survival, yet its dynamics and impacts can vary
3 widely across species depending on their evolutionary histories, life-history traits, and
4 demographic trajectories. To investigate these differences, we analysed the genomes of
5 three species that experienced extreme and well-documented population bottlenecks, the
6 Mauritius parakeet, the Mauritius kestrel, and the pink pigeon, and compared them to 36
7 species spanning the avian phylogeny with varied IUCN Red List statuses. For each species,
8 we assessed nucleotide diversity, genetic load, and inbreeding coefficients based on runs of
9 homozygosity (F_{ROH}). We found a negative correlation between nucleotide diversity and F_{ROH} ,
10 but neither metric was a good predictor of the species' Red List status. Rather, the effective
11 population size to census size ratio (N_e/N_c) showed a strong correlation to Red List status.
12 Species with larger historical effective population sizes showed greater heterozygosity but
13 carried a higher heterozygous load, highlighting the importance of historical demography for
14 contextualising species' vulnerability to genomic erosion. We also found significant
15 differences in genetic load between taxonomic groups (parrots, pigeons and falcons),
16 possibly due to differences in life-history traits and demographic histories, underscoring the
17 importance of interpreting genomic erosion dynamics in an evolutionary context. By
18 anchoring our study on three evolutionarily divergent endangered species from Mauritius,
19 we show how multispecies comparisons can contextualize extreme bottlenecks within a
20 broader evolutionary framework, thereby identifying both general patterns of genomic
21 erosion and species-specific vulnerabilities.

1 Introduction

2 Genetic diversity is an essential component of a species' ability to adapt and persist under
3 changing environmental conditions (Spielman et al. 2004; Allendorf et al. 2013; Kardos et al.
4 2021). For small or isolated populations, maintaining genetic diversity is particularly
5 challenging, as reduced effective population size (N_e) diminishes the efficacy of natural
6 selection, intensifies genetic drift, and leads to increased inbreeding. These processes
7 ultimately lead to genomic erosion, characterised by reduced genetic diversity and the
8 accumulation or fixation of deleterious mutations (van Oosterhout et al. 2022). As
9 inbreeding becomes more frequent, recessive deleterious mutations are increasingly
10 exposed, intensifying negative effects and leading to inbreeding depression (Charlesworth
11 and Willis 2009; Blomqvist et al. 2010; Hasselgren et al. 2021). These processes collectively
12 reduce fitness and adaptive potential, heightening vulnerability to environmental changes
13 and threatening the long-term persistence of the population (Blomqvist et al. 2010;
14 Hasselgren et al. 2021; Jackson et al. 2022; van Oosterhout et al. 2022; Jeon et al. 2024).
15 Additionally, even populations that have partially recovered demographically retain the
16 genetic legacy of past bottlenecks, known as "drift debt", which manifests as a time lag
17 between population decline and loss of genome-wide variation (Dussex et al. 2023; Gilroy et
18 al. 2017; Pinto et al. 2024). Recent analyses have shown that species are losing genetic
19 diversity worldwide (Exposito-Alonso et al. 2022; Shaw et al. 2025), highlighting the need for
20 cross-species comparisons to improve our understanding of genomic erosion in biodiversity
21 conservation.

22 With the continuous and rapid production of genomic data for wild species worldwide,
23 conservation genomics can now take advantage of high-resolution tools to assess genetic
24 diversity and genetic load (Lewin et al. 2018; Wright et al. 2020; van Oosterhout et al. 2022;
25 Theissinger et al. 2023). For species at risk of extinction, such insights are critical for guiding
26 conservation interventions aimed at reducing genetic load and enhancing population
27 viability (e.g., vaquita (Morin et al. 2021), kākāpō (Dussex et al. 2021), pink pigeon (Speak et
28 al. 2024)). Genome-wide comparisons can also provide insights into an endangered species'

1 susceptibility to introgression from closely related species (Rieseberg 2001; Serrato-
2 Capuchina and Matute 2018; Fontdevila 2019), and opportunities for genetic rescue
3 (Whiteley et al. 2015; Bell et al. 2019). Additionally, using genomic resources across multiple
4 species within a comparative framework may provide valuable insight into how evolutionary
5 and demographic histories shape genomic patterns over both short and long timescales
6 (Grueber 2015). This approach can elucidate how evolutionary history interacts with
7 genomic traits, such as genetic diversity, genetic load, or structural variations, to influence
8 species' long-term viability and extinction risk.

9 The Mauritius parakeet (*Alexandrinus [Psittacula] eques*), Mauritius kestrel (*Falco*
10 *punctatus*), and pink pigeon (*Nesoenas mayeri*) exemplify how species can recover
11 demographically from near extinction but remain genetically imperilled. These birds,
12 endemic to Mauritius—a species-rich archipelago in the Indian Ocean that has witnessed
13 over 100 species extinctions in recent centuries (Florens 2013)—experienced some of the
14 most extreme population bottlenecks ever recorded in wild populations. Only four Mauritius
15 kestrels remained by 1974, the pink pigeon declined to ~10 individuals by 1990, and the
16 Mauritius parakeet to just ~20 individuals by 1986 (Jones and Swinnerton 1997; Jones 2013;
17 Jones et al. 2013). Intensive conservation management facilitated their demographic
18 recovery to current free-living adult population sizes of approximately 250 Mauritius kestrels,
19 500 pink pigeons, and 650 Mauritius parakeets (Jones and Swinnerton 1997; Jones 2010;
20 Nicoll et al. 2021) (Figure 1D). Although these species belong to evolutionarily distant
21 lineages, they underwent similar demographic trajectories of collapse and recovery,
22 providing independent yet comparable case studies to examine the genomic consequences
23 of population decline and recovery across birds.

24 Despite these recoveries, the legacy of the extreme historical population collapses can
25 jeopardise their long-term viability, as genetic diversity in these species continues to decline
26 due to the accrued drift debt (Tollington et al. 2013; Jackson et al. 2022). These species are
27 also at risk of accumulating an increased genetic load of deleterious mutations, as has been
28 shown in the pink pigeon (Jackson et al. 2022). Beyond genetic challenges, ecological
29 pressures such as habitat loss and degradation persist, compounded by threats like

1 emerging infectious diseases, which can affect individual fitness and population viability
2 (Tollington et al. 2015).

3 This study investigates the interplay between genome-wide diversity, genetic load,
4 demographic history, and conservation status across a diverse set of avian species. Using
5 recently generated, high-quality chromosome-level reference genomes for three focal
6 Mauritian species – the Mauritius parakeet, pink pigeon and Mauritius kestrel – we compared
7 them to 36 species spanning the avian phylogeny. Placing these species in a broader
8 phylogenetic context allowed us to distinguish general temporal trends from lineage-
9 specific outcomes and to evaluate how such insights can inform conservation assessments
10 and prioritisation. By further focusing on species within the same orders as the Mauritian
11 taxa, we explored potential lineage-specific differences in genomic metrics to contextualise
12 the genetic risk of the Mauritius species against the backdrop of their phylogenetic
13 background and to inform conservation priorities for other vulnerable birds.

1 **Materials and Methods**

2 **Dataset**

3 The reference genomes from three bird species endemic to Mauritius—the Mauritius
4 parakeet (Morales, Groombridge, et al. 2024), the pink pigeon (Morales, Van Oosterhout, et
5 al. 2024), and the Mauritius kestrel (Morales, Norris, et al. 2024)—were recently sequenced
6 and reported. All three genomes were generated from samples collected post-bottleneck,
7 from 2020 to 2021. To build a comparative dataset, 36 additional bird species were selected
8 based on the availability of relatively high-quality reference genomes, prioritizing assemblies
9 with higher scaffold N50, larger average scaffold size, and lower scaffold count within each
10 taxonomic group, while also ensuring a comprehensive representation across the avian
11 phylogeny (Figure 1B). Although no strict thresholds were applied, the majority of selected
12 genomes had scaffold N50 values >2 Mb and >85% of their genome contained within
13 scaffolds >500 kb; a small number of species with slightly lower metrics were included to fill
14 key phylogenetic gaps. Metadata for all 39 species, including current census population
15 sizes, IUCN conservation statuses, and assembly statistics are compiled in Table S1.

16 **Mapping and variant calling**

17 Raw reads used for assembling the reference genomes were downloaded from NCBI (see
18 Table S1 for Assembly IDs) and aligned to the corresponding genomes. NGS short reads were
19 mapped using BWA (v0.7.17) mem (Li and Durbin 2009) with default parameters. Read
20 duplicates were marked with GATK (4.4.0.0) MarkDuplicates (DePristo et al. 2011). PacBio
21 HiFi reads were mapped and sorted using pbmm2 v1.5.0
22 (<https://github.com/PacificBiosciences/pbmm2>) with the parameter “--preset HIFI”. GATK
23 HaplotypeCaller was used to call variants for each alignment. Only SNPs were kept for
24 further analyses.

25 **Depth**

1 After mapping the raw reads to each reference genome, we estimated the average genome-
2 wide and per scaffold depth in each genome using MosDepth v0.3.3 (Pedersen and Quinlan
3 2018).

4 **Sex chromosome removal**

5 Each reference genome was mapped to the chicken genome (assembly GRCg6a) with
6 minimap2 v2.1 (Li 2018). Any scaffold mapped to chicken sex chromosomes for more than
7 20% was treated as potential regions from sex chromosomes and removed for further
8 analyses. Any additional scaffolds annotated in the reference genomes as sex
9 chromosomes were also removed.

10 **Heterozygosity**

11 We estimated genome-wide heterozygosity using ANGSD (Korneliussen et al. 2014). We first
12 obtained genotype likelihoods on scaffolds larger than 500 kb and only considered sites with
13 a depth of depth between $\frac{1}{3}$ (-setMinDepth) and two times (-setMaxDepth) the average depth
14 for each sample. We assumed that the reference and ancestral states were the same. We
15 applied the following parameters: -uniqueOnly 1 -remove_bads 1 -only_proper_pairs 1 -C 50
16 -baq 0 -minMapQ 30 -minQ 20 -setMinDepth \$minDP -setMaxDepth \$maxDP -doCounts 1 -
17 GL 2 -doSaf 1. Next, we calculated the folded site frequency spectrum (SFS) with realSFS.

18 To compare different estimations of heterozygosity, we also estimated genome-wide
19 heterozygosity directly from the VCF files with a custom pipeline. First, we divided scaffolds
20 into sliding windows of size 100 kb (with a slide of 50 kb) using bedtools makewindows
21 v2.30.0 (Quinlan and Hall 2010). Next, we obtained the total number of callable
22 heterozygous and total callable genotypes per window using bcftools v1.20 (Danecek et al.
23 2021), tabix v1.14 (Li 2011), and vcfhetcount from vcflib (Garrison et al. 2022). Genotypes
24 were considered callable if their read depth was between $\frac{1}{3}$ and 2 times the average depth
25 per sample and had a minimum genotype quality (GQ) of 30 or reference genome quality
26 (RGQ) of 10, indels and multiallelic sites were excluded. Only non-missing and quality
27 filtered sites (callable) were considered in each window and used as total callable genotypes

1 in the denominator. Windows with less than 50% callable sites relative to the window size
2 were removed for analysis.

3 **Runs of Homozygosity (ROH)**

4 As some reference genomes were assembled with only Pacbio long reads, and no short-read
5 data are available for the same individual, commonly used methods like ROHan (Renaud et
6 al. 2019) could not be applied to identify ROH. To address this limitation, we developed a
7 custom method for this analysis. Given the varying fragmentation levels of the assemblies
8 (Table S1), for each species, we retained only scaffolds with a minimum size of 5 Mb. As a
9 result, two species (Red-faced mousebird, *Urocolius indicus* and Wilson's storm petrel,
10 *Oceanites oceanicus*) were excluded. We identified ROH based on per-window
11 heterozygosity estimates (see above). Using the R package bedtoolsr (Patwardhan et al.
12 2019), we concatenated windows with a heterozygosity lower than $5e^{-4}$ bp⁻¹ (Figure S1),
13 except for two genomes with exceptionally low average heterozygosity (the flightless
14 cormorant, *Nannopterum harrisi*, and Mauritius kestrel), for which a lower threshold of $1e^{-4}$
15 bp⁻¹ was used. Adjacent homozygous regions were merged if separated by a gap shorter than
16 100 kb, and only ROHs with a minimum size of 500 kb were retained. The inbreeding
17 coefficient (F_{ROH}) was calculated as the ratio of the total length of ROH segments to the total
18 length of the analyzed genome (scaffolds > 5 Mb). We also estimated heterozygosity for the
19 analyzed scaffolds per species, both including and excluding ROHs. To obtain the
20 heterozygosity outside ROHs, we subtracted the windows that fall within a ROH for the
21 estimation.

22 To validate our custom method, we compared our ROH estimates with those from ROHan
23 for five species for which short-read data were available. ROHan was employed using a
24 window size of 100Kb and a rohmu of $5e^{-4}$ to mimic the parameters used in the custom
25 method.

26 **Genetic load**

27 To compare genetic load across species, we used Combined Annotation-Dependent
28 Depletion (CADD) score annotations (Kircher et al. 2014). CADD score integrates multiple

1 genome annotations to rank the deleteriousness of any possible single-nucleotide variant,
2 including conservation metrics (e.g., GERP, Cooper et al. 2005), regulatory and transcript
3 information, and protein-based scores (e.g., SIFT, Ng and Henikoff 2003). While CADD
4 annotation of deleteriousness of mutations is generally consistent with regular functional
5 annotation based on protein-coding information (Fontseré et al. 2025) such as SnpEff
6 (Cingolani et al. 2012), CADD can also rank mutations in the introns and intergenic regions.
7 We used the CADD score calculated for chicken genome (Groß et al. 2020) and transferred
8 them to evolutionary conserved regions of the genome (ultraconserved elements, UCEs) in
9 our target species. UCEs are highly conserved in vertebrates over a long evolutionary period,
10 especially in birds (Cummins et al. 2024). Though mainly in non-protein coding regions
11 (introns or lncRNA genes), mutations in UCEs, especially with a high CADD score, are
12 expected to have a strong deleterious effect (Speak et al. 2024). We extracted UCE regions
13 and corresponding flanking regions from each reference genome and from the chicken
14 genome (GRCg6a), and performed a multi-species alignment for each UCE, using the
15 recommended pipeline of Phyluce v1.7.3 (Faircloth 2016) (see Figure S2 for detailed pipeline).
16 Each genome was converted from fasta to 2bit format using UCSC FaToTwoBit (Casper et al.
17 2018). The UCE probe file was downloaded from [https://github.com/faircloth-lab/uce-](https://github.com/faircloth-lab/uce-probe-sets/tree/master/uce-5k-probe-set)
18 [probe-sets/tree/master/uce-5k-probe-set](https://github.com/faircloth-lab/uce-probe-sets/tree/master/uce-5k-probe-set), and used to extract and validate UCE regions per
19 species. The CADD score file of the chicken genome was downloaded from
20 <https://osf.io/c97ez>. For each species, CADD scores were lifted from the chicken genome
21 for homozygous (relative to chicken) and heterozygous sites across UCE regions with
22 customised scripts partially adapted from LoadLift (Speak et al. 2024). Heterozygous sites
23 were extracted from VCF files and filtered using bcftools with the same parameters used for
24 heterozygosity estimations (see above). Only heterozygous sites with one allele equal to the
25 corresponding site in the chicken genome were kept for further analyses.

26 To quantify genetic load in each genome, we counted the number of heterozygous sites and
27 homozygous substitutions with CADD scores ≥ 20 in UCE regions, representing the top 1%
28 most deleterious sites in the chicken genome. To control for the evolutionary distance to the
29 chicken among species, we rescaled the counts of sites with CADD scores ≥ 20 by dividing

1 them with the counts of substitutions with CADD scores < 3 , the latter representing nearly-
2 neutral sites. The rescaled ratios of heterozygous sites and homozygous substitutions were
3 used as inference of heterozygous and homozygous load. We distinguished these two
4 classes because, according to theory (Bertorelle et al. 2022), deleterious homozygous
5 positions are expressed, approximating the realised load, whereas (recessive) heterozygous
6 positions are not expressed, approximating the masked load. However, in the absence of
7 precise estimates of dominance coefficients, these are only approximations, and we
8 therefore prefer to refer to them as the homozygous and heterozygous load.

9 To account for potential lineage-specific adaptive substitutions that have occurred since the
10 divergence with chicken, homozygous substitutions that were shared by 20 or more species
11 were excluded, as these are more likely to reflect long-term adaptive changes rather than
12 harmful mutations. To further confirm that we were correctly retaining sites that have not
13 changed since the divergence with chicken, we compared three species (saker falcon, *Falco*
14 *cherrug*; budgerigar, *Melopsittacus undulatus*; and rock pigeon, *Columba livia*) included in
15 the phylogenetic tree by (Feng et al. 2020), to their closest reconstructed ancestral nodes in
16 the tree, which correspond to genus or family level. The command “hal2fasta” from HAL
17 tools v2.3 (Hickey et al. 2013) was used to extract the sequences of the ancestral nodes from
18 the genome-level alignment from this phylogenetic tree of 363 bird species. We extracted
19 the reconstructed full sequences from the closest ancestral nodes and cut them into 200-
20 bp short sequences with 20-bp step sliding windows. The reads were mapped to the chicken
21 genome with BWA. For each species, we confirmed that homozygous substitutions had at
22 least one ancestral read mapped to the chicken genome, and the ancestral state matched
23 the chicken sequence. Homozygous substitutions with CADD scores above 20 are
24 concentrated at the terminal branches of the phylogenetic tree of birds (Figure S3),
25 indicating that they are more likely to be deleterious substitutions than lineage-specific
26 adaptations. Although we cannot rule out lineage-specific adaptive substitutions when
27 measuring homozygous load, focusing on sites with CADD > 20 within the most conserved
28 regions provides a higher likelihood of targeting truly deleterious variation (Rentzsch et al.
29 2019; Speak et al. 2024; Fontseré et al. 2025) (Figure S3). As above, the counts of

1 substitutions with CADD scores < 3 , considered as nearly-neutral sites, were used to rescale
2 the counts of sites with CADD scores ≥ 20 .

3 **Demographic history**

4 We inferred historical fluctuations of effective population size (N_e) for each species using
5 PSMC (Li and Durbin 2011) with the parameters “-N30 -t5 -r5 -p 1+1+1+1+30*2+4+6+10”
6 (Hilgers et al. 2025) and estimated the harmonic N_e mean from 10 kya to 100 kya for further
7 analyses. The generation times and mutation rates used for PSMC can be found in Table S1.
8 Generation times were retrieved from IUCN Red List (IUCN 2024), and the source of mutation
9 rates were listed in Table S1.

10 **Statistical and phylogenetic comparative analyses**

11 To explore the relationships among genome-wide heterozygosity, F_{ROH} , N_e , and genetic load
12 across species while accounting for phylogenetic signals, we reconstructed the
13 phylogenetic relationships among the studied species and incorporated this inference into
14 two statistical frameworks. The phylogeny was reconstructed from a subset of the UCE
15 dataset described above (see *Genetic Load* section). Using the software AMAS (Borowiec
16 2016), we selected and concatenated 1,526 UCE sequences, retaining only loci with $\leq 2\%$
17 missing data and $>30\%$ parsimony-informative sites. As previously published phylogenies
18 did not include the target Mauritius species, we used IQ-TREE (Minh et al. 2020) to infer a
19 maximum-likelihood tree using the edge-linked partition model (Chernomor et al. 2016)
20 constraining deeper relationships based on the topology from Stiller et al. (2024) This
21 approach allowed us to integrate our focal species into a well-supported, coalescent-
22 informed avian phylogeny. Using this inferred phylogenetic tree, we assessed different
23 univariate models with a phylogenetic generalised least squares (PGLS) approach
24 (Freckleton et al. 2002). These analyses were conducted using the R packages *ape* (Paradis
25 et al. 2004; Paradis and Schliep 2019), *caper* (Orme et al. 2023) and *nlme* (Pinheiro et al.
26 2014). When PGLS indicated a non-zero lambda (λ) value, suggesting a significant
27 phylogenetic signal, we further examined these effects using a Bayesian phylogenetic

1 generalised linear mixed model (pGLMM) (Hadfield and Nakagawa 2010). In this framework,
2 the phylogenetic relationship among species was modelled as a random effect. pGLMM
3 analyses were performed using the R packages *ape* and *MCMCglmm* (Hadfield 2010).

4 **Genomic synteny**

5 We inferred multi-genome synteny for chromosome-level reference genomes for pigeons
6 (three species in Columbidae), parrots (five species in Psittaciformes), and falcons (six
7 species in *Falco*) separately using ntSynt v1.0.2 (Coombe et al. 2024) with the divergence
8 range (-d) set to 10. Synteny results were visualised using scripts from ntSynt based on the
9 R package *gggnomes* (Hackl et al. 2024).

10 **Identification of Transposable Elements**

11 To annotate repetitive elements (RE) in the genomes of the pink pigeon, Mauritius kestrel,
12 and Mauritius parakeet, we produced *de novo* libraries of RE for each species using
13 RepeatModeler2 (Flynn et al. 2020). We combined the *de novo* libraries with previously
14 published manually curated libraries of RE from the Collared flycatcher (*Ficedula albicollis*)
15 and Blue-capped cordon-bleu (*Uraeginthus cyanocephalus*) from Storer et al. (2021), and
16 from the Emu (*Dromaius novaehollandiae*), Anna's hummingbird (*Calypte anna*), and
17 Kākāpō (*Strigops habroptilus*) from Peona et al. (2021). Using the resulting custom libraries,
18 we annotated the RE from the genomes using RepeatMasker version 4.0.8 (Smit et al. 2015).
19 We repeated this process for three, five and four additional species of Columbiformes,
20 Falconiformes and Psittaciformes, respectively, to enable comparisons of proportions of RE
21 across species.

22 **Results**

23 **Genome-wide diversity and inbreeding**

24 The sequencing depth across the dataset ranged between 15x and 96x (mean = 46, SD = 19).
25 We estimated genome-wide heterozygosity with both genotype likelihoods in ANGSD and by
26 SNP-calling, resulting in very similar estimates (adjusted $R^2 = 0.78$; Table S1, S2, Figure S4).
27 We used heterozygosity estimates from ANGSD for all subsequent analyses, except for the

1 estimation of ROHs (see Material and Methods). Neither heterozygosity or F_{ROH} estimates
2 showed significant correlation with the quality of the genomes (e.g., N50) or depth (Figure
3 S5). Our in-house method produced consistent ROH results to those from ROHan (Figure
4 S6), validating our approach.

5 Consistent with recent demographic change, genome-wide heterozygosity showed a strong
6 negative correlation with inbreeding coefficient F_{ROH} (Figure 1C; PGLS: $\lambda = 0$, $R^2 = 0.46$, $F_{1-28} =$
7 26.56 , $p < 0.001$). Samples with domestic or pet origins (Figure 1C, Table S1) are outliers with
8 higher F_{ROH} compared to wild samples with similar levels of heterozygosity (Figure 1C), and
9 higher heterozygosity outside of ROH regions compared to genome-wide heterozygosity
10 (Figure S7); we therefore excluded them from further analyses. IUCN Red List status did not
11 correlate with genome-wide heterozygosity, F_{ROH} (Figure S8) or genetic load (Figure S9).

12 Comparing historical N_e (between 10 kya and 100 kya estimated from PSMC) to current
13 census size (N_c) reveals the magnitude of recent demographic change, with elevated values
14 indicating more abrupt declines. The N_e/N_c ratio ($\text{Log}(N_e)/\text{Log}(N_c)$) was significantly lower
15 (Wilcoxon two-sample test $p < 0.001$) in non-threatened species (Least Concern, mean =
16 0.91 , $SD = 0.23$) compared to threatened species (remaining IUCN status categories, mean
17 = 1.49), yet more varied ($SD = 0.52$). N_e/N_c ratio showed a strong linear correlation with
18 IUCN status (Figure 1D, GLM: $R^2 = 0.43$, $F_{1-24} = 12.49$, $p < 0.001$), when numerically coded
19 from 0 Critically Endangered to 4 Least Concern. To disentangle the contribution of each
20 component, we tested log-transformed N_c and N_e separately (Figure S8). In these tests, only
21 N_c was significant ($p = 0.0186$, $R^2 = 0.27$), whereas N_e was not. However, the N_e/N_c ratio
22 explained more variance than either component alone ($p < 0.001$, $R^2 = 0.43$), indicating that
23 the ratio captures additional, meaningful variation. Moreover, the N_e/N_c ratio reveals
24 discrepancies that are not evident from N_c alone. For example, the pink pigeon and the
25 whooping crane (*Grus americana*) both exhibit unusually high N_e/N_c ratios (2.19 and 2.59 ,
26 respectively) compared to other species within the same IUCN categories (Vulnerable and
27 Endangered, respectively). These elevated ratios point to a history of intense demographic
28 decline despite currently recovered census sizes, underscoring that the severity of
29 underlying genomic erosion is not apparent with N_c or N_e alone.

1 Historical demographic trends (N_e) have a significant positive correlation with genome-wide
2 heterozygosity (Figure 2A; PGLS: $\lambda = 0$, $R^2 = 0.47$, $F_{1-22} = 19.65$, $p = 2.1e^{-4}$). In contrast, F_{ROH}
3 showed no significant correlation with historical N_e (Figure 2D; PGLS: $\lambda = 0$, $R^2 = 0.11$, $F_{1-22} =$
4 2.82 , $p = 0.11$). This lack of correlation is not surprising as the inbreeding coefficient is
5 expected to have a nonlinear relationship with N_e (Reed et al. 2003), because inbreeding
6 increases rapidly in small populations but approaches equilibrium asymptotically as N_e
7 grows. Furthermore, our analysis focused only on long ROHs (> 500 Kb), which reflect
8 population history within tens to hundreds of generations ago.

9 Species with higher genetic diversity or a lower inbreeding coefficient tended to carry a
10 higher heterozygous load, calculated as the corrected ratio of heterozygous sites with a
11 CADD score above 20 (Figure 2B; PGLS: $\lambda = 0$, $R^2 = 0.61$, $F_{1-30} = 45.99$, $p = 1.6e^{-7}$, and Figure
12 2E; PGLS: $\lambda = 0$, $R^2 = 0.19$, $F_{1-28} = 6.74$, $p = 0.015$). In contrast, estimated homozygous load,
13 calculated as the corrected ratio of homozygous substitutions with a CADD score above 20,
14 showed a statistically significant but weak association with heterozygosity (Figure 2C; PGLS:
15 $\lambda = 0.81$, $R^2 = 0.16$, $F_{1-30} = 5.61$, $p = 0.0245$), and no association with F_{ROH} (Figure 2F; PGLS: λ
16 $= 0.86$, $R^2 = 0.02$, $F_{1-28} = 0.61$, $p = 0.4424$). Because $\lambda \approx 0.8$ indicated phylogenetic signal in
17 the residuals, we refitted these models using a phylogenetic GLMM (pGLMM) with a
18 random effect for shared ancestry. This model recovered the same fixed-effect pattern, as
19 heterozygosity remained significant and F_{ROH} non-significant, but revealed that phylogenetic
20 variance was negligible compared to residual variance ($\sigma^2_{phylo} \approx 4.1 \times 10^{-14}$; $\sigma^2_{species} \approx$
21 1.0×10^{-14} ; Table S3). Thus, although residuals appeared phylogenetically structured in the
22 PGLS, shared ancestry explained little additional variation once predictors were included,
23 indicating that phylogenetic relatedness is not a major determinant of homozygous load
24 variation. Although statistically significant, the association between homozygous load and
25 heterozygosity remained weak, and the absence of a positive correlation between
26 homozygous load and F_{ROH} was unexpected (Kyriazis et al. 2025). This pattern may reflect the
27 influence of deep-time factors such as lineage-specific mutation rates, adaptive

1 substitutions, or life-history differences. Moreover, because only one individual per species
2 was analyzed, it remains difficult to distinguish fixed substitutions accumulated through
3 deep phylogenetic time from genuinely deleterious homozygous alleles (see Discussion).

4 **Genomic features within and across taxonomic groups**

5 Despite similar distribution ranges and histories of population decline in the past decades
6 (Figure 1A), the three Mauritius species showed contrasting levels of genetic heterozygosity,
7 inbreeding coefficients (Figure 1C, 3AB), and homozygous load (Figure 3C). The Mauritius
8 kestrel had the lowest heterozygosity of all samples (8.33×10^{-5} het x bp⁻¹) and the second
9 highest F_{ROH} (0.71) among the wild species included in this study, with 50% of its genome in
10 very long ROHs (>10 Mb), as evidence of sustained recent inbreeding after recovering
11 demographically from a bottleneck of only four individuals. The Mauritius parakeet had the
12 second lowest heterozygosity (8.07×10^{-4} het x bp⁻¹) among parrots, closely following another
13 extremely bottlenecked species, the critically endangered Kākāpō (*Strigops habroptilus*).
14 However, the Mauritius parakeet's F_{ROH} , while high (0.40), is lower than that of the Kākāpō
15 (0.69), with 24.7% of the Mauritius parakeet's genome in ROHs longer than 10 Mb, evidence
16 of their extreme bottleneck of ~12 individuals. The pink pigeon exhibits a heterozygosity of
17 2.38×10^{-3} het x bp⁻¹, the lowest among the analysed pigeons, but higher than more than
18 half of the species included in the study and nearly 30 times greater than the Mauritius
19 kestrel. Additionally, the pink pigeon showed an F_{ROH} of 0.26, with 12.3% of its genome in
20 ROHs of a length longer than 10 Mb (Figure S7).

21 Reflecting a deeper evolutionary process, the differences in genetic diversity of Mauritius
22 species were associated with the differences between their taxonomic groups (Figure 3).
23 Falcons exhibit lower heterozygosity (one-side Wilcoxon test $p=0.07$) than the other two
24 taxonomic groups. Likewise, falcons carry 23.7% less homozygous load than the parrots
25 ($p=0.001$) and 29.7% less than the pigeons ($p=0.005$). No significant difference of F_{ROH} found
26 between taxonomic groups. Within their respective taxonomic groups, the three Mauritius
27 species showed the lowest genome-wide heterozygosity (Figure 3A) and the highest F_{ROH}
28 (Figure 3B). Genetic diversity estimates carry the signal of ancestral population size, as the

1 three Mauritius species had relatively low population sizes within their respective taxonomic
2 groups (Figure 3D). However, the pink pigeon had a larger historical population than most
3 studied species, including falcons and parrots, which is reflected in its higher heterozygosity
4 compared to the average levels in the other taxonomic groups (Figure 3A). This reveals the
5 importance of considering genetic diversity within the context of a species' long-term
6 evolutionary history and taxonomic group. Note that all species that we have included from
7 Falconiformes are from the same genus, *Falco*, with a divergence time of 12 million years
8 (Kumar et al. 2022), which could explain the small deviations for heterozygosity and
9 homozygous load, whereas the divergence time of the study Columbiformes and
10 Psittaciformes species was roughly 16 and 55.6 million years, respectively (Figure S10).

11 We examined synteny and repetitive element content in the three Mauritius species to
12 ensure that their differences did not confound interspecific comparisons. All exhibited
13 conventional avian genome structures, with conserved synteny to their closest relatives
14 (Figure S10) and typical repetitive element proportions (15–20%; Figure S11; Hughes &
15 Piontkivska 2005), consistent with previous reports of lower repeat content in birds relative
16 to mammals.

17 Discussion

18 By analysing 39 avian genomes spanning diverse taxonomic groups, we show that the
19 dynamics of genetic diversity, genetic load, and inbreeding are shaped by both recent
20 demographic changes and deep evolutionary history. While the genomic effects of recent
21 population decline have been well documented (van der Valk, Diez-del-Molino, et al. 2019;
22 Hasselgren et al. 2021; Khan et al. 2021; Cavill et al. 2024), we show how deep demographic
23 history also exerts a long-lasting influence on patterns of genomic erosion. As a result,
24 species from different taxonomic groups exhibit distinct levels of heterozygosity and genetic
25 load, underscoring the need to account for both demographic history and phylogenetic
26 context when comparing genomic metrics. Using three Mauritian species as focal case
27 studies, we illustrate how comparative analyses can uncover conservation-relevant patterns
28 that would be overlooked in single-species studies. Despite challenges in standardizing

1 genomic metrics across diverse taxa, our findings demonstrate how evolutionary history
2 constrains the interpretation of genomic metrics widely used in conservation, highlighting
3 the value of comparative frameworks for advancing biodiversity conservation.

4 **Conservation status is shaped by recent and long-term history**

5 Genetic diversity has been considered a classical indicator for population resilience and risk
6 of extinction (Breed et al. 2019; DeWoody et al. 2021; Teixeira and Huber 2021; Jeon et al.
7 2024). Consistent with this expectation, we observed a negative correlation between
8 genome-wide heterozygosity (a proxy of genetic diversity), and F_{ROH} (a proxy of inbreeding)
9 (Figure 1C), reflecting intensified inbreeding and genetic drift in recently small populations
10 (Brüniche-Olsen et al. 2018; Grossen et al. 2020). Reference genomes sequenced from
11 domestic or pet samples had elevated F_{ROH} , despite relatively high heterozygosity outside
12 ROHs, highlighting how recent inbreeding can bias genome-wide heterozygosity estimates
13 and the importance of checking sample origin when using public genomic data (Figure S7).

14 Over longer evolutionary timescales (10,000 to 100,000 years ago), genetic diversity was
15 strongly correlated with historical population size (Figure 2A), indicating that present-day
16 genomic variation continues to reflect ancient demographic history. This suggests that
17 species' genetic susceptibility to future habitat and environmental change is associated with
18 its ancient demographic history, even prior to the accelerated recent environmental changes
19 induced by human activity (Tan et al. 2023). F_{ROH} on the other hand, did not show a strong
20 correlation with the historical population size (Figure 2D), as it should instead reflect the
21 effect of recent demographic change (Ceballos et al. 2018). Consequently, joint monitoring
22 of demographic, environmental, and genetic change – using complementary genomic
23 metrics – is essential for evaluating short- and long-term risks. This is particularly important
24 for species with historically low genetic diversity, as they may remain more vulnerable to
25 future environmental shifts even if current population sizes appear stable (Ellstrand and
26 Elam 1993; van der Valk et al. 2019; Brüniche-Olsen et al. 2021; Liu et al. 2025; Willi et al.
27 2006).

1 Data on modern census population sizes (N_c) are undoubtedly crucial in conservation
2 assessments (Shaffer 1981; Lande 1988; Willi et al. 2006; Frankham et al. 2014), with the
3 rate of demographic decline being one of the major factors considered by the IUCN Red List
4 rating (Frankham et al. 2014; McNeely et al. 1990). However, the N_e/N_c ratio, reflecting the
5 balance between long-term genetic diversity and current population size, can also have a
6 prominent role in conservation assessments (Frankham 1995; Kalinowski and Waples 2002).
7 Elevated N_e/N_c ratios based on current N_e likely reflect genetic erosion that has already
8 occurred, while elevated ratios based on historical N_e reflect recent demographic declines
9 that have not yet resulted in a proportional loss of genome-wide diversity. The latter ratio
10 reflects the time-lag between population decline and genetic diversity loss (Gargiulo et al.
11 2024), resulting from the drift debt (Gilroy et al. 2017; Dussex et al. 2023; Pinto et al. 2024;
12 Liu et al. 2025), and serves as an early warning sign of an imminent population collapse
13 (Amos and Balmford 2001; Wilder et al. 2023). In this study, we use historical N_e estimated
14 via PSMC, enabling a comparison across many species without the need for population-level
15 sampling. We find that elevated N_e/N_c ratios are associated with higher IUCN risk categories
16 (Figure 1D). Although the correlation between IUCN status and N_e/N_c ratio is mainly driven
17 by N_c (Figure S8), as IUCN rating is partly based on current population sizes, the N_e/N_c ratio
18 has a stronger correlation to IUCN status than N_c alone (Figure S8), suggesting that it
19 captures additional demographic-genetic dimensions. Notably, species such as the pink
20 pigeon and whooping crane exhibit unusually high N_e/N_c ratios relative to their IUCN
21 category, revealing discrepancies that may signal severe ongoing genomic erosion, as a
22 result of a sharp historical demographic decline despite demographic recovery. This
23 highlights the value of integrating genomic data into conservation assessments to better
24 capture long-term genetic threats, as previously discussed for these species (Jackson et al.
25 2022; Fontseré et al. 2025). One potential caveat is the uncertain sampling time of the
26 biological materials used to develop the reference genomes, which could bias our analyses
27 of IUCN status, since nine out of 39 species had status changes within the past 20 years.
28 Our findings indicate that the N_e/N_c ratio, even when based on historical N_e , is not only a
29 meaningful indicator of conservation status (Figure 1D), but also a potential flag for

1 discrepancies between genomic erosion and current IUCN status. This underscores the
2 importance of understanding and incorporating long-term demographic history into
3 conservation assessments to better capture latent genetic risks.

4 **Interpreting genetic load patterns across species**

5 Our results highlight that the relationship between diversity and load must be interpreted in
6 light of evolutionary timescale and demographic context. We found a strong positive
7 correlation between the relative number of heterozygous deleterious sites – a proxy for
8 masked load – and genome-wide heterozygosity (Figure 2B). Therefore, similarly to genetic
9 diversity, masked load is also shaped by demographic history. Population decline often
10 leads to the expression of masked genetic load, driven by genetic drift and reduced purging
11 (van der Valk, Diez-del-Molino, et al. 2019; Dussex et al. 2023). With habitat loss predicted
12 to intensify in the near future, resulting in accelerated population declines and loss of
13 genetic diversity (Exposito-Alonso et al. 2022), species with currently higher diversity may
14 face rapid exposure of these deleterious mutations before effective purging can occur,
15 increasing the risk of fitness reductions and jeopardising population viability (van
16 Oosterhout et al. 2022). Therefore, estimating heterozygous load remains highly informative,
17 as it integrates demographic and selective history and may ultimately help predict
18 population fitness once empirical links are established.

19 Our results reveal that species with lower genetic diversity exhibit reduced homozygous load
20 (Figure 2C). This contrasts population-genetics expectations that small low-diversity
21 populations accumulate more deleterious mutations through genetic drift (Kimura et al.
22 1963; Bertorelle et al. 2022; Robinson et al. 2023), and with empirical studies (Khan et al.
23 2021; Wang et al. 2023), based on standing variation under constant selection coefficients.
24 Several factors may explain this apparent discrepancy.

25 First, our estimates rely on single individuals per species, which limits the resolution of
26 polymorphic deleterious alleles and sensitivity to recent demographic effects. As we are
27 comparing single genomes per species spanning >60 million years of avian evolution, our
28 estimates of homozygous load primarily reflect long-term evolutionary accumulation of

1 substitutions in conserved regions, a mixture of mildly deleterious and lineage-specific
2 adaptive changes (Grossen et al. 2020; Dussex et al. 2023; Kardos et al. 2023; Wang et al.
3 2023). The difficulty of distinguishing between these categories likely weakens cross-
4 species correlations with diversity and inbreeding. Improved ancestral state inference and
5 population-level sampling will be required to disentangle fixed deleterious substitutions
6 from adaptive changes and to accurately quantify realized load within species.

7 Moreover, differences in life-history traits may modulate the rate of deleterious allele
8 accumulation. Species with long generation times experience fewer generations over
9 comparable evolutionary periods, potentially slowing the accumulation of weakly
10 deleterious alleles, whereas species with short generation times but large population sizes
11 may maintain more efficient purifying selection. However, these relationships are complex,
12 as generation time often covaries with population size and other ecological factors (Chao
13 and Carr 1993; Sæther et al. 2005; Plough 2016).

14 Finally, because our lifted-over CADD annotations are based on noncoding regions
15 ultraconserved across birds, they provide reliable indicators of evolutionary constraint, but
16 the direct functional consequences of mutations in these regions remain incompletely
17 understood. Therefore, our estimates should be interpreted as comparative indicators of
18 evolutionary constraint rather than as absolute measures of fitness impact.

19 **Lineage-specific patterns across taxonomic groups**

20 The three Mauritian species exhibit low genetic diversity and high inbreeding (F_{ROH}) within
21 their respective taxonomic groups, consistent with their severe population bottlenecks.
22 These metrics highlight an ongoing risk of inbreeding depression despite their successful
23 conservation management (Jones et al. 1995; Jones and Swinnerton 1997; Tollington et al.
24 2013; Nicoll et al. 2021). Although absolute levels of heterozygosity and homozygous load
25 differ among the three species, the similarly high F_{ROH} values indicate comparable levels of
26 recent inbreeding across the Mauritian taxa (Figure 3B), suggesting the need for future
27 population monitoring and management focused on reducing the risk of inbreeding.

1 Placing these patterns in a broader evolutionary context, the contrasts among taxonomic
2 groups reveal the interplay between long-term demographic history and deep-time
3 evolutionary processes. Falcons as a group show consistently low heterozygosity and
4 homozygous load, whereas parrots and pigeons display higher overall genomic diversity.
5 This pattern mirrors variation in ancestral effective population size inferred from PSMC
6 trajectories (Figure 3D), indicating that ancient demography has left a strong imprint on
7 present-day diversity. By contrast, F_{ROH} estimates based on long ROHs show similar values
8 across taxonomic groups (Figure 3B, pairwise Wilcoxon tests were not significant), as these
9 capture recent inbreeding rather than long-term demographic history.

10 Life-history traits likely mediate these taxonomic differences. Parrots have long generation
11 times, low reproductive rates, and high parental investment (Jones and Swinnerton 1997;
12 Jones 2010; Jones et al. 2013), making them particularly vulnerable to genomic erosion.
13 These traits slow the recovery of genetic diversity after bottlenecks and exacerbate the
14 accumulation of homozygous load. In contrast, pigeons have shorter generation times and
15 higher reproductive rates (Jones 2013), facilitating faster recovery and preserving higher
16 genetic diversity despite similar population collapses. Falcons exhibit intermediate traits,
17 with low reproductive rates but shorter generation times and the ability to disperse to new
18 environments (Jones et al. 1995; Cartwright et al. 2014; Nicoll et al. 2021), which can limit
19 genetic drift and inbreeding but may not fully mitigate the effects of historically small
20 population sizes.

21 Together, these results illustrate that genomic erosion cannot be interpreted outside its
22 phylogenetic and life-history context, and they highlight the need to deepen our
23 understanding of how life-history traits influence genetic diversity (Germain et al. 2023) and
24 load.

25 **Future directions to benefit conservation genomics**

26 As whole-genome data become more accessible (Feng et al. 2020; Stiller et al. 2024), the
27 integration of genomic-derived metrics (e.g., demographic reconstructions, heterozygosity,
28 F_{ROH} , N_e/N_c) with demographic, ecological and environmental data will substantially

1 improve conservation assessments and planning. Expanding the availability and taxonomic
2 breadth of reference genomes will further increase the utility of genomic resources in
3 conservation biology (Grueber 2015; Supple and Shapiro 2018; Mc Cartney et al. 2024).
4 Given the substantial differences of genome-wide features observed between groups (Figure
5 3, S10, S11), it is advantageous, even in the absence of a species-specific reference genome,
6 to identify a closely related reference genome to minimize mapping bias and improve
7 inference accuracy (Prasad et al. 2022). However, population-level data remain essential, as
8 a single individual cannot fully represent the genetic diversity of an entire species.
9 Incorporating population-level data also allows for more robust estimates of realised genetic
10 load by leveraging site frequency distributions (Grossen et al. 2020; Bertorelle et al. 2022).
11 Although the importance of genetic diversity is well established, understanding the fitness
12 effects of deleterious alleles is central to predicting species' adaptive potential and
13 persistence (Kardos et al. 2021). Future progress will require combining genomic data with
14 direct fitness measures, temporal datasets tracking load dynamics, and improved methods
15 to identify deleterious mutations (Bosse et al. 2019; van der Valk, de Manuel, et al. 2019;
16 Bertorelle et al. 2022; Fontseré et al. 2025).
17 Integrating demographic history changes is also critical for interpreting genetic diversity
18 trends. While genomic inference with modern samples reveals population history in both the
19 long term (N_e) and short term (recent inbreeding with F_{ROH}), historical genetic data provides
20 critical pre-decline information in accurately assessing trends in population size and genetic
21 load in a more recent, crucial time scale (van der Valk et al. 2019; Femerling et al. 2023; Cavill
22 et al. 2024; Dehasque et al. 2024; Silver et al. 2024; Fontseré et al. 2024). Such data are
23 invaluable for identifying rapid losses of genetic diversity and increases in load, which may
24 otherwise go undetected until demographic impacts become severe (Díez-del-Molino et al.
25 2018).
26 Although the relationships among genetic diversity, demographic history, and deleterious
27 variation are well established in theory, our findings underscore the importance of
28 considering evolutionary history, demographic processes, and life-history traits when
29 applying genetic measures in conservation. Our comparative analyses indicate that low

1 genetic diversity or high load does not carry equivalent implications across taxa, and that
2 evolutionary context is essential for interpreting genomic risk. Comparative analyses across
3 lineages provide a unique chance to evaluate how recent demographic collapse interacts
4 with deep-time history, helping to refine expectations for genetic recovery and to better
5 contextualize genomic data for guiding future conservation strategies in an era of rapid
6 environmental change.

7

ACCEPTED MANUSCRIPT

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15 Data Availability

16 The scripts used in this study are available on GitHub: [PachecoMC/CompConGen](https://github.com/PachecoMC/CompConGen).

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27

1 **Figure 1. Demographic trajectory of the three Mauritius species and phylogenetic, genetic diversity, and Ne/Nc ratio**
 2 **distribution of the 39 species used in this study. A** Demographic trajectory of the wild population derived from field
 3 monitoring of adult individuals over time. Note that the three species have been monitored in different ways so presented
 4 trends are approximations of their total numbers. **B** Phylogenetic relationship among the avian orders sampled in this study.
 5 Tree topology follows Stiller et al. (2024) and branch lengths are not time-calibrated and do not reflect divergence times.
 6 The orders of the three Mauritius species are marked in bold. Each circle represents a sampled species within its respective
 7 order. The colour and initials indicate the IUCN Red List category of each species. **C** Genome-wide heterozygosity (circles)
 8 and runs of homozygosity-based inbreeding coefficient (F_{ROH} ; diamonds) for each species. Colour coding corresponds to
 9 IUCN Red List categories. Domestic species are denoted with lighter colours and in grey (outer line in the dots and in their
 10 name in x-axis). **D** Correlation between the Ne/Nc ratio after log-transform ($\text{Log}(\text{Ne})/\text{Log}(\text{Nc})$) and IUCN Red List categories.
 11 The effective population size (Ne) was estimated as the harmonic mean of PSMC values from 10 kya to 100 kya, whereas
 12 the census population size (Nc) was obtained from IUCN Red List data. Photo credits: Samantha Cartwright for the
 13 Mauritius kestrel (*Falco punctatus*), Jacques de Speville for the Mauritius parakeet (*Alexandrinus eques*), and Gregory Guida
 14 for the pink pigeon (*Nesoenas mayeri*).

15
 16 **Figure 2. Comparison between genetic diversity metrics, genetic load, and effective population sizes.** The dashed line
 17 represents the linear correlation when $p < 0.05$. **A** Correlation between genome-wide heterozygosity and effective
 18 population size (Ne), with Ne estimated as the harmonic mean of PSMC values between 10 kya and 100 kya. **B** Correlation
 19 between heterozygous load and genome-wide heterozygosity. Heterozygous load is defined as the ratio of heterozygous
 20 substitutions with CADD > 20 to homozygous substitutions with CADD < 3. **C** Correlation between homozygous load and
 21 genome-wide heterozygosity. Homozygous load is defined as the ratio of counts of filtered homozygous substitutions with
 22 CADD > 20 and the number of filtered homozygous substitutions with CADD < 3. **D** Correlation between inbreeding
 23 coefficient (based on runs of homozygosity; F_{ROH}) and Ne. **E** Correlation between heterozygous load and inbreeding
 24 coefficient. **F** Correlation between estimated homozygous load and inbreeding coefficient.

25
 26 **Figure 3. Genetic diversity, genetic load, and demographic history of Falconiformes, Psittaciformes, and**
 27 **Columbiformes. A** Genome-wide heterozygosity in $\text{het} \times \text{bp}^{-1}$, **B** inbreeding coefficient, and **C** homozygous load distribution
 28 across the orders of the three target species. The inbreeding coefficient (F_{ROH}) was estimated using runs of homozygosity,
 29 and homozygous load was based on the ratio of homozygous substitutions with CADD scores above 20 to those with CADD
 30 scores below 3. **D** Demographic histories are shown as variation in Ne (effective population size) inferred with PSMC. The
 31 falcons had the lowest historical Ne (5.0×10^4 , harmonic mean for 10 to 100 kya) on average, while the parrots having higher
 32 Ne (7.6×10^4) and pigeons having the highest Ne (2.3×10^5) Thick lines refer to Mauritius species. Only species with
 33 chromosomal-level assemblies were included.

34

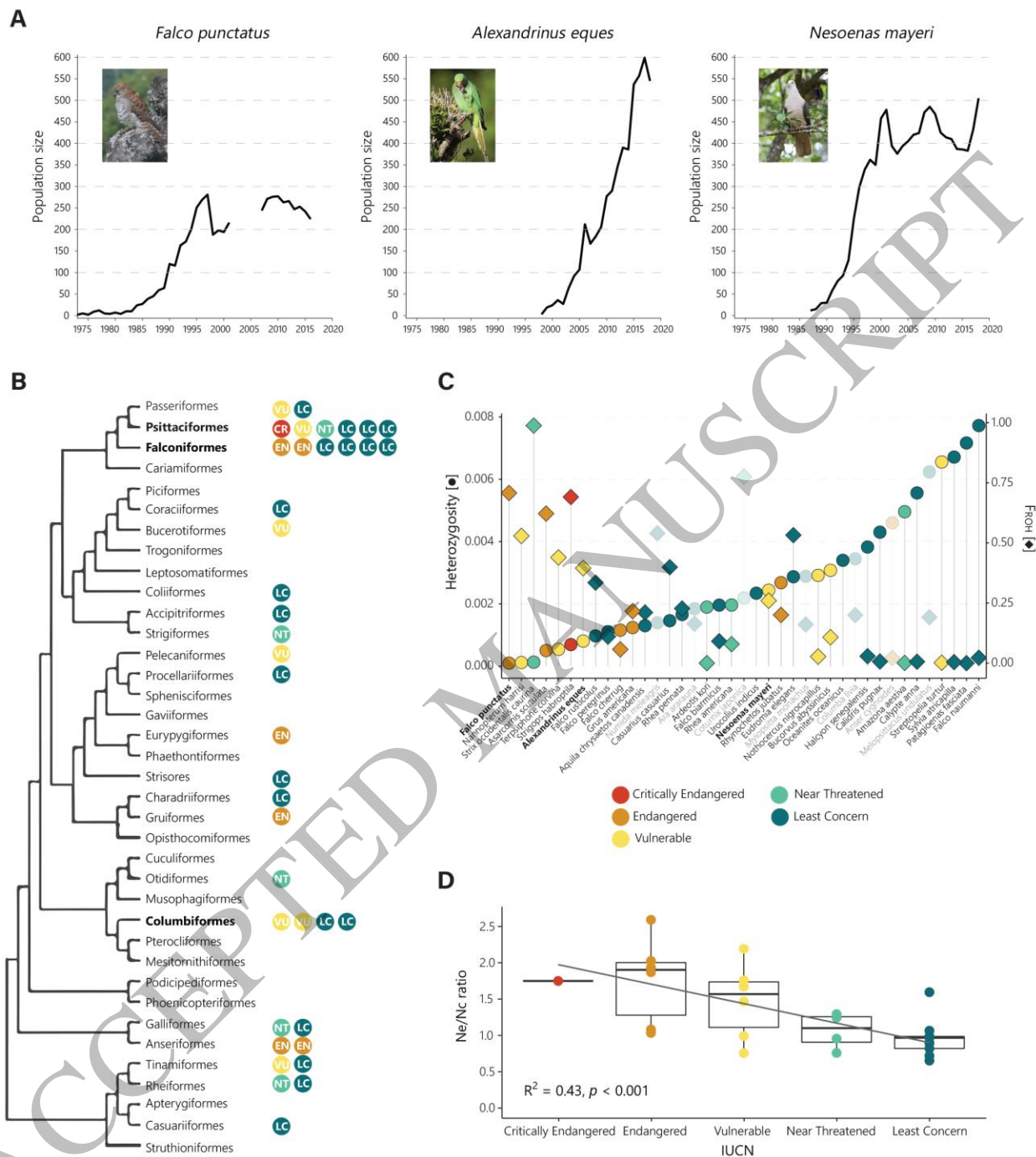


Figure 1
165x184 mm (x DPI)

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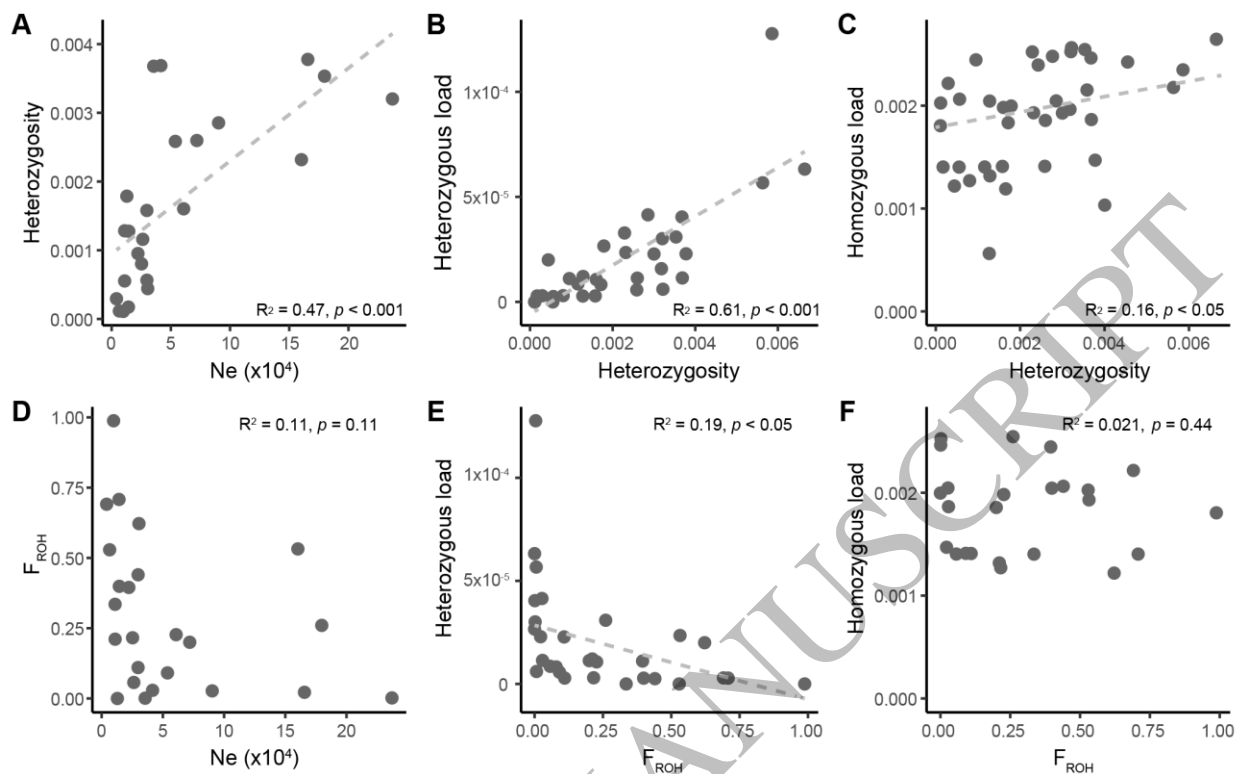


Figure 2
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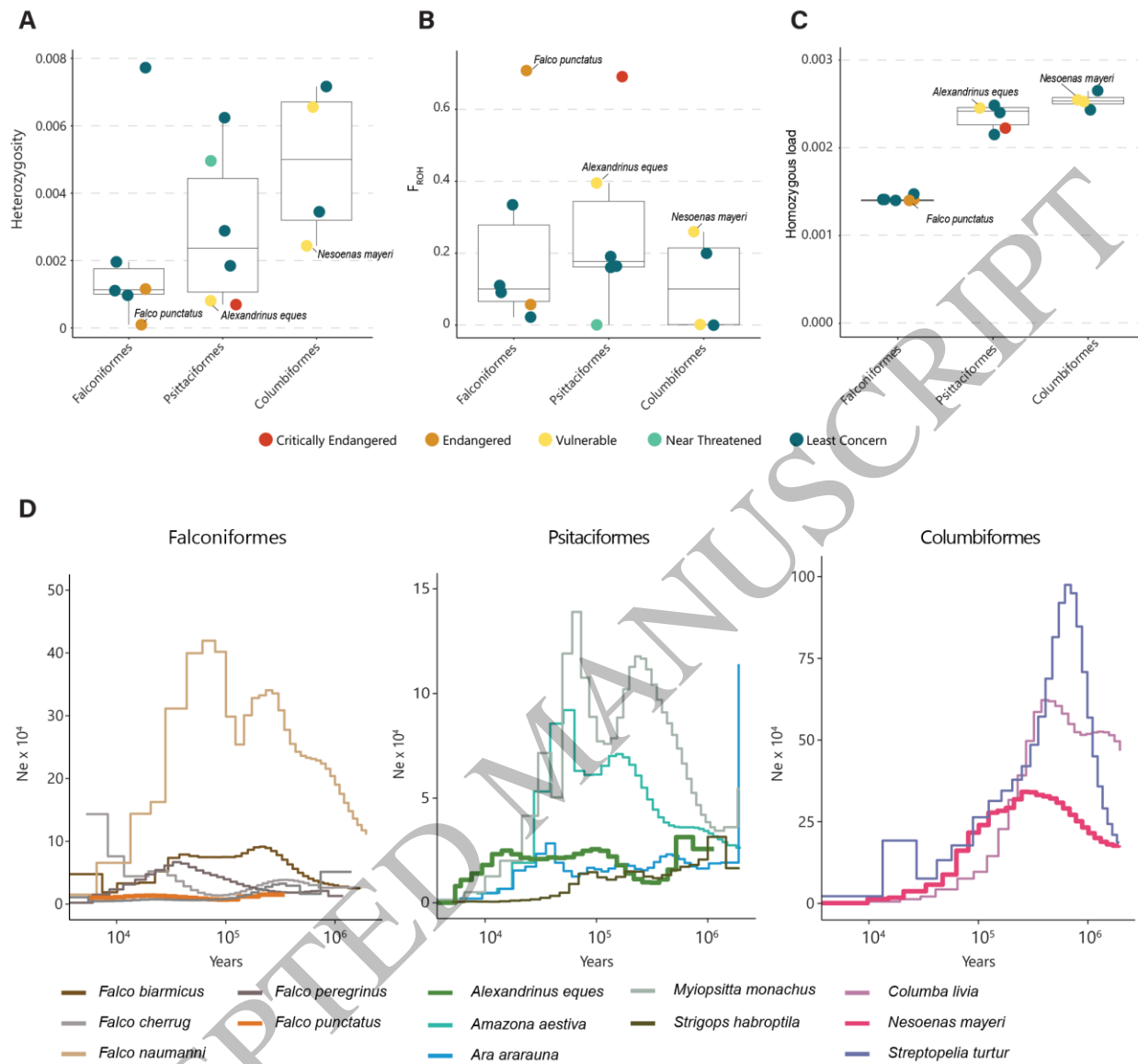


Figure 3
165x154 mm (x DPI)

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