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Silent erosion: impact of forest logging on genetic diversity in tropical understorey birds

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Abstract

Anthropogenic habitat disturbance can erode genetic diversity long before population declines become apparent, potentially contributing to extinction debt. However, empirical assessments of genetic erosion following anthropogenic habitat degradation remain scarce. Here, we investigated whether selective logging, the most pervasive anthropogenic disturbance in tropical forests, affects genetic diversity in tropical forest biota. We re-sequenced whole genomes of 99 understorey songbirds from ten forest specialist species captured in both primary and selectively logged forests of Borneo. The study species are all sedentary and weak flyers but differ in their susceptibility to forest logging. The within-species comparisons of whole genomes between primary and selectively logged forests showed reduced nucleotide diversity and higher levels of inbreeding in a common understorey rainforest inhabitant, *Malacocincla sepiaria*. We also found a substantial amount of homozygosity in the local population of that same species as well as in another, *Malacopteron cinereum*, regardless of forest type, indicating reduced standing genetic diversity due to historical bottlenecks. Nine out of ten species, including those considered more sensitive to the environmental conditions of selectively logged forests, showed no reduction in genetic diversity, indicating that selectively logged forests retain substantial conservation value for many rainforest birds. Nonetheless, our findings indicate that genetic erosion can occur within a few decades of habitat disturbance even in apparently common tropical bird species, raising concerns about silent population-genetic processes that might threaten the long-term persistence of seemingly abundant species in selectively logged forests.

Keywords

Genetic erosion, genetic diversity, forest logging, population genomics, bird

Significance statement

Selective logging is the most pervasive anthropogenic disturbance in tropical forests, but whether it leads to the erosion of genetic diversity in forest organisms is a key unresolved question. By comparing re-sequenced whole genomes of ten species of understorey songbirds between old-growth primary forests and selectively logged forests in Borneo, we show the first evidence of reduced nucleotide diversity and higher levels of inbreeding in a common rainforest songbird species in selectively logged forests. Our findings raise concerns about silent population-genetic processes that might threaten the long-term persistence of seemingly abundant species in selectively logged forests.

Introduction

Human activity is responsible for a global biodiversity crisis that has resulted in the Sixth Extinction Event (Ceballos and Ehrlich 2023). A realistic evaluation of its impacts is paramount for guiding conservation action and to assess the potential effects this crisis may have on basic planetary processes. However, most efforts to quantify the magnitude of biodiversity loss have focused on direct impacts resulting in visually observable data, measured via such approaches as population censuses or extinction surveys (Edwards et al. 2011; Paez et al. 2022). At the same time, it is known that the impacts of habitat loss or degradation can take many years to crystallize in the form of observable extinctions or declines. They can build up in the background, accruing extinction debt, which only materializes years or decades later through the sudden disappearance of species (Kuussaari et al. 2009).

The mechanisms underlying extinction debt remain poorly understood, but it has been suggested that the resultant time lag in declines or extinctions is intertwined with population-genetic processes (Figueiredo et al. 2019). Reduced survival and reproductive success due to anthropogenic habitat disturbance cause the loss of genetic variants. Such loss of allelic diversity can decrease a species' adaptive potential, ultimately leading to populations' inability to deal with rapid environmental change (Gargiulo et al. 2024). In its worst form, diversity loss leads to inbreeding depression, with concomitant repercussions through the accumulation of genetic load (Dussex et al. 2023). These insights suggest that genetic diversity scans may be an invaluable tool of the future to flag populations at risk (DeWoody et al. 2021; Schmidt et al. 2023). And yet, there is a lack of comprehensive studies that have investigated the impact of habitat loss or degradation directly on genetic diversity.

The most pervasive form of anthropogenic disturbance in tropical forest is selective logging. Over 400 million hectares (~25%) of the remaining tropical forests are zoned for selective harvesting of large, commercially valuable trees (Blaser et al. 2011; FAO 2025). Compared to old-growth undisturbed forests, selectively logged forests are dominated by fast-growing pioneer species, saplings, and elevated abundance of climbing lianas and bamboos (Imai et al. 2019). Although selectively logged forests retain high levels of species richness (Edwards et al. 2011; Putz et al. 2012), the local abundances of species change as interior specialists decline and edge-tolerant species increase in abundance (Costantini et al. 2016). Studies on tropical understorey birds of selectively logged forests found differences in movement behaviour, body size and physiology compared to conspecifics in primary undisturbed forests (Messina et al. 2020a; Cosset et al. 2021; Messina et al. 2021).

In this study, we tested the hypothesis that selective logging leads to loss of genetic diversity in those species that are sensitive to this kind of forest disturbance. We assessed whether apparently non-sensitive species may additionally be subject to the silent effects of genetic diversity loss. We included in our study 10 species of understorey songbirds showing increasing, decreasing, or stable trends of relative population abundance from old-growth primary forest towards selectively logged forest in Malaysian Borneo (Table 1). The study species belong to the families Pellorneidae (six babbler species), Timaliidae (three babbler species), and Pycnonotidae (one bulbul species). Babblers are strictly insectivorous, while the sole bulbul species included in our study is frugivorous. All our study species are forest specialists, highly sedentary and do not exhibit a strong dispersal capability.

Results

An average of 298,339 SNPs per species were retained after filtering. The species with the highest number of SNPs was *Stachyris maculata* (n SNPs = 546,464) and with the lowest number *Tricholestes criniger* (n SNPs = 119,737; Table 1).

Visualizations of PCA results and Admixture analyses showed no clear pattern of segregation of populations between logged and primary forests across all species (Fig. S1 and S2). Levels of nucleotide diversity (π) ranged from 0.009 for *S. poliocephala* in both primary and logged forests to 0.02 for *M. sepiaria* in primary forest (Table S1). The analysis of effect sizes (ES) pointed to a significantly reduced π in logged versus primary forest in *M. sepiaria* (ES-π = -1.62; confidence interval-π = -2.95 – -0.3; Fig. 2). These findings were supported by analyses of inbreeding (F), which exhibited a higher signal in logged compared to primary forest in *M. sepiaria* (ES-π = 0.81; confidence interval-π = -0.36 – 1.99; Fig. 2, Table S2). All other species displayed comparable levels of π and F between forest types. A visualization of π ratios between logged and primary forests via Manhattan plots did not point to any substantial chromosomal regions characterized by a reduced or elevated nucleotide diversity in primary or logged forest populations (Fig. S3).

We found no significant differences in ROH numbers between primary and logged forest for any species (Table S1; Table S2). However, when testing for differences in ROH numbers between species regardless of forest type, we detected a significantly higher number of ROHs in *M. sepiaria* and *M. cinereum* compared to the other species, with *M. sepiaria* showing significantly more ROHs even than *M. cinereum* (Fig. 3; Table S3).

Discussion

In this study we provide for the first time evidence of genetic erosion in a common bird species inhabiting selectively logged tropical forests. This finding adds to those reporting loss of genetic diversity in various vertebrate species following relatively recent land-use changes and other anthropogenic disturbances (Shaw et al. 2025). For example, Chattopadhyay et al. (2019) found a drastic decline in genetic diversity in a population of Sunda fruit bats (*Cynopterus brachyotis*) in Singapore, commencing at the onset of industrialisation on the island. Overall, such results indicate that genetic erosion may occur just a few decades after the onset of habitat disturbance even in species considered common.

Loss of genetic diversity has previously been found in tropical understorey birds inhabiting forest fragments (Cros et al. 2020). In particular, insectivorous birds showed a stronger reduction in heterozygosity than frugivorous birds, probably because of their reduced dispersal capabilities. In our study, we detected a loss of nucleotide diversity and increased levels of inbreeding in *M.*

sepiaria, a territorial insectivore with a weak flight ability. Previous research conducted in our study area showed that *M. sepiaria* is more likely to move shorter distances in logged forests than in pristine forest (Cosset et al. 2021). This pattern may arise because the species avoids forest gaps or perceives a higher risk of predation in selectively logged forests. Such constrained movement within logged forest interiors may limit gene flow, thereby contributing to the observed increase in inbreeding and the loss of genetic diversity. However, reduced movement in logged forests was also found in other species included in this study that do yet not show loss of genetic diversity, suggesting that movement patterns may be only one of the factors contributing to reduced genetic diversity in *M. sepiaria*.

Other evidence suggests that selectively logged forests constitute a low-quality habitat for *M. sepiaria.* The species shows significantly reduced body size in selectively logged forests compared to primary forests (Messina et al. 2021), as well as higher trophic mean level, possibly due to increased feeding on predatory arthropods (Hamer et al. 2015). Furthermore, recent findings indicate that *M. sepiaria* has been declining in abundance over time in both primary and selectively logged forests in our study area (Costantini et al. 2025). While in primary forests the species maintains an extensive network of co-occurrence with other understorey birds, suggesting a key role in the ecological network, in selectively logged forests its co-occurrence with other species also declines. This pattern further indicates the species' vulnerability to both abiotic and biotic changes associated with forest selective logging.

Our analyses revealed substantial homozygosity in local populations of *M. sepiaria* and *M. cinereum*, regardless of forest type. Runs of homozygosity (ROH) are identical chromosomal segments inherited from both parents, arising more frequently with increasing parental relatedness and shared ancestry within a population (Broman and Weber 1999; Martin et al. 2023). Because our ROH analyses likely reflect historical reductions in effective population size rather than very recent inbreeding events, these results suggests that the entire local populations of *M. sepiaria* and *M. cinereum* may have experienced a regional bottleneck which could have reduced their long-term adaptive potential (Barrett and Schluter 2008). This pattern is particularly pronounced in *M. sepiaria,* which exhibited lower genetic diversity in selectively logged forests compared to primary undisturbed forests, potentially reflecting a reduced capacity to cope with anthropogenic environmental change.

Our data show that nine out of the ten species of understorey birds, including two showing negative population abundance trends, have managed to maintain levels of genetic diversity in selectively logged forests similar to those in primary forests. These findings support the high biodiversity value of selectively logged forests for long-term conservation. However, based on species-specific population dynamics, some species may require more time to show signs of genetic erosion, keeping in mind that the most recent major logging intervention occurred only roughly two decades ago. Further studies combining long-term data on genetic variation with demographic parameters are needed to shed more light on the long-term conservation value of selectively logged forests.

An important caveat, differences in genetic diversity among species could partly reflect phylogenetic bias. Closely related taxa, such as species within the Pellorneidae, may share similar demographic histories or life-history traits that influence levels of genetic variation. However, testing for a phylogenetic signal would require a larger comparative dataset.

In conclusion, we show reduced nucleotide diversity and higher levels of inbreeding in a common rainforest songbird species, *M. sepiaria*, about four decades after the onset of selective logging. Furthermore, we found a substantial amount of homozygosity in the local population of

M. sepiaria and *M. cinereum*, regardless of forest type, indicating reduced standing genetic diversity. Overall, our findings raise concerns about silent population-genetic processes that might threaten the long-term persistence of these seemingly abundant species in selectively logged forests.

Materials and Methods

Study area and data collection

The study area was located within the Yayasan Sabah logging concession in Sabah, Malaysian Borneo. We conducted fieldwork for avian blood collection in primary old-growth tropical forest within the Danum Valley Conservation Area (4°57045.2″N, 117°48010.4″E), and in adjacent selectively logged rainforests (Fig. 1). These lowland evergreen forests are dominated by valuable timber tree species of the family Dipterocarpaceae. Timber harvesting occurred twice: the first logging rotation (from 1976 to 1991) removed trees more than 0.6 m in diameter using tractors and high-lead cables, yielding about 120 m^3 ha^{-1} (range: 73-166 m^3). The second logging rotation (from 2001 to 2007) extracted trees more than 0.4 m in diameter, adding ~31 m^3 ha^{-1} (15-72 m^3) of timber (Edwards et al. 2011). Following the second harvest, the heavily disturbed forest was left to recover naturally.

Most of the avian blood samples for DNA extraction were collected in 2023, but some in 2014. Three additional samples of *T. criniger* from a previous unpublished study were collected in 2017 and 2018. Fieldwork took place from early June to late August in each year. We set three plots in old-growth primary forests and three plots in twice-selectively logged forests, located at least 500 m away from the nearest road to avoid edge effect. Based on a previous study, our plots are representative of the different environmental conditions found in unlogged and selectively logged forests (Senior et al. 2018). Plots within the same type of forest were at least 1.8 km apart (mean primary forest = 6.64 km; mean logged forest = 4.04 km). Plots between primary forest and selectively logged forest were at a distance between ~12.5 km and ~22 km (Fig. S1), ensuring that dispersal of juveniles between forest types is rare (we had no recaptures between forest types; Cosset et al. 2021). Within each plot, three parallel transects were established 250 m apart. Each transect consisted of fifteen 12-m nets set up end-to-end. All nets were operated simultaneously from 06:00 to 12:00 h on two consecutive days, after which they were relocated to the next plot. Each plot was surveyed three times per field season.Every captured bird was marked with a unique numbered ring and released after data and/or blood sample collection. Species name, ring number, day and time of capture were recorded. Blood samples (~15 µl) were taken from the brachial vein of adult birds only using non-heparinized capillary tubes. The blood was immediately transferred into a vial and stored on ice during the time of mist netting. After transfer to the field laboratory, we added ethanol to each vial at an approximate ratio of 1:20 between blood and ethanol. The vials were then stored in a fridge.

We included in our study 10 species of forest understorey birds belonging to three different families: six species of the babbler family Pellorneidae, three species of the babbler family Timaliidae, and one species of the bulbul family Pycnonotidae. Species were selected based on their capture rates and their relative population abundance index (see below) between primary and selectively logged forest (Table 1) (Messina et al. 2020b; Messina et al. 2021). Babblers are strictly insectivorous and hunt for prey either on the ground or in the lower forest strata (up to 3 meters), depending on species. The sole bulbul is a frugivore feeding between the understorey and midstorey levels of the forest (Wilman et al. 2014). The study species are highly sedentary and do not exhibit strong dispersal capabilities.

All experimental procedures were approved by the Sabah Biodiversity Council (access licence number: JKM/MBS.1000-2/2 JLD.16(132)). Samples were exported under the export licences JKM/MBS.1000-2/2 JLD.3(45) and JKM/MBS.1000-2/3 JLD.5(37).

Relative Population Abundance Index

We used species' capture rates in the study area (same plots and transects) from 2014 to 2023, with the exception of the years 2020 and 2021 due to Covid-19 restrictions, to estimate the relative population abundance (RPA) index of each species as follows: ([abundance in logged forest – abundance in primary forest]/[abundance in logged forest + abundance in primary forest]) (Table 1). Abundance data were corrected for sampling effort (number of captures/expected effort [nets*hours]). Recaptured individuals were included in the abundance counts because recapture rates are low and similar between unlogged and logged forests (Messina et al. 2020b; Cosset et al. 2021). The RPA index is positive for species with a higher abundance in logged forest and negative for species with a higher abundance in primary forest.

Laboratory procedures, sequencing and mapping

Using DNA extracted from blood samples of 96 individual birds equally subdivided between primary and logged forests, we sequenced whole genomes at an overall mean coverage of 14.2 × (min = 12.77 ×; max = 15.81 ×). Additionally, three samples of *T. criniger* from a previous unpublished study sequenced at an average coverage of ~10 × were included in this study, adding up to a total of 99 samples (Table 1). Sample sizes were equitable across species, consisting of five to seven individuals per forest type, except for *S. maculata* which was represented by three individuals per forest type.

DNA was extracted using a Magnetic Animal Tissue Genomic DNA Kit (TIANGEN, Beijing, China), following the manufacturer's protocol. Genomic library preparation and genome sequencing were performed at NOVOGENE laboratory in Cambridge, United Kingdom, using paired-end sequencing on an Illumina NovaSeq X Plus PE150 platform (350-bp reads). Briefly, the genomic DNA was randomly sheared into shorter fragments, which were then end-repaired, A-tailed, and further ligated with Illumina adapters. The resulting fragments with adapters were size-selected and PCR amplified before proceeding to purification. The library was quantified through Qubit and qPCR, and its size distribution was characterized with a fragment analyzer. DNA for the three additional samples was extracted using the DNAeasy Blood and Tissue Kit (Qiagen Hilden, Germany) following the manufacturer's protocol. Libraries were prepared and then sequenced on DNBSEQ PE150 by BGI Genomics.

We assessed raw data quality of the Illumina reads using FastQC v0.12.1. We then mapped the sequences to reference genomes using the software BWA-MEM v2.2.1, and used SAMtools v1.3.1 to filter files with a minimum required MAPQ score of 20 (Li et al. 2009; Vasimuddin et al. 2019). The babbler species were mapped to a chromosome-level reference genome of *Sylvia borin* (Genbank assembly: GCA_014839755.1; Prost et al. 2025), the phylogenetically closest species that had a chromosome-level genome available during our study at the time (Cai et al. 2019). In contrast, the sole bulbul species was mapped to a scaffold level genome of the closely related *Alophoixus pallidus*, obtained from the B10K consortium (see Acknowledgements). Aligned data were then pre-processed using Picard v2.27.5 for assignment of read groups and removal of PCR duplicates.

SNP calling and population genomic analysis

To call SNPs we used the mpileup command of BCFtools v1.17 (Li and Durbin 2009; Lefouili and Nam 2022). First, we obtained a vcf file containing all SNPs (unfiltered) and invariant sites for each species separately. Then, we used vcftools to filter out indels, low quality SNPs (QUAL < 20), and sites for which the read depth was three times higher than the species average depth of coverage or below 3 (https://www.htslib.org/workflow/filter.html). We retained only SNPs that were genotyped in ≥90% of individuals (--max-missing 0.9), except for *T. criniger* for which the threshold was set at ≥70% of individuals (--max-missing 0.7) to avoid excessive loss of SNPs after filtering. This way, we obtained a filtered dataset with invariant sites and SNPs. Then, we created a vcf file containing only variant sites setting the minor allele count to 1 (--mac 1).

First, to visualize species' genomic variation across the two populations (i.e., primary and logged forest) we ran principal component analyses (PCA) for each species. The PCAs were implemented on the datasets including variant sites only. Then, to estimate the number of subpopulations (K) that make up the total population in the study area for each species, we conducted admixture analyses after filtering the datasets containing variant and invariant sites (--max-missing 0.5 --maf 0.05 --thin 100000) and using PLINK to generate bed files.

Subsequently, we calculated the inbreeding coefficient F (--het function) and runs of homozygosity (ROH) for each species. These analyses were implemented on the datasets including variant sites only, using PLINK v1.9 (Purcell et al. 2007). Following sensitivity analyses (Fig. S4), analyses of ROH were implemented with the flags --homozyg-density 25 --homozyg-gap 500 --homozyg-het 1 --homozyg-window-snp 50 --homozyg-window-het 5 --homozyg-window-missing 5 --homozyg-window-threshold 0.05 --homozyg-snp 50 --homozyg-kb 500 (Meyermans et al. 2020). Finally, we used the single nucleotide polymorphism (SNP) dataset that included invariant sites for calculating nucleotide diversity (π) with Pixy v1.2.7 at a window size of 200 kb (Korunes and Samuk 2021).

Statistical analysis

To assess any significant difference between primary and logged forests in inbreeding coefficient F and nucleotide diversity π, we calculated standardized Hedges' *g* effect sizes for each species. Effect sizes were calculated from means, standard deviations and sample sizes (number of individuals) of the parameters of each species in both primary and logged forest. Following Cohen (1988), the magnitude of the effect sizes can be considered small (Hedges $g = 0.2$, explaining 1 % of the variance), intermediate (Hedges $g = 0.5$, explaining 9% of the variance) or large (Hedges $g = 0.8$, explaining 25% of the variance). Effect sizes are statistically significant when their confidence intervals do not overlap zero.

For each species, we calculated the ratio of π between logged and primary forest. Then, we attempted to identify loci particularly affected by a reduction in nucleotide diversity by visualizing the π ratios on Manhattan plots. The x-axis of the Manhattan plots represented the main chromosomal regions for each species except for *T. criniger*, whose genome had been mapped at scaffold level. Manhattan plots were implemented in the CMplot package of R (LiLin-Yin 2015).

We ran a Wilcoxon test for each species to assess differences in ROH between primary and logged forest. Finally, we ran a linear regression to assess differences between species in the number of ROH, regardless of forest type. Thus, the linear regression included the number of ROH as a dependent variable and the species as an independent variable. Pairwise comparison between species was implemented through the 'emmeans' function of the homonym package (Lenth et al. 2023). All statistical analyses were run in R.

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Data availability

Raw sequencing reads have been deposited in the NCBI Sequence Read Archive (SRA) under BioProject accession number PRJNA1450337 and are publicly available at the following link: https://www.ncbi.nlm.nih.gov/search/all/?term=PRJNA1450337. The codes used in this manuscript have been deposited in Zenodo and are publicly available at the following link: https://zenodo.org/records/20640237.

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Table 1 – Species names follow the classification by Eaton et al. (2021). The relative population abundance (RPA) index is negative for species with lower abundance in logged as compared to primary forest and positive for species with higher abundance in logged forest (ranging from -1 to 1). The two species for which we expected a loss of genetic diversity are indicated by asterisks. For all species except *T. criniger*, SNPs were retained if they were genotyped in at least 90% of individuals; for *T. criniger* the threshold was 70%. Abbreviations: UNL – primary (unlogged); LOG – logged; n SNPs – number of single nucleotide polymorphisms.

Species scientific name	**Species common name**	**Sample size**	**Sample size UNL**	**Sample size LOG**	**RPA index**	**Mean genomic coverage (×)**	**Total genomic sites**	**n SNPs**
*Kenopia striata**	Striped wren babbler	10	5	5	-0.26	14.55	1,192,592	377,512
Malacocincla sepiaria	Horsfield's babbler	10	5	5	0.13	12.77	652,481	377,512
*Malacopteron cinereum**	Scaly-crowned babbler	10	5	5	-0.15	13.23	804,711	315,455
Pellorneum bicolor	Ferruginous babbler	10	5	5	0.15	14.12	996,629	305,600
Pellorneum capistratoides	Bornean black-capped babbler	10	5	5	0.24	15.29	881,358	316,355
Pellorneum poliogene	Leaflitter babbler	10	5	5	0.13	15.81	394,143	149,932
Cyanoderma bicolor	Bicolored babbler	10	5	5	0.16	13.47	956,482	259,208
Stachyris maculata	Chestnut-rumped babbler	6	3	3	0.03	13.45	2,508,264	546,464
Stachyris poliocephala	Grey-headed babbler	10	5	5	0.23	14.44	1,047,259	280,131
Tricholestes criniger	Hairy-backed bulbul	13	7	6	-0.01	14.92	175,572	119,737

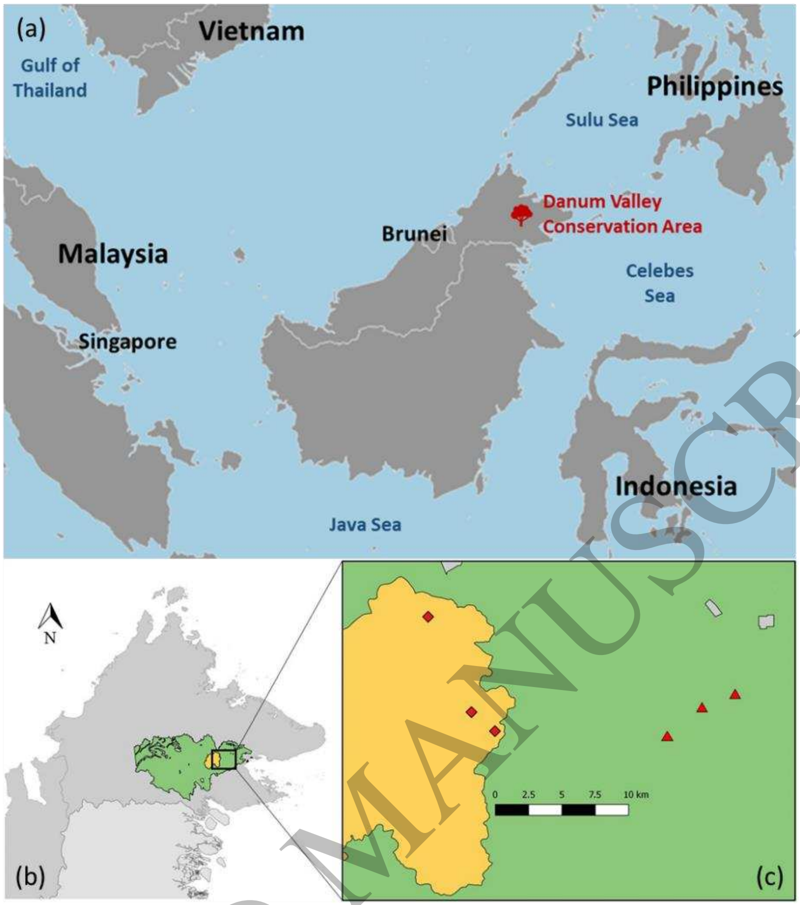


Figure 1 – (a) Danum Valley Conservation Area in the Malaysian state of Sabah, Borneo. (b) The green area corresponds to the Yayasan Sabah logging concession, and the yellow area corresponds to the Danum Valley Conservation Area and Palum Tambun watershed reserve. (c) Distribution of study plots between unlogged forest (square symbols) and selectively logged forest (triangular symbols); grey areas are plantations. This image was previously published in Messina et al. (2020b).

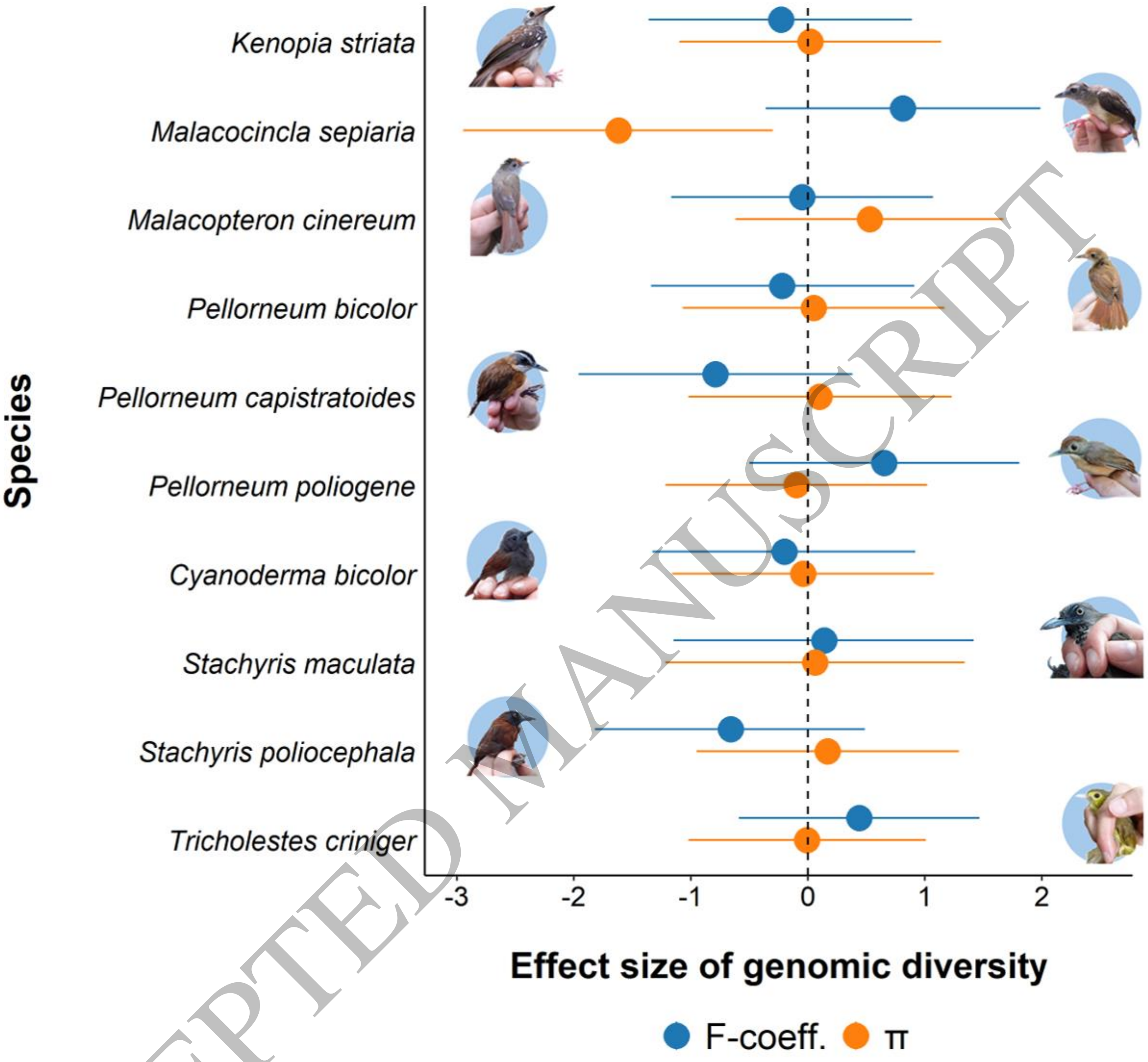


Figure 2 – Effect sizes ± confidence intervals of inbreeding coefficient (F) and nucleotide diversity (π) between primary (unlogged) forest and selectively logged forest for each species. For F (=blue), values greater than zero indicate a higher signal for inbreeding in selectively logged as compared to primary forest. For π (=orange), values less than zero indicate a reduced nucleotide diversity in selectively logged as compared to primary forest.

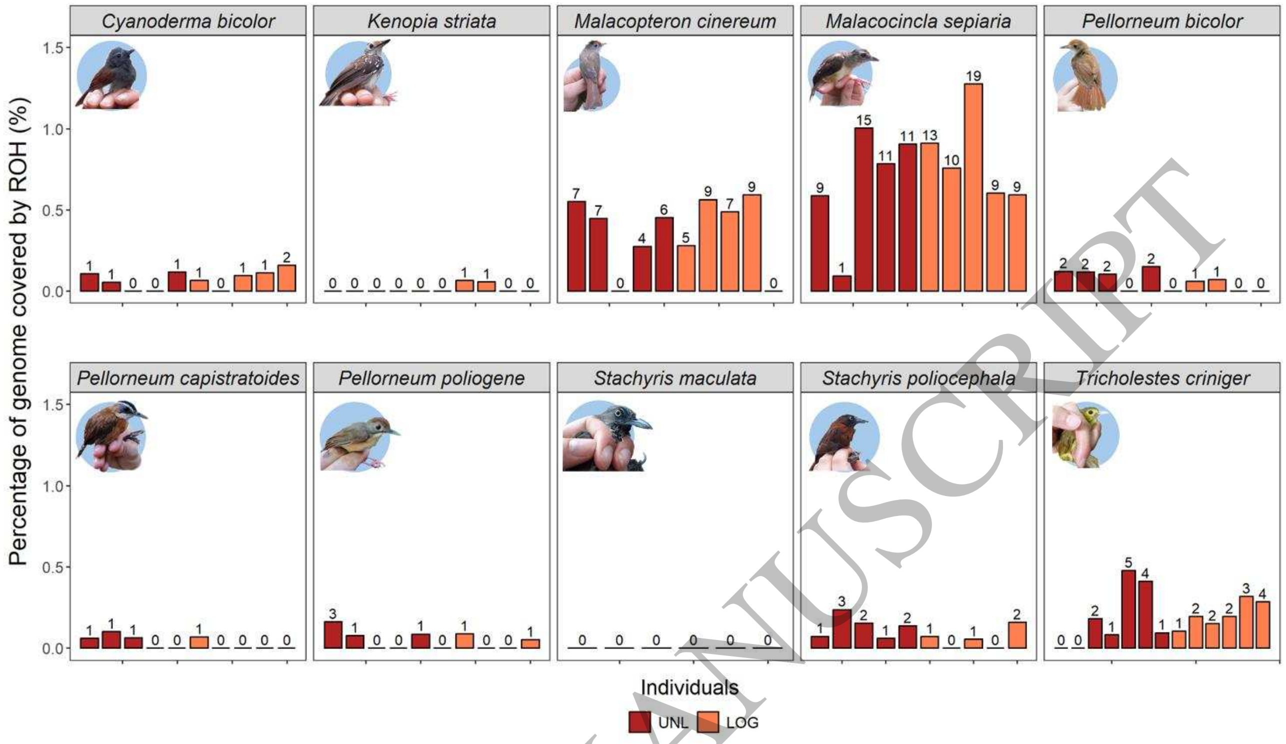
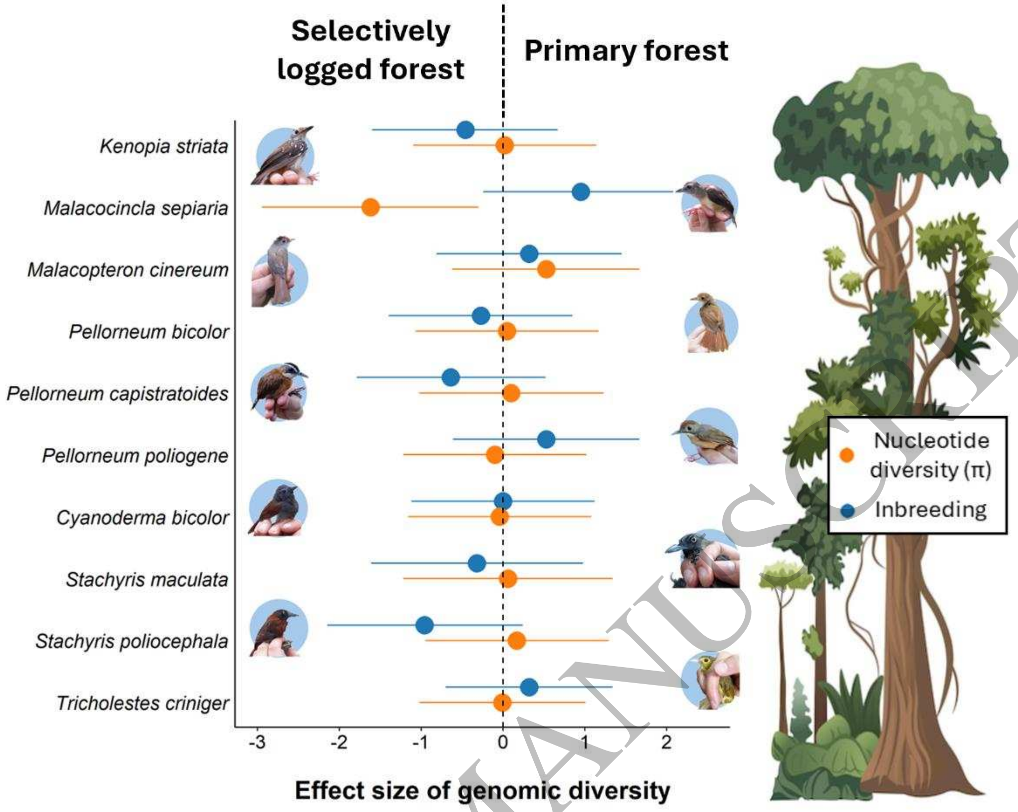


Figure 3 – Runs of homozygosity (ROH) for each of the 10 species. Each bar represents an individual, with the number of ROH reported above. The height of each bar indicates the individual percentage of the genome covered by ROH, calculated as: [(individual sum of kb covered by ROH/genome size of the reference species) * 100]. The genome size of the reference species *Sylvia borin* corresponds to 1,045,652.18 kb, while that of *Alophoixus pallidus* corresponds to 1,101,612.124 kb. Red indicates birds from old-growth primary forest (UNL), while orange indicates birds from selectively logged forest (LOG). Because SNPs in *T. criniger* were retained if genotyped in at least 70% of individuals (as compared to a 90% threshold for all other species), ROH estimates for this species may not be directly comparable and could be inflated relative to the others.



Graphical Abstract