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RESEARCH ARTICLE

DNA metabarcoding reveals population-specific links between diet and fledging success in a recovering threatened bird, the Mauritius parakeet

Rebecca Louch[1,2,3,4] | Simon Tollington[1,5] | Sion Henshaw[6] | Vikash Tatayah[6] | Carl Jones[5,6] | John Ewen[3] | Claire Raisin[5] | Deborah A. Dawson[3] | Lucy S. Knowles[3] | Kathryn H. Maher[3] | Kevin Ruhomaun[7] | Nicolas Zuël[8] | Jim Groombridge[1]

[1]School of Natural Sciences, Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent, UK; [2]Chester Zoo, Chester, UK; [3]Institute of Zoology, Zoological Society of London, Regents Park, London, UK; [4]NERC Environmental Omics Facility, School of Biosciences, University of Sheffield, Sheffield, UK; [5]Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey, UK; [6]Mauritian Wildlife Foundation, Vacoas, Mauritius; [7]National Parks and Conservation Service, Réduit, Mauritius and [8]Ebony Forest, Chamarel, Mauritius

Correspondence
Rebecca Louch
Email: rebeccalouch@gmail.com

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Abstract

1. Populations of threatened species frequently persist in suboptimal landscapes comprising degraded, altered and restored habitats. Such habitat mosaics may influence diet, potentially impacting fitness.
2. We investigated dietary variation in the Mauritius ('echo') parakeet (*Alexandrinus eques*), a threatened species that exists in two isolated populations exhibiting differing habitat quality. DNA metabarcoding of faecal samples identified plant taxa consumed, while reproductive data allowed assessment of nest-level diet-fitness relationships.
3. We identified 83 plant taxa in 206 faecal samples and discovered significant dietary differentiation between the two populations. Despite historical declines in native vegetation across both ranges, parakeet diets in the North population contained significantly higher native species richness (4.7 vs. 1.9 species per sample). Consumption of endemic *Gaertnera* spp. was positively associated with reproductive success in the South, while supplementary food enhanced reproduction in the North, suggesting population-specific dietary strategies.
4. *Synthesis and applications*: Our findings suggest that restoration of native/endemic habitat in modified landscapes can directly improve reproductive success in a threatened endemic bird. Conservation strategies must consider the impact of dietary components on reproductive fitness. Conservation managers on Mauritius should consider prioritising protection of key endemic food plants while maintaining tailored supplementary feeding regimes based on local conditions. This

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approach has broad applicability for threatened species conservation in modified habitats worldwide.

KEYWORDS
conservation management, DNA barcode library, DNA metabarcoding, fledging success, habitat restoration, Mauritius parakeet, reproductive success, supplementary feeding

1 | INTRODUCTION

Habitat modification and loss through anthropogenic activities profoundly impact ecosystems worldwide, leading to the decline of native species (Haddad et al., 2015; Vergara-Tabares et al., 2020). As landscapes transform, species face novel ecological pressures affecting their access to key habitat resources including food. This can manifest through both direct habitat alteration and non-native species proliferation (Bartley et al., 2019; Schirmel et al., 2016; Traveset & Richardson, 2014), with invasive plants particularly impacting herbivore diet composition (Atwood et al., 2020). While some species exhibit dietary flexibility in response to these changes (Wong & Candolin, 2015), the extent to which dietary adjustments impact species' fitness varies considerably between species and the changes occurring in their habitat (Bartley et al., 2019).

Conservation managers employ multiple strategies to address these challenges, from habitat restoration and invasive species control to supplementary feeding programmes (Baider & Florens, 2011; Blanco et al., 2011; Ewen et al., 2015; Murray et al., 2016; Tollington et al., 2019). While these interventions can support species' nutritional needs (Harrison et al., 2010; Murray et al., 2016), their interactions with natural foraging behaviour remain poorly understood. Supplementary feeding can alter these natural foraging patterns and/or mask the importance of native food resources (Blanco et al., 2011; Harrison et al., 2010; Oro et al., 2013; Robb et al., 2008), underscoring the need to understand how these changes influence fitness outcomes and ultimately long-term population viability. This goal is particularly important for birds, where food quality and availability impact parental provisioning to nestlings (Tremblay et al., 2005; Wilkin et al., 2009) and can directly impact reproductive success through egg production, chick growth and fledging survival (Brightsmith et al., 2010; Koutsos et al., 2001; Martin, 1987; Reynolds et al., 2003).

The challenges of maintaining dietary quality become especially acute for species inhabiting islands, where ecosystems often face extensive habitat modification and high rates of species introductions (Whittaker & Fernández-Palacios, 2007). Island endemic species have frequently evolved specialised relationships with native plant communities (Olesen et al., 2012) and may be particularly vulnerable when these relationships are disrupted by habitat alteration. Understanding how island endemics respond to such changes through dietary adaptations, and the consequences for their fitness, is critical for developing effective long-term conservation strategies in highly threatened island ecosystems.

The Mauritius ('echo') parakeet (*Alexandrinus eques*), a parrot endemic to Mauritius, provides an ideal opportunity to examine these questions. Mauritius has experienced extensive forest modification, with less than 2% of intact native forest now remaining (Page & D'Argent, 1997). Within this altered landscape, the Mauritius parakeet persists in two distinct areas in the North and South of the Black River Gorges National Park. While both populations occupy ranges that contain fragments of Mauritius' best-preserved native forest, the North population's habitat is dominated by invasive species such as *Psidium cattleyanum* and *Ligustrum robustum*, whereas the South is dominated by non-native *Syzygium jambos* (Virah-Sawmy et al., 2009). Historical forest surveys revealed significant degradation across both population ranges. For example, in one study area within the North population range, native tree density declined by 70% between 1939 and 1999, with substantial reductions in species richness (Virah-Sawmy et al., 2009).

Conservation management of the Mauritius parakeet varies between populations through two main interventions. First, conservation management areas (CMAs) have been established to differing extents in both ranges—these are fenced sections where invasive plants are periodically removed to promote native species recovery (MWF, 2020). Second, supplementary feeding is provided at different intensities: daily in the North and weekly in the South population. Previous research has shown that Mauritius parakeets nesting closer to supplementary feeding stations incorporate more supplementary food into their diet, which correlates with improved reproductive success (Tollington et al., 2019). However, a detailed understanding is needed of how management through CMAs affects dietary breadth, whether supplementary feeding influences natural foraging patterns, and how these interact with reproductive outcomes.

Understanding these relationships requires detailed analysis of dietary information that is seldom available. However, recent avian dietary studies (e.g. Fablet et al., 2024; Schumm et al., 2023; Shutt et al., 2021; Stenhouse et al., 2023; Tang et al., 2022) have demonstrated how DNA metabarcoding technology can facilitate this by enabling taxonomic resolution exceeding that possible through traditional methods (Ando et al., 2020; Pompanon et al., 2012), and revealing dietary breadth in threatened and declining birds that would be undetectable through conventional approaches (Fablet et al., 2024; Schumm et al., 2023; Stenhouse et al., 2023; Tang et al., 2022). For example, metabarcoding of blue tit (*Cyanistes caeruleus*) faecal samples identified 432 invertebrate MOTUs from 793 samples, overcoming the difficulties in prey identification that limit traditional approaches (Shutt et al., 2020).

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To date, while DNA metabarcoding has been applied to numerous threatened bird species, no studies have linked nest-level dietary composition to reproductive outcomes in threatened island birds. A key distinction of the present study is that faecal samples were collected directly from known individual chicks during routine nest monitoring visits, meaning that the dietary signal can be attributed to specific breeding pairs and directly linked to their reproductive output. The closest parallel, Jarrett et al. (2020), linked blue tit diet composition to reduced chick mass and offspring numbers in urban compared to forest habitats. This study therefore addresses a critical gap in understanding how diet might impact fitness in threatened island birds.

Using DNA metabarcoding of faecal samples, this study investigates dietary patterns and their impacts on reproductive output in the Mauritius parakeet, across different levels of habitat modification and management intensity. We hypothesise that: (1) dietary composition will differ significantly between North and South populations reflecting potential differences in resource availability between the two areas, (2) dietary composition of birds nesting inside CMAs will consist of more native plant species than those outside, and (3) consumption of native plant species will positively correlate with reproductive output, as measured by the number of fledglings per brood (Tollington et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study species and sites

The Mauritius parakeet (*A. eques*) inhabits forest in the North and South of the Black River Gorges National Park in Mauritius (20°23′ S, 57°23′ E), across two populations separated by deep gorges and a high plateau, with genetic analyses confirming significant population differentiation and limited gene flow between them (Raisin et al., 2012; Tollington et al., 2013) (Figure 1). The North population ('Grand Gorges') inhabits areas with five CMAs, while the South population ('Bel Ombre') contains three CMAs. These protected areas range from 0.06 to 0.23 km^2 in size (MWF, 2020) and are fenced sections where invasive plants are removed to promote native plant recovery. Two reintroduced populations in the South-East and South-West of Mauritius lack data and were not included in this study.

Mauritius parakeets are monogamous with high nest site fidelity, breeding from October to February. Females lay one to four eggs and incubate for approximately 25 days while males provide food (Jones & Duffy, 1993; Young, 1987), with chicks typically fledging between February and March (Thorsen & Jones, 1998). Intensive monitoring includes several visits per season to record eggs hatched, chicks

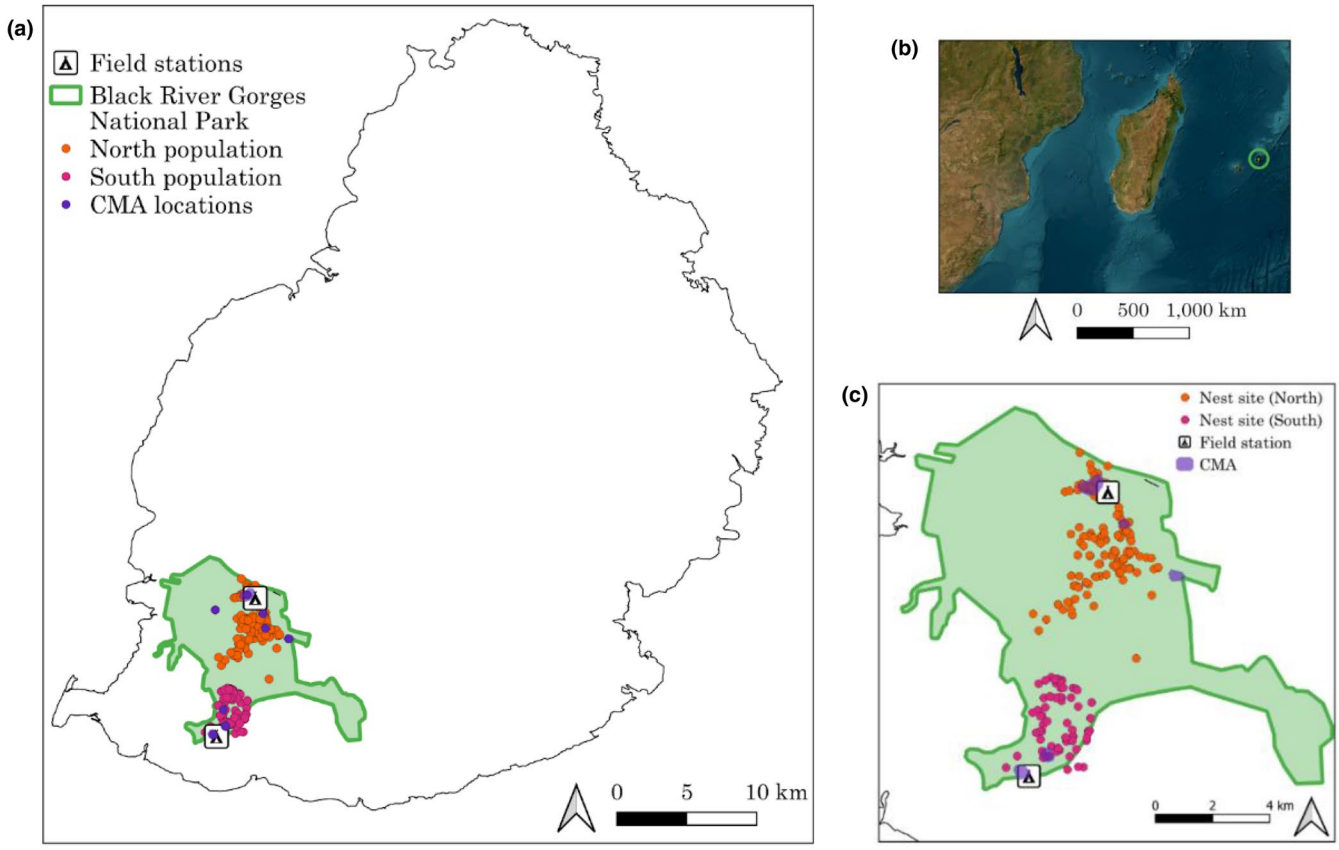


FIGURE 1 (a) Distribution of Mauritius parakeet populations in Black River Gorges National Park. Field stations, nest site locations, and CMA locations are shown within the park boundary. (b) Mauritius's location relative to mainland Africa and Madagascar. (c) Nest site distribution across the two populations.

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fledged and breeding pair identity. Their diet consists of fruit, tree bark, flowers and leaves, supplemented by commercial parrot food provided at designated feeding stations. The parrot food is provided daily in the North and weekly in the South, reflecting demand—the North population has a significantly higher proportion of supplementary food in their diet (Tollington et al., 2019).

2.2 | Sampling and DNA extraction

Faecal samples ($n = 209$) were collected from 157 Mauritius parakeet chicks at approximately 45 days old during routine nest site visits across three breeding seasons (2020–2022), from the North ($n = 150$ samples) and South ($n = 59$ samples). Where a chick defecated more than once during handling, multiple samples were collected from the same individual. Whilst samples were collected from known individual chicks, the dietary signal reflects the combined provisioning behaviour of both parents at the nest (Duffy, 1993; Young, 1987), rather than the food preferences of individual birds.

Chicks were temporarily removed from the nest in sterilised fabric bags for routine health checks, during which morphometric measurements, blood samples and feather samples were collected. Faecal samples were collected opportunistically and directly from the bags as chicks defecated during handling, ensuring samples could be attributed to known individual chicks and therefore reflected the diet of their parents. Samples were immediately transferred to pre-labelled zip-lock bags containing self-desiccating silica gel and stored away from direct sunlight in the field prior to transport. Upon return to the UK, samples were stored at −20°C at the National Environment and Omics Facility (NEOF), University of Sheffield, prior to DNA extraction.

All chicks were fitted with two uniquely coded identification rings (one per leg) to allow individual identification in the field and at feeding stations. Reproductive success was measured as the number of fledglings per brood, recorded during routine nest monitoring visits. Nests were visited multiple times per season: initially to confirm eggs, followed by health checks during the chick stage, and a final visit at the expected fledging stage to count the number of successfully fledged chicks. During each visit, data recorded included clutch size, egg age (determined by candling), hatching success, and chick morphometrics including body weight, wing feather length and tail length. Blood and feather samples were also collected from chicks during health check visits for ongoing monitoring and research purposes.

Of the 209 faecal samples, 39 were collected from within CMAs and 170 from outside CMAs, with all CMA samples coming from the North population. Only one active nest was located inside a CMA in the South population during the study period, and we were not able to obtain samples from it.

Dried faecal samples were homogenised using autoclaved metal beads and TissueLyser (Qiagen, Hilden, Germany). DNA was extracted from at least 10 mg of homogenised sample using the QIAamp DNA Stool Mini Kit (Qiagen, Manchester, UK) following the manufacturer's protocol. To control for potential contamination, one DNA extraction negative was included in each extraction session.

PCR amplification was carried out in 20 μL reaction volumes containing 10 μL of QIAGEN Multiplex PCR Master Mix, 2 μL each of UniPlantF and UniPlantR 5 μM primers (Moorhouse-Gann et al., 2018), 5 μL ddH_2O and 1 μL of DNA template (10 ng/μL). The PCR program consisted of initial denaturation at 95°C for 10 min, followed by 40 cycles of 95°C for 30 s, 56°C for 30 s and 72°C for 1 min, with final extension at 72°C for 10 min. A second PCR added Fi5 and Ri7 unique identifier Illumina adapters (Integrated DNA Technologies, USA) to the amplicons. Sequencing was performed at the Centre for Genomic Research (University of Liverpool, UK) on an Illumina MiSeq platform using a V2 250 bp paired-end read kit.

The UniPlantF and UniPlantR primers used in this study were validated by Moorhouse-Gann et al. (2018) against a Mauritian plant ITS2 database, demonstrating in silico coverage of 88% of Mauritian species and in vitro amplification success of 99% of 169 Mauritian species tested.

Sampling methods were approved by the Research Ethics Committee of the School of Anthropology and Conservation, University of Kent. All samples were collected with support from trained field staff at the Mauritian Wildlife Foundation (MWF) and the National Parks and Conservation Service (NPCS) as part of routine monitoring (NPCS permit: NP-46/3 V5). Samples were transported from Mauritius to the UK under APHA Import Permit ITIMP21.0404, CITES Export permits MU 220195 and MU 220125, and CITES Import permit 598437/02 and Import notification 020113.

2.3 | Plant DNA reference library

We compiled a DNA barcode reference library specific to Mauritian plants targeting the Internal Transcribed Spacer 2 (ITS2) region using S2F and S3R markers (Chen et al., 2010). The library was constructed using: (1) samples collected from mainland Mauritius, primarily from arboretums and conservation areas; (2) specimens from the herbarium collection at Kew Gardens; and (3) sequences downloaded from the NCBI GenBank database, including those from Moorhouse-Gann et al. (2018).

Of the known 691 plant species on Mauritius (Baider et al., 2010), plant sampling was prioritised based on known occurrence in Mauritius parakeet diet from prior observations by MWF, endemism to Mauritius or the Mascarene Islands (Atkinson & Sevathian, 2024) and existing barcode availability (Sayers et al., 2022). Species assignment was verified for each sequence by BLASTn searches against all other sequences in the library and the GenBank database (Altschul et al., 1990). If the sequence's top bit score matched exclusively to a single species, the sequence was identified to species level, with hierarchical assignment criteria applied for ambiguous matches (Hleap et al., 2021).

The ITS2 reference library achieved species-level assignment for 71.4% of sequences, genus-level for 87.6% and family-level for 95.4%, consistent with published assessments of ITS2 as a plant DNA barcode (Chen et al., 2010; Moorhouse-Gann et al., 2018). Species-level

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discrimination was not always possible within certain genera including *Syzygium*, *Coffea* and *Labourdonnaisia*, where pairwise sequence identity between species was 99%–100%, likely reflecting limited interspecific variation in the ITS2 region within these genera rather than misidentification. For full details of reference library construction, sequencing success rates and species assignment results, see Supplementary Information S1.

2.4 | Bioinformatics

Raw sequencing reads were processed using the DADA2 pipeline (Callahan et al., 2016) implemented in R v4.3.1 (R Core Team, 2023). Cutadapt v4.5 (Martin, 2011) was used to remove primer sequences and then DADA2 functions were used to filter and de-noise the data, resulting in amplicon sequence variants (ASVs) without OTU clustering (full bioinformatics pipeline parameters are provided in Supplementary Information S2).

Taxonomic assignment was performed using our custom reference library (minimum bootstrap confidence 50). ASVs not assigned by the custom library were subjected to BLASTn searches against the NCBI nucleotide database (*e*-value ≤0.00001, minimum 90% identity). BLAST results were processed using MEGAN6 (Huson et al., 2016) with a top percent threshold of 10 and naive LCA algorithm to assign taxonomy. Non-plant hits were excluded, and the top hit per ASV was retained based on bit score. ASV read counts were subsequently aggregated to species level for downstream analyses.

Contaminant species were identified and removed using the 'decontam' package (Davis et al., 2018). Following recommendations by Drake et al. (2022) and Tercel et al. (2022), we additionally filtered the data by removing ASVs with 10 or fewer reads. Additionally, for each taxon detected in negative control samples, we subtracted the maximum observed read count from all true samples to account for potential contamination.

In total, 7,969,910 raw reads were generated across all samples. The DADA2 pipeline produced 2699 ASVs, of which 1899 (70.4%) were assigned to at least family level. Following aggregation to species level and sequential filtering steps including decontamination, read count thresholds and negative control correction, 83 plant taxa were retained in the final dataset. Mean reads per sample in the final dataset were 27,590 (range 0–86,325), with 5,715,383 reads retained after filtering. The composition of sequence reads per identified plant taxon is provided in Supplementary Information S1.

2.5 | Statistical analysis

Plants were categorised as native or non-native based on established classifications (POWO, 2025). Species richness and Shannon diversity were calculated after rarefying to a standardised read depth of 10,000 reads. Following filtering and rarefaction, 144 of the 157 individuals sampled were retained for diversity analyses (North $n=108$, South $n=36$; within CMA $n=27$, outside CMA $n=117$). Wilcoxon rank-sum tests then compared these metrics between populations and within or outside of a CMA.

Factors influencing plant diversity in individual birds were analysed using generalised linear mixed models (GLMMs) with brood ID as a random effect to account for the non-independence of siblings. Response variables included total species richness (excluding supplementary food species), Shannon diversity and native species richness. Predictors included population (North or South), CMA status (whether the nest site was located inside or outside of a CMA), distance to nearest CMA (straight-line distance in km, from nest site coordinates to CMA border), distance to feeding station (straight-line distance in km) and Season (breeding year). Models were fitted using the 'glmmTMB' package (Brooks et al., 2017) with negative binomial distribution for count data and Gaussian distribution for Shannon diversity. Models included 144 individuals from 117 broods.

To analyse relationships between diet composition and reproductive output, we performed GLMs with the number of fledglings per brood as the response variable. Fledgling number is a widely used proxy for reproductive output in avian studies, integrating multiple aspects of breeding performance (Ricklefs & Bloom, 1977), and has been used previously as a measure of reproductive output in Mauritius parakeet research (Tollington et al., 2019). Dietary detections were aggregated to the brood before analysis: where more than one chick was sampled from a brood, a plant taxon was recorded as present if detected in at least one sampled chick. Each brood therefore contributed a single observation. Plant species detected in at least 20 broods, and identified to at least genus level, were included as predictor variables, along with population (North or South), CMA status (whether the nest site is located inside or outside of a CMA), distance to nearest CMA (straight-line distance in km, from nest site coordinates to CMA border), Season (breeding year) and distance to supplementary feeding station (straight-line distance in km). Models were fitted using base R glm() with a Gaussian distribution, for the entire dataset and for each population separately. Of the 117 broods represented in the dietary dataset, 95 had complete reproductive outcome data and were included in these models (North $n=67$, South $n=28$).

In each case, model selection was based on AICc values with models restricted to ΔAICc <7 before model averaging (Bolker et al., 2009; Burnham et al., 2011). The significance of model-averaged coefficients was assessed using 95% confidence intervals, and we calculated weighted t-statistics following Cade (2015) to evaluate the relative importance of variables.

3 | RESULTS

3.1 | Plant DNA reference library and diet composition

The plant DNA reference library consisted of 296 Sanger consensus sequences generated in this study representing 147 plant species (132 native to Mauritius, 15 introduced), plus 371 sequences

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obtained from GenBank, including those uploaded by Moorhouse-Gann et al. (2018) in a DNA metabarcoding study based on Round Island and Île Aux Aigrettes (islets off the coast of Mauritius). The downloaded sequences represent 143 additional species (70 native to Mauritius, 67 introduced). This produced a total of 290 plant species—42% of the estimated 691 plant species documented in Mauritius (Baider et al., 2010).

Of the 209 faecal samples from 157 individual parakeets, 206 samples from 155 individuals were retained following filtering, and 144 individuals met the rarefaction threshold for inclusion in diversity analyses. DNA metabarcoding identified 83 plant taxa in these samples, with 74 plant taxa detected in samples from the North population and 43 in the South. The identified taxa consisted of 44 plant families and 75 genera, with 68 taxa identified to species level. Of these, 21 were categorised as endemic, 22 as native, 29 as non-native, 3 as supplementary food-derived species and 8 remained uncategorised due to higher-level taxonomic identification.

The most prevalent plant species across all samples was *Gaertnera* spp. (endemic, present in 51% of samples), followed by *Triticum urartu* (non-native supplementary food species, 49% of samples), *Tabernaemontana persicariifolia* (endemic to Mauritius and Réunion Island, 49%), *Olea lancea* (native, 47%) and *Tridax procumbens* (non-native, 46%). The most common species in the North was *T. urartu*, followed by *O. lancea* (native) and *T. persicariifolia*. In the South, the most common species was an unknown species in the Asteraceae family, followed by *T. procumbens* (non-native) and *Gaertnera* spp. (endemic). Figure 2 visualises the occurrence of each plant taxon in samples from each population.

Out of 38 plant species previously understood to be in the Mauritius parakeet diet from direct field observations, 29 were present in our DNA reference library. Of these, 11 species (38%) and 19 genera (66%) were detected in the faecal samples. Of the 83 plant taxa detected, 72 had not previously been recorded in Mauritius parakeet diet from field observations, representing a substantial expansion of the known diet of this threatened species.

3.2 | Native versus non-native species consumption

Native species richness was significantly higher than non-native species richness in the North population (4.7 ± 0.3 vs. 2.1 ± 0.2 species per sample; Wilcoxon rank sum test, $p < 0.001$). In the South population, there was no significant difference between native and non-native species richness (1.9 ± 0.2 vs. 1.7 ± 0.2 species per sample; $p > 0.05$).

There was no significant difference in native species richness between samples from within CMAs and outside CMAs (Wilcoxon rank sum test, $p > 0.05$), although overall species diversity (Shannon index) was higher within CMAs. Note that this CMA comparison applies only to the North population, as no samples were collected from CMAs in the South population.

3.3 | Alpha and beta diversity

Alpha diversity was significantly higher in the North ($n = 108$) than the South ($n = 36$) for both observed species richness (Wilcoxon rank-sum test, $p = 0.024$) and Shannon diversity ($p < 0.001$) (Figure 3). Species richness within CMAs ($n = 27$) was significantly higher than outside CMAs ($n = 117$) for both observed species richness ($p = 0.005$) and Shannon diversity ($p = 0.003$).

Beta diversity analysis revealed significant differences in diet composition between the North and South populations (PERMANOVA, $p < 0.001$), and between individuals within and outside CMAs (PERMANOVA, $p < 0.01$). Principal coordinates analysis (PCoA) of Jaccard distances visualised these compositional differences, with the first two axes explaining 23.8% and 12.8% of variation respectively (Figure 4).

3.4 | Factors influencing dietary diversity

GLMMs predicting dietary diversity revealed that birds in the North population had significantly higher total plant species richness (Estimate = 0.34, 95% CI: 0.11–0.57, $p = 0.003$), Shannon diversity (Estimate = 0.42, 95% CI: 0.16–0.68, $p = 0.001$), and native species richness (Estimate = 2.27, 95% CI: 1.28–3.26, $p < 0.001$) compared to the South (Table 1).

Neither CMA presence nor distance to feeding station had significant effects on species richness or Shannon diversity. Breeding season showed negative effects on observed species richness (2021: Estimate = −0.23, $p = 0.022$; 2022: Estimate = −0.27, $p = 0.035$) and native species richness (2021: Estimate = −1.01, $p = 0.028$). Population was the strongest and most consistent predictor of dietary diversity across all measures.

3.5 | Diet composition and reproductive success

In the North population (Table 2), consumption of the supplementary food component *T. urartu* showed a positive association with fledgling numbers (Estimate = 0.57, 95% CI: 0.10–1.05), while *Labourdonnaisia calophylloides* (endemic to Mauritius and Réunion Island) had a negative effect (Estimate = −0.46, 95% CI: −0.88 to −0.04).

In the South population (Table 3), consumption of endemic *Gaertnera* spp. was positively associated with fledgling numbers (Estimate = 0.79, 95% CI: 0.38–1.20), while two non-native species—*Homalanthus populifolius* (Estimate = −0.73, 95% CI: −1.34 to −0.12) and *L. robustum* (Estimate = −1.17, 95% CI: −1.83 to −0.51)—were negatively associated with reproductive success.

Breeding season had a negative effect on fledgling numbers in the North population (Estimate = −0.32, 95% CI: −0.60 to −0.04) but showed no significant effect in the South. The full averaged model

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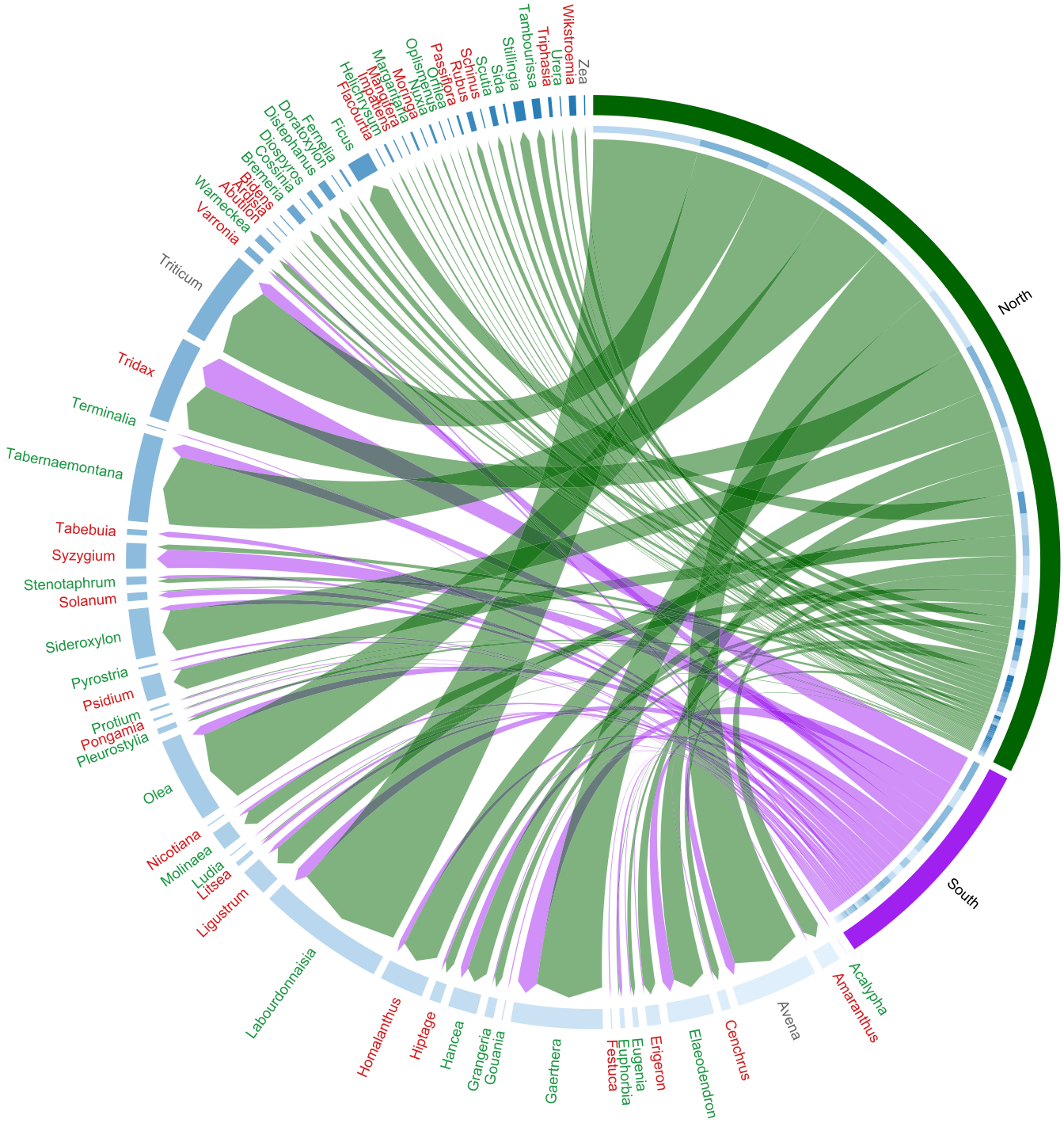


FIGURE 2 Distribution of plant genera found in the diet of Mauritius parakeets in the North (dark green) and South (purple) populations of Black River Gorges National Park, Mauritius. Chords connect population arcs to genus arcs, indicating presence of that genus in the respective population. Chord width is proportional to the frequency of occurrence of each genus across samples. Genus labels are coloured by native status: Green = native or endemic; red = non-native; grey = genus present in supplementary food.

indicated that across all birds, consumption of *Gaertnera* spp. was a positive predictor of reproductive success (Estimate = 0.50, 95% CI: 0.14–0.87), while *L. calophylloides* (Estimate = −0.49, 95% CI: −0.88 to −0.10) and *H. populifolius* (Estimate = −0.45, 95% CI: −0.85 to −0.06) showed negative associations.

4 | DISCUSSION

This study, to our knowledge, is the first to link dietary composition to reproductive success in a threatened island bird, and the first characterisation of Mauritius parakeet diet using DNA metabarcoding. While

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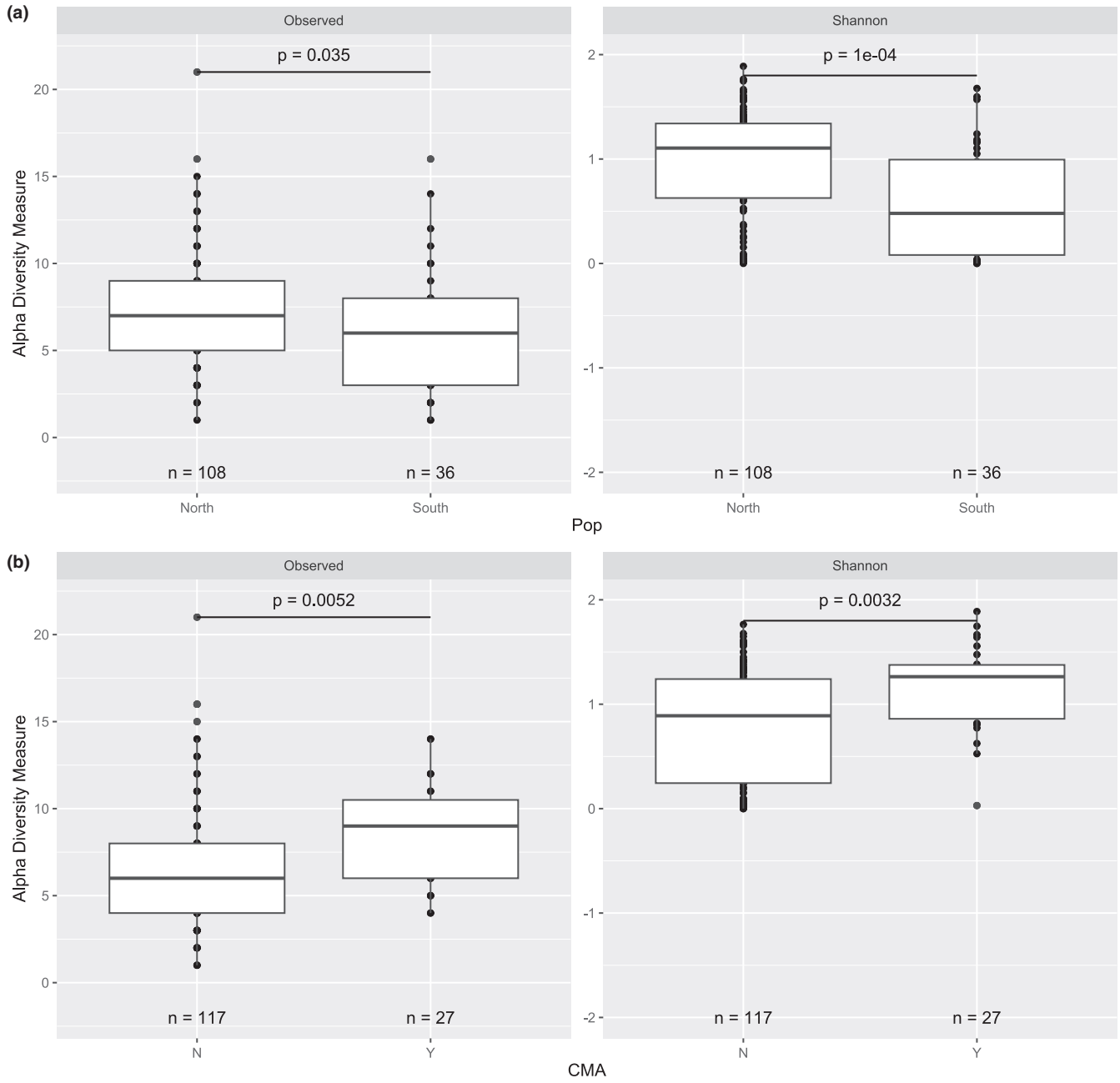


FIGURE 3 Alpha diversity of plant species in Mauritius parakeet faecal samples. (a) Comparison of observed species richness and Shannon diversity between North ($n = 108$) and South ($n = 36$) populations. (b) Differences in alpha diversity metrics between nests located outside (N, $n = 117$) and inside (Y, $n = 27$) conservation management areas (CMA). *p*-values were calculated using Wilcoxon rank-sum tests.

DNA metabarcoding has been increasingly applied to characterise diets of threatened species, including the critically endangered red-headed wood pigeon (Ando et al., 2013) and endangered species such as the Sichuan partridge (Tang et al., 2022) and black-faced spoonbill (Lee et al., 2021), these studies have focused on dietary characterisation without examining relationships between diet composition and nest-level reproductive outcomes.

We revealed distinct patterns in Mauritius parakeet diet across two populations. The North population had significantly higher native plant diversity in the diet. Diet composition was associated with reproductive success in both populations, but differently: endemic plant consumption was positively associated with fledgling number in the South, whilst supplementary food consumption was the strongest predictor in the North.

4.1 | Improved understanding of dietary breadth through metabarcoding

DNA metabarcoding substantially expanded our understanding of Mauritius parakeet dietary breadth. While previous field observation methods documented 38 plant species in their diet, we identified

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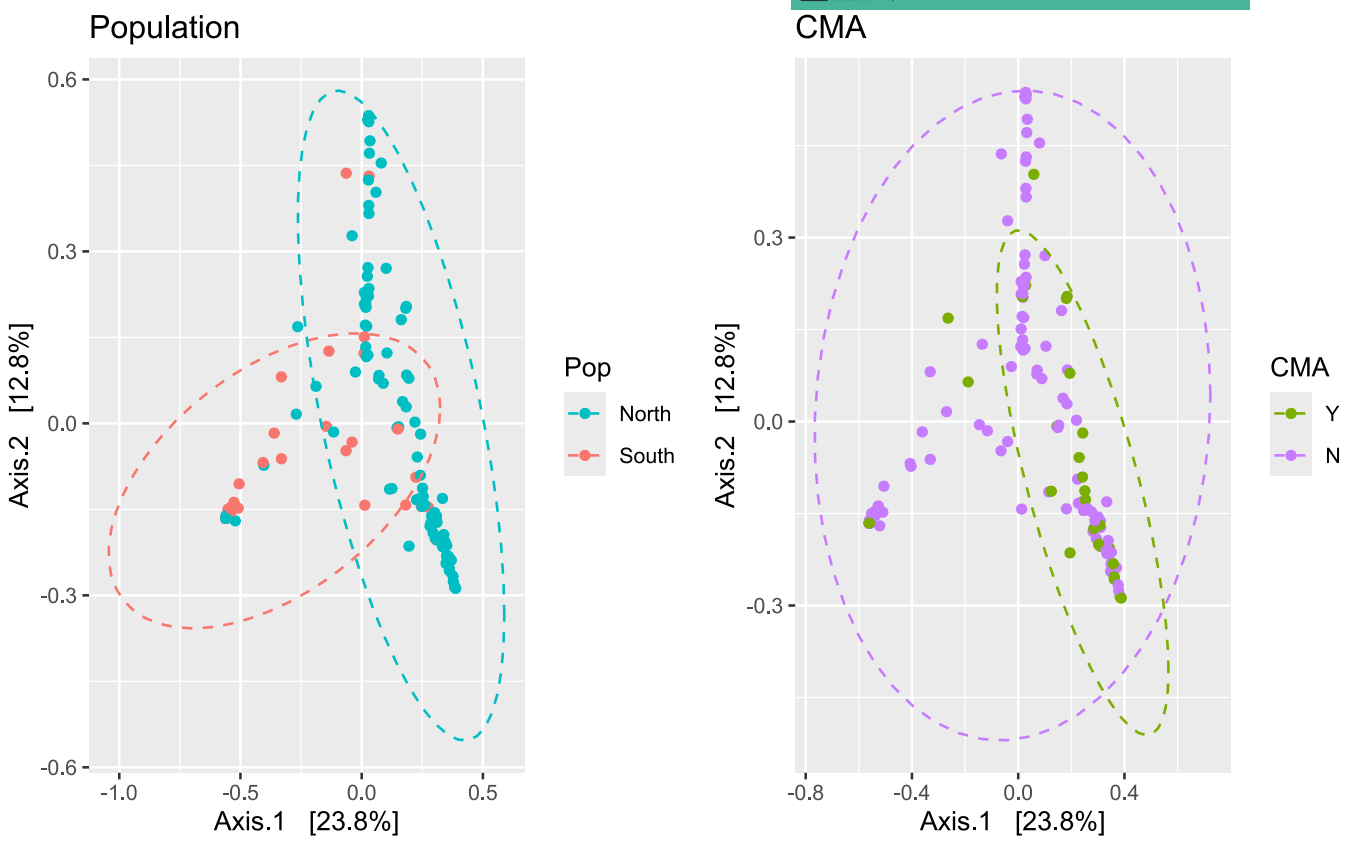


FIGURE 4 Principal coordinates analysis (PCoA) plots illustrating dietary composition differences among samples based on Jaccard dissimilarity. Left panel shows samples colour-coded by population (North: blue, South: pink). Right panel shows the same samples colour-coded by presence inside (Y: green) or outside (N: purple) conservation management areas (CMAs). Each point represents an individual bird (North $n = 108$, South $n = 36$; within CMA $n = 27$, outside CMA $n = 117$). Axis 1 explains 23.8% of the variation and Axis 2 explains 12.8%. Dashed ellipses represent 95% confidence intervals for each group. Closer points indicate more similar diets, while distant points represent more divergent dietary compositions.

83 taxa, with only 11 species overlapping between observational and molecular methods. This difference aligns with findings from Goldberg et al. (2020), who found DNA metabarcoding revealed considerably more dietary components than previous methods in ground squirrels.

This expanded dietary profile has implications for understanding a species' ecological flexibility and potential resilience to habitat modification. With more than twice as many food plants identified than previously known, Mauritius parakeets appear to have a broader dietary niche than earlier assumed. Dietary plasticity in parrots has been shown to influence their capacity to respond to anthropogenic pressures (Renton et al., 2015), with dietary generalists more likely to thrive in modified ecosystems (Ducatez et al., 2015), and behavioural plasticity allowing threatened parrots to persist in human-modified landscapes (Salinas-Melgoza et al., 2013).

An unexpected finding was the relatively low detection of dominant invasive plants across samples. Despite *P. cattleyanum* and *L. robustum* being highly invasive and widespread across the species' range (Lorence & Sussman, 1986; Virah-Sawmy et al., 2009), these species appeared infrequently in dietary samples. This may partly reflect phenological mismatch: *P. cattleyanum* fruits primarily during the austral winter (June–August) in Mauritius (Kueffer & Mauremootoo, 2004), whilst the Mauritius parakeet breeding season occurs from October to February, limiting availability during the critical chick-provisioning period.

Beyond phenological constraints, birds may preferentially consume native fruits even when invasive fruits are more abundant (Gallinat et al., 2020), potentially reflecting more suitable nutritional profiles and more familiar chemical and visual signals in native species (Kessler & Kalske, 2018; Lomáscolo & Schaefer, 2010; Smith et al., 2013). Plant DNA detected in faecal samples may originate from a range of plant tissues beyond fruit, including flowers, leaves, buds and young shoots, all of which are known components of Mauritius parakeet diet (Jones et al., 2013). The low detection of invasive species may therefore reflect avoidance across multiple tissue types rather than fruit consumption alone.

Our finding that endemic *Gaertnera* spp. consumption positively correlates with reproductive output in the South population supports the interpretation that selective foraging for native species may confer fitness benefits in modified island habitats. Together, these findings support the importance of prioritising native and endemic plant species in habitat restoration efforts, particularly those that align with the species' breeding phenology.

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TABLE 1 Model coefficients and statistics for predictors of plant diversity measures in Mauritius parakeet diet.

Response variable	Parameter	Estimate	SE	*p*-value	CI 2.5%	CI 97.5%	*t* abs	*t* ratio	var *t*
Observed (excluding SF species)	Intercept	1.70	0.17	<0.001	1.37	2.03	10.26	1	0
	Pop North	**0.34**	**0.12**	**0.003**	**0.11**	**0.57**	**2.94**	**1**	**0**
	Season 2021	**−0.23**	**0.10**	**0.022**	**−0.43**	**−0.03**	**2.29**	**0.78**	**0**
	Season 2022	**−0.27**	**0.13**	**0.035**	**−0.52**	**−0.02**	**2.11**	**0.72**	**0**
	Nearest feeder	−0.05	0.09	0.563	−0.23	0.13	0.58	1	0
	Nest in CMA	0.13	0.13	0.312	−0.13	0.39	1.01	1	0
	Nearest CMA	0.06	0.12	0.618	−0.18	0.30	0.50	1	0
Shannon	Intercept	1.54	0.19	<0.001	1.17	1.91	8.06	1	0
	Pop North	**0.42**	**0.13**	**0.001**	**0.16**	**0.68**	**3.19**	**1**	**0**
	Season 2021	−0.21	0.12	0.082	−0.45	0.03	1.74	0.55	0
	Season 2022	−0.26	0.15	0.088	−0.55	0.04	1.71	0.54	0
	Nearest feeder	−0.02	0.11	0.859	−0.24	0.20	0.18	1	0
	Nest in CMA	0.26	0.16	0.108	−0.06	0.58	1.61	1	0
	Nearest CMA	0.02	0.15	0.881	−0.27	0.31	0.15	1	0
Native species	Intercept	2.75	0.73	<0.001	1.31	4.19	3.74	1	0
	Pop North	**2.27**	**0.51**	**<0.001**	**1.28**	**3.26**	**4.48**	**1**	**0**
	Season 2021	**−1.01**	**0.46**	**0.028**	**−1.91**	**−0.11**	**2.20**	**0.49**	**0**
	Season 2022	−0.93	0.58	0.109	−2.07	0.21	1.60	0.36	0
	Nearest feeder	−0.28	0.43	0.516	−1.12	0.56	0.65	1	0
	Nest in CMA	0.54	0.61	0.381	−0.66	1.74	0.88	1	0
	Nearest CMA	0.40	0.56	0.480	−0.70	1.50	0.71	1	0

Note: Results shown are from generalised linear mixed models with brood ID as random effect. Includes model coefficient estimates, standard errors (SE), *p*-values, 95% confidence intervals and *t*-statistics (absolute *t*-value, *t*-ratio relative to maximum *t*-value and variance in *t*-values) indicating relative predictor importance. Negative binomial models were used for species counts (Observed and Native species) and Gaussian model for Shannon diversity. Variables for which 95% confidence intervals do not cross zero are shown in bold.

4.2 | Population differences in diet composition

Despite historical vegetation surveys showing higher dominance of non-native species in the North (Florens et al., 2012; Lorence & Sussman, 1986; Virah-Sawmy et al., 2009), the North population had higher native species richness per sample than the South. The more frequent supplementary feeding in the North (daily vs. weekly in the South) may provide a reliable nutritional buffer during the breeding season, potentially reducing energetic constraints and allowing birds to exploit a wider variety of natural food resources opportunistically (Harrison et al., 2010; Murray et al., 2016). Additionally, the greater number and spatial extent of CMAs in the North may collectively create more foraging opportunities across the landscape—birds may be selectively foraging for native plants within CMAs while nesting outside of them, or targeting scattered native resources rather than abundant invasives. In contrast, the South population's lower native plant diversity could reflect both less frequent supplementary feeding and their fewer, smaller CMAs in a landscape where, among patches of good quality forest, large areas are dominated by *S. jambos* (Virah-Sawmy et al., 2009). Disentangling these mechanisms would require experimental approaches beyond the scope of this study.

4.3 | Diet composition and reproductive success

We found contrasting relationships between diet and reproductive success across the two populations. In the North, supplementary food consumption (*T. urartu*) had a positive association with fledgling numbers, while in the South, endemic *Gaertnera* spp. consumption correlated with greater reproductive success, and two non-native species, *H. populifolius* and *L. robustum*, were negatively associated with fledging success.

Fledgling number per brood was our measure of reproductive success, consistent with its use in previous Mauritius parakeet research (Tollington et al., 2019) and its widespread application as a metric of avian breeding performance (Ricklefs & Bloom, 1977). Fledgling number has been used as a key measure of reproductive output in recent studies linking food availability and diet quality to breeding success in birds (Berzins et al., 2020; Halliwell et al., 2023; Ruffino et al., 2014). Fledgling production integrates multiple components of the breeding attempt—hatching success, chick survival, and parental provisioning capacity—and is sensitive to dietary conditions during the chick-rearing phase, which is the period captured by our faecal sampling at approximately 45 days old. Given the three-season study window (2020–2022), survival to recruitment was not obtainable, making

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TABLE 2 Model-averaged coefficient estimates, standard errors (SE), 95% confidence intervals and *t*-statistics for predictors of fledgling numbers in the North population.

Variable (North model)	Estimate	SE	*p*-value	CI 2.5%	CI 97.5%	*t*_abs	*t*_ratio	var.*t*
Intercept	650	285	0.03	82	1219	—	—	—
Season	**−0.32**	**0.14**	**0.03**	**−0.60**	**−0.04**	**2.37**	**0.94**	**0.15**
Labourdonnaisia calophylloides	**−0.46**	**0.21**	**0.03**	**−0.88**	**−0.04**	**1.71**	**0.66**	**0.21**
Triticum urartu	**0.57**	**0.24**	**0.02**	**0.10**	**1.05**	**1.50**	**0.60**	**0.42**
Homalanthus sp.	−0.17	0.24	0.49	−0.82	0.08	0.92	0.36	0.38
CMA	−0.36	0.33	0.28	−1.07	0.06	0.73	0.30	0.41
Sideroxylon puberulum	0.08	0.18	0.66	−0.14	0.77	0.62	0.24	0.31
Syzygium jambos	0.15	0.33	0.64	−0.24	1.37	0.34	0.14	0.19

Note: Variables for which 95% confidence intervals do not cross zero are shown in bold.

TABLE 3 Model-averaged coefficients estimates, standard errors (SE), 95% confidence intervals and *t*-statistics for predictors of fledgling numbers in the South population.

Variable (South model)	Estimate	SE	*p*-value	CI 2.5%	CI 97.5%	*t*_abs	*t*_ratio	var.*t*
Intercept	88.76	212.66	0.69	−351.37	528.88	—	—	—
***Gaertnera* sp.**	**0.79**	**0.20**	**0.00**	**0.38**	**1.20**	**3.61**	**0.94**	**0.19**
Ligustrum robustum	**−1.17**	**0.32**	**0.00**	**−1.83**	**−0.51**	**2.89**	**0.75**	**0.71**
***Homalanthus* sp.**	**−0.73**	**0.29**	**0.02**	**−1.34**	**−0.12**	**1.85**	**0.48**	**0.31**
Tabernaemontana persicariifolia	−0.07	0.18	0.70	−0.85	0.22	0.78	0.21	1.01
Season	−0.04	0.11	0.70	−0.26	0.18	0.43	0.12	0.04
Hancea integrifolia	−0.06	0.17	0.74	−0.88	0.27	0.37	0.11	0.29

Note: Variables for which 95% confidence intervals do not cross zero are shown in bold.

fledgling number the most proximate and practically obtainable outcome variable in this system.

The population-specific relationships between diet and fledgling numbers could reflect differences in habitat composition and management intensity. The lack of a significant effect of breeding season in the South, contrary to the North, further emphasises how differently these populations respond to environmental and dietary factors.

The strong positive relationship between endemic *Gaertnera* spp. consumption and reproductive success in the South population has potentially significant ecological implications. It suggests that despite extensive habitat modification and the presence of supplementary feeding, endemic plant species can remain important for the reproductive success of threatened birds. However, as data on plant availability and nutritional composition are lacking in this system, causal mechanisms cannot be established from the current study alone.

While the nutritional composition of Mauritian *Gaertnera* species has not been comprehensively characterised, members of the Rubiaceae family have been shown to contain significant levels of phenolic compounds with antioxidant activity in Mauritian endemic flora (Soobrattee et al., 2008). Phenolic antioxidants may buffer against oxidative stress during energetically demanding periods such as chick-rearing (Alonso-Alvarez et al., 2004; Wiersma et al., 2004), though available phytochemical data are based on leaf tissue and nutritional composition of consumed plant parts may differ. Dedicated nutritional studies on this genus are needed to substantiate this interpretation.

4.4 | Conservation management areas

While we predicted CMAs would increase native species consumption through invasive plant removal (MWF, 2020), our findings suggest more complex patterns. Initial Wilcoxon tests suggested that CMAs increased overall plant species diversity in the parakeet diet but did not specifically enhance native species consumption. When examined in more complex models that included both presence within CMAs and distance to nearest CMA, along with other predictors, neither measure significantly predicted species richness or native species consumption.

This unexpected result may reflect how parakeets use the landscape: since their foraging ranges extend beyond CMA boundaries, birds may be accessing native plant resources across the habitat mosaic regardless of nesting location relative to CMAs. Rather than shifting dietary consumption solely towards native species, CMAs may effectively increase the total diversity of food resources available across the broader landscape.

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4.5 | Synthesis and applications

This study represents the first investigation to link nest-level dietary composition to reproductive success in a threatened island bird using DNA metabarcoding. Our findings provide partial support for two of our three hypotheses and have implications for conservation management of species in modified landscapes.

Consistent with our first hypothesis, diet composition differed significantly between the North and South populations, reflecting differences in resource availability or dietary preferences. This population-level divergence demonstrates how local habitat conditions may shape foraging behaviour within a single species.

Our second hypothesis—that birds nesting inside CMAs would consume more native species—was not supported. CMA presence at nest sites did not significantly alter nest-level dietary composition, suggesting CMAs might influence foraging opportunities at the landscape scale rather than through nest-site proximity alone.

Our third hypothesis was partially supported, but with important population-specific differences. Native plant consumption positively correlated with reproductive success in the South, whilst supplementary food was the strongest predictor in the North. The difference in supplementary feeding frequency between populations—daily in the North versus weekly in the South—likely contributes to this difference, with the North population showing greater benefit from supplementary food as a reliable and abundant resource. These results highlight that supplementary feeding remains an important management intervention for the North population and that reduction in provisioning frequency could negatively impact reproductive output. At the same time, the importance of *Gaertnera* spp. in the South demonstrates that native plant conservation remains essential even where supplementary feeding is provided.

For landscapes with remnant endemic plant populations, even small patches may provide critical resources for threatened species, particularly for island endemic species that may have evolved specialised relationships with native flora (Olesen et al., 2012; Schrader et al., 2024). Small habitat remnants in heavily modified landscapes can support disproportionate biodiversity value (Lindenmayer, 2019; Wintle et al., 2019).

Conservation managers should identify and protect endemic plant patches within broader restoration efforts, potentially using CMAs as reservoirs for native plant diversity while facilitating access to these resources for wildlife. For the Mauritius parakeet, expanding the number and size of CMAs in the South population could therefore be beneficial given the link between native plant consumption and reproductive success.

Generally, island bird management decisions should be informed by population-specific dietary studies identifying key food plants linked to fitness outcomes. This approach has broad applicability for threatened bird conservation in modified habitats worldwide.

4.6 | Limitations and future directions

While DNA metabarcoding provided unprecedented resolution of dietary composition, the relationship between sequence read abundance and actual biomass consumption remains uncertain, limiting our ability to quantify the relative importance of different food items (Pompanon et al., 2012; Thomas et al., 2016). Additionally, the incompleteness of our plant DNA reference library could mean that our dietary analysis underestimates true diversity.

A critical limitation is the absence of plant availability and phenology data across both population ranges, meaning dietary patterns may reflect resource availability rather than active food preferences.

The difference in sample sizes between the North ($n = 150$) and South ($n = 59$) populations reflects population size rather than unequal sampling effort; approximately 57% of all monitored nests were successfully sampled in both populations (North: 57 of 100; South: 29 of 50). The smaller absolute sample size in the South may nonetheless limit statistical power for population-specific comparisons, and these results should be interpreted with appropriate caution.

Although rarefaction was applied at the read depth level to standardise sequencing effort within samples, the larger sample size in the North population may have increased the probability of detecting rarer plant taxa. Comparisons of per-sample diversity metrics are less affected by this than comparisons of total species pools, but results for infrequently detected species exclusive to the North should be interpreted with caution. The North population also occupies a larger geographic range than the South, which may have contributed to higher dietary diversity by increasing access to a broader variety of plant resources, though without foraging range data we cannot quantify this effect.

Although the UniPlantF/UniPlantR primers have been shown to amplify 99% of Mauritian plant species in vitro (Moorhouse-Gann et al., 2018), primer mismatches may have contributed to the non-detection of some taxa, particularly within families that showed low sequencing success in our reference library construction such as Ebenaceae and Phyllanthaceae. Future studies should consider trialling additional markers such as rbcL or trnL to improve coverage.

AUTHOR CONTRIBUTIONS

Rebecca Louch, Simon Tollington, John Ewen, Claire Raisin, Jim Groombridge and Carl Jones conceived the ideas and designed methodology; Kevin Ruhomaun provided research permits and CITES permits for sample export; Rebecca Louch collected the data, with fieldwork support from Vikash Tatayah, Sion Henshaw, Nicolas Zuël and Kevin Ruhomaun; Deborah A. Dawson, Kathryn H. Maher and Lucy S. Knowles supported the laboratory methods and analysis of the metabarcoding data; Rebecca Louch analysed the data with input from Simon Tollington, John Ewen and Jim Groombridge; Rebecca Louch led the writing of the manuscript with supervision from Jim Groombridge, Simon Tollington and John Ewen. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The ITS2 DNA barcode reference library sequences generated for this study have been deposited in GenBank under accession numbers PX704139–PX704419. Sequencing and species assignment data are provided in Table S1.1 and Table S1.2. Study data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.m905qfvjj (Louch et al., 2026).

ORCID

Rebecca Louch https://orcid.org/0000-0001-9698-1824
Claire Raisin https://orcid.org/0000-0002-5074-4150

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1.1. Plant species list with sequencing and species assignment results.

Table S1.2. Number of reads and mean reads where detected per taxa, after filtering for contaminants using R package 'decontam'.

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