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RESEARCH

Extinction and loss of genetic diversity in a pantropical seabird population in the southwestern Atlantic Ocean

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Abstract

Seabirds are highly mobile organisms but often exhibit philopatric behavior, with each colony potentially forming a distinct breeding unit, leading to genetic structuring. Molecular markers are valuable tools for detecting genetic distinctiveness and supporting conservation strategies. The pantropical red-footed booby (*Sula sula*) nests in trees and currently has a single breeding site in the southwestern Atlantic Ocean at the Fernando de Noronha Archipelago, Brazil. The species was extirpated from Trindade Island, 1200 km off the Brazilian coast, due to forest destruction, and is now classified as "Endangered" in Brazil. This study compared the genetic structure and diversity between the extinct Trindade population and the extant Noronha population. Blood samples from Noronha and interdigital membrane samples from museum specimens from Trindade were analyzed using microsatellite markers. The Trindade population exhibited greater genetic diversity than Noronha, holding exclusive alleles. Additionally, the two colonies shared ancestry, with subtle signs of genetic segregation. This ancestry may be related to gene flow and a founder effect from Trindade individuals in the Noronha population. Ultimately, the extinction of the Trindade population led to the loss of a different genetic profile and reduced genetic diversity of red-footed boobies in the southwestern Atlantic Ocean. These findings highlight the importance of investigating evolutionary processes and dynamics within species for assessing anthropogenic impacts on biodiversity and conservation. Translocating red-footed boobies to Trindade Island could restore its ecological function and potentially prevent the imminent extinction of two endemic frigatebird species, which nest on trees and are kleptoparasitic on boobies.

Keywords Conservation · Genetic diversity · Gene flow · Microsatellites · Population structure · Suliformes

Introduction

Different factors can influence the genetic structure and diversity of populations. Populations can be genetically similar or distinct as a result of stochastic events (e.g. genetic drift) and deterministic processes (e.g. natural selection) (Griffiths 2013), as well as the influence of gene flow between them. Altough natural populations may form a single genetically homogeneous unit (Bilton et al. 2001) due to the effect of gene flow (Young et al. 2013), the absence or reduction of gene flow can lead to genetic differentiation (Hartl and Clark 2006) when populations become isolated and evolve independently. Panmictic populations have been documented for seals (Coltman et al. 2007), fish (Coimbra et al. 2020), and penguins (Nims et al. 2008), while in the southwestern Atlantic Ocean, populations of the Franciscana dolphin (*Pontoporia blainvillei*) (Gariboldi et al. 2016) and loggerhead sea turtles (*Caretta caretta*) (Reis et al. 2010) are genetically isolated. Therefore, studies on interpopulation genetic structure and diversity are essential for understanding species' evolutionary histories (Taylor and Friesen 2012) and developing effective conservation management plans (Frankham 2010).

Molecular markers, such as simple sequence repeats (SSRs or microsatellites), are useful for assessing interpopulation variation and detecting genetic structure. These markers are multi-allelic, co-dominant, exhibit high levels of polymorphism, and can be used in modern and ancient DNA samples when analyzed with appropriate precautions (e.g. specific program applications) (van Oosterhout et al.

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2004). Additionally, primers developed for one species can often be applied to related taxa (Moura et al. 2017). SSR markers have been successfully employed to detect genetic distinctiveness in various animal populations, including marine mammals (Durante et al. 2022), sea turtles (Roden et al. 2023), and seabirds (Nunes and Bugoni 2017; Danckwerts et al. 2021).

Most seabird species breed on islands and archipelagos and are highly philopatric (Schreiber and Burger 2001), despite their ability to fly long distances (Egevang et al. 2010; Fijn et al. 2013). As a result, genetic distinctiveness between populations is expected, as observed in the masked booby (*Sula dactylatra*, Suliformes) (Steeves et al. 2005; Muraro et al. 2024) and the Northern fulmar (*Fulmarus glacialis*, Procellariiformes) (Burg et al. 2003). However, some species show low or even non-existent genetic structure, such as the brown noddy (*Anous stolidus*, Charadriiformes) (Mazzochi et al. 2024) and the magnificent frigatebird (*Fregata magnificens*, Suliformes) (Hailer et al. 2010), likely due to gene flow from migrating individuals. Thus, the genetic structure of seabirds is complex and lacks a single pattern, even among closely related groups (Friesen et al. 2007).

The red-footed booby, *Sula sula*, is a suliform seabird (Chesser et al. 2010) with a pantropical distribution. During foraging, individuals can fly long distances (Mendez 2017) in search of fish and cephalopods (Seki and Harrison 1989). The species exhibits polymorphic plumage, characterized by two primary morphotypes: light and dark. The subspecies *S. sula sula* inhabits the Atlantic Ocean. In the southwest (SW) Atlantic Ocean, particularly Brazilian waters, the species historically bred on Trindade Island and the Fernando de Noronha Archipelago. However, currently, only Noronha is used as a breeding site (Schulz-Neto 2004; Mancini et al. 2016), with individuals nesting throughout the archipelago. Globally classified as “Least Concern” (IUCN 2018), the red-footed booby is listed as “Endangered” in Brazil (MMA 2014). The species is vulnerable to habitat destruction due to its reliance on trees and shrubs for nesting and the laying of a single egg per breeding season (Nelson 1978). Additionally, more than 12 colonies have gone extinct in the Indian Ocean in the last century (Carboneras 1992). In Brazil, the Trindade colony went extinct in the 1970s due to habitat destruction primarily caused by the introduction of goats and fires that destroyed nesting trees (Fonseca-Neto 2004).

The extinction of seabird colonies compromises genetic diversity and reduces species fitness (Danckwerts et al. 2021). This loss potentially affects entire ecosystems: seabirds are essential for transferring nutrients between marine and terrestrial environments (Signa et al. 2021) and influence other species. On Trindade Island, the loss of the red-footed booby colony may have affected two critically endangered frigatebird species, *Fregata trinitatis* and *Fregata minor nicolli* (Olson 2017). These frigatebirds exhibit kleptoparasitic behavior (Nuss et al. 2016), relying on fish stolen from boobies or other species. The absence of the red-footed booby may limit the food supply for these endemic frigatebirds, whose populations consist of only a few dozen individuals (Mancini et al. 2016). Efforts to restore colonies and recover seabird ecological functions have included chick translocations in other ocean basins (e.g. Pacific Rim Conservation 2018). However, such initiatives require thorough research, including genetic analyses to evaluate the fitness and genetic characteristics of each population (Freifeld et al. 2016). For this, scientific museum collections offer invaluable biological material from extant and extinct populations, providing insights into genetic variability and supporting evaluations of translocation feasibility (Schander and Halanych 2003).

In this study, we evaluated and compared the genetic diversity and structure of red-footed booby populations from Noronha and the extinct Trindade colony using SSR markers. We aim to assess whether these populations represent genetically distinct units and evaluate the impact of Trindade’s extinction on the species’ genetic diversity in the SW Atlantic Ocean.

Materials and methods

Study area and taxon sampling

The two historical breeding sites of red-footed boobies in the SW Atlantic Ocean are separated by 1,880 km. The Fernando de Noronha Archipelago (Fig. 1), located 360 km off the Brazilian coast, hosts the only existing colony of the species. Despite historical environmental degradation (Pessenda et al. 2008), Noronha supports diverse vegetation, including trees, shrubs, and herbaceous species (Mello and Oliveira 2016), providing suitable nesting sites for red-footed boobies, magnificent frigatebirds, and black noddies (*Anous minutus*). In contrast, the red-footed booby population on Trindade Island (Fig. 1), situated 1,140 km from the Brazilian coast, became extinct in the 1970s, after three centuries of habitat degradation due to the introduction of pigs and goats and the use of fire. The island now features only scattered patches of low vegetation, inconsistent with the reproduction needs of the species (Alves 1998).

Between 2011 and 2018, adult breeding red-footed boobies were captured at nest sites across various locations in Noronha (Table S1) for blood sample collection ($n=34$). Each bird was individually banded to avoid resampling and then released back to its nest. For the Trindade population, samples were obtained from taxidermized specimens housed at the National Museum of UFRJ (Federal University of Rio

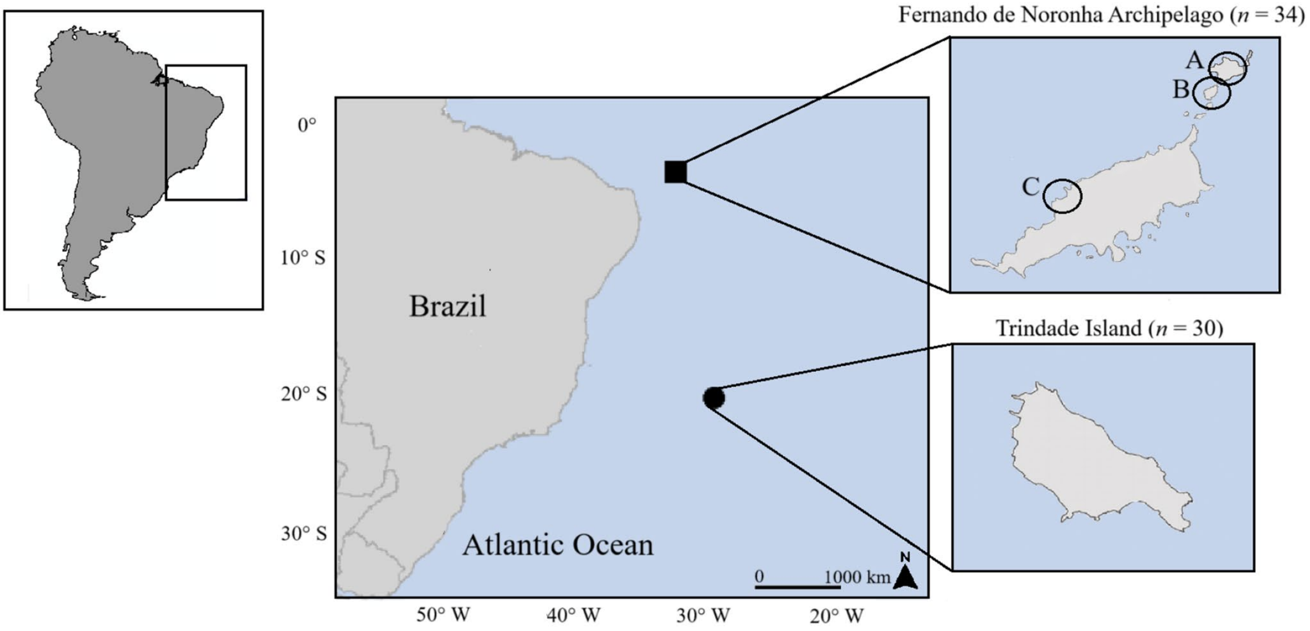


Fig. 1 Breeding sites of red-footed booby (*Sula sula*) in the southwest Atlantic Ocean: the Fernando de Noronha Archipelago is the only current breeding site for the species, while Trindade Island represents an extinct population. Samples from Noronha were collected at Rata Island (A), Meio Island (B), and Sancho Beach (C). The sampling sites on Trindade Island are not specified

de Janeiro, Brazil), collected during expeditions between 1914 and 1988 (Supplementary Material Table S1). A small fragment of the interdigital membrane was extracted from each specimen ($n=30$), as this tissue is highly vascularized.

DNA extraction and microsatellite amplification

DNA was extracted from blood samples ($n=34$) using the DNeasy Blood & Tissue QIAGEN® kit, following the manufacturer's protocol. For interdigital membrane samples ($n=30$), an adapted protocol combining the QIAquick PCR Purification kit and QIAamp DNA Micro kit was employed (unpublished data). All DNA samples were quantified using a Biodrop® spectrophotometer. Eight microsatellite loci were amplified from total genomic DNA. Detailed PCR protocols can be found in Supplementary Material 1.1. PCR products were isolated, amplifications were verified using 2% agarose gel electrophoresis, and only samples with defined and clear bands were kept. The resulting PCR products were genotyped at Macrogen® in Seoul, South Korea. To ensure consistency, 5–10% of previously genotyped samples were included in each subsequent genotyping batch.

Microsatellite analysis

Genotyping peaks were analyzed using the Peak Scanner program (Applied Biosystems). Only high-quality genotypes with well-defined peaks were included in the analyses. The presence of null alleles was assessed with the MICRO-CHEKER 2.2.3 program (van Oosterhout et al. 2004). Genetic diversity indices were calculated using Arlequin 3.5 (Excoffier and Lischer 2010), FSTAT (Goudet 1995), and GenePop 4.4 (Rousset 2008). Linkage disequilibrium tests between pairs of loci were performed in Arlequin 3.5.

Population structure between the two colonies was examined using multivariate and Bayesian techniques. Principal Coordinate Analysis (PCoA) was performed in GenAlEx 6.5 (Peakall and Smouse 2012) for multivariate analysis. For Bayesian analysis, STRUCTURE 2.3.4 was used to determine the most likely number of genetic groups (K) (Pritchard et al. 2000). The ΔK method (Evanno et al. 2005) was applied to identify the optimal K value through STRUCTURE HARVESTER Web 0.6.94 (Earl and vonHoldt 2012). A bar graph representing individual assignments to different clusters was generated using DISTRUCT 1.1 (Rosenberg 2004). To complement Evanno's method, which may not effectively detect $K=1$, the Puechmaille method (2016) was implemented via STRUCTURE SELECTOR (Li and Liu 2018). Additionally, the BOTTLENECK 1.2.02 program (Piry et al. 1999) was used to assess whether the populations were in mutation-drift equilibrium (Cornuet and Luikart 1996). Further analytical details are provided in Supplementary Material 1.2.

Table 1 Characterization of microsatellite markers for red-footed booby (*Sula sula*) populations from the Fernando de Noronha Archipelago and Trindade Island, southwestern Atlantic Ocean. It includes the number of samples (*n*), the number of alleles identified at each site, and diversity parameters: allelic richness (A_r), expected (H_E) and observed (H_O) heterozygosity, gene diversity, and the number of exclusive alleles

Population	*n*	Alleles	A_r	H_E	H_O	Gene diversity	Exclusive alleles
Noronha	34	14	1.66	0.31	0.34	0.15	2
Trindade	30	24	2.83	0.26	0.27	0.25	17

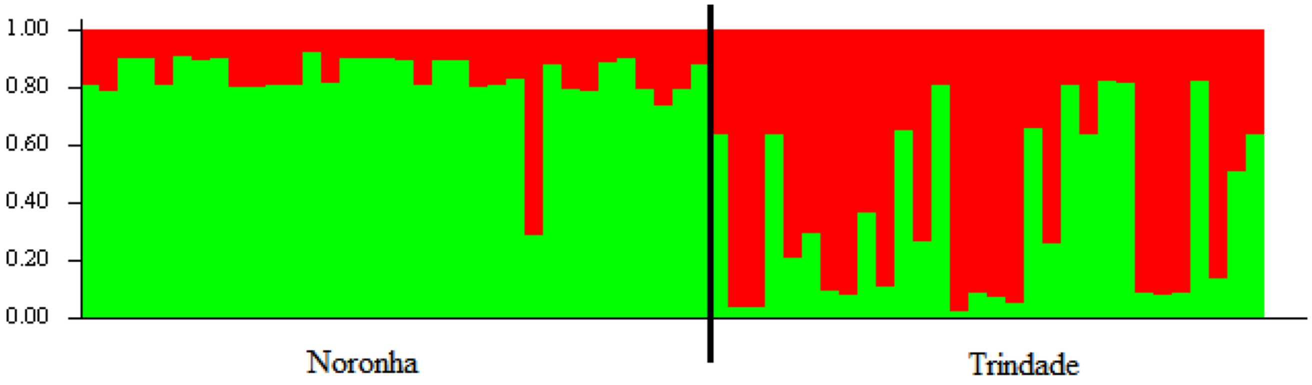


Fig. 2 Bayesian estimates of population structure for red-footed boobies (*Sula sula*) from the Fernando de Noronha Archipelago ($n=34$) and the extinct population of Trindade Island ($n=30$), based on eight microsatellite loci. The analysis revealed two groups (K = 2). Each vertical line represents an individual, with colored segments indicating the proportional representation of genetic group

Results

As the results of the sample sequences included in the different genotyping runs were consistent, all batches of samples were included in the analysis. None of the analyzed loci exhibited linkage disequilibrium. Null alleles were detected at a single locus. However, analyses showed no significant differences when this locus was included or excluded, so it was retained for subsequent analysis.

Genetic diversity indices

A total of 26 alleles were identified across the eight SSR loci analyzed. All loci were variable in the Trindade population, where as only four were variable in Noronha. The Trindade population exhibited a greater number of alleles ($n=24$; Table 1) compared to Noronha ($n=14$; Table 1). The mean number of alleles per locus was higher in Trindade (3) than in Noronha (1.75). Despite a higher overall number of alleles, many in Trindade ($n=16$) had low frequencies (between 0.01 and 0.19) and were considered rare (with frequencies lower than 0.5). Allelic richness (A_r) was also higher in Trindade (2.83 alleles) compared to Noronha (1.66 alleles) (Table 1). Trindade exhibited higher genetic diversity (0.25) and a greater proportion of exclusive alleles (65.4%) than Noronha (0.15 and 7.7%, respectively).

Observed heterozygosity (H_O) exceeded expected heterozygosity (H_E) in both colonies (Table 1). The test for heterozygote deficiency was significant for Trindade ($p=0.009$), indicating deviations from Hardy-Weinberg equilibrium (HWE). Population reduction tests revealed a heterozygote deficit in Trindade, while Noronha showed no significant deficits. The pairwise population genetic distance (R_{ST}) value was low (0.02) and not significant ($p=0.33$).

Genetic structure

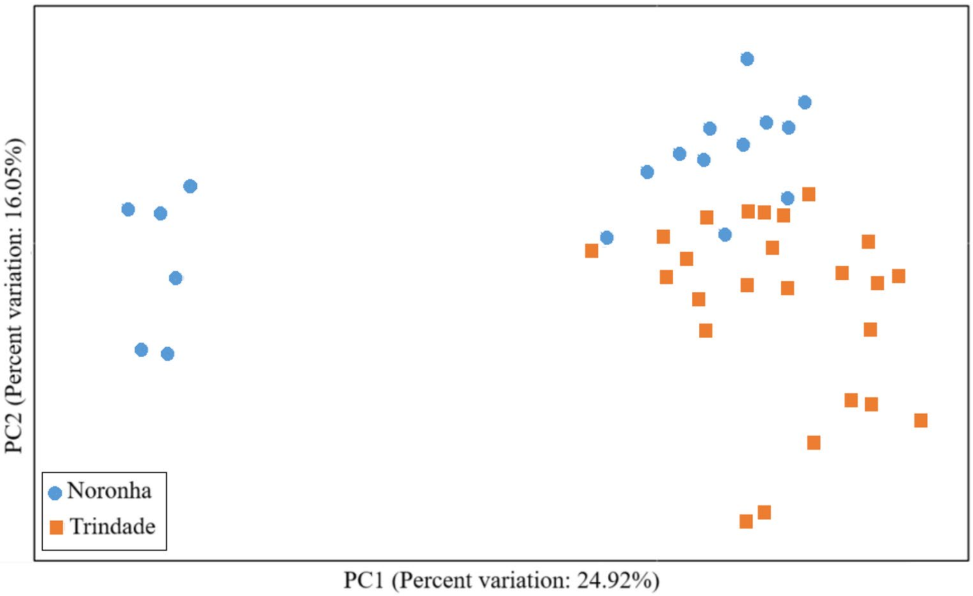
The highest value of ΔK (Evanno et al. 2005) indicated two genetically distinct populations (K = 2; Fig. 2) corresponding to Noronha and Trindade, further supported by the Puechmaille method. Despite this distinction, a relevant proportion of shared ancestry was observed between the two colonies. Principal Coordinate Analysis (PCoA) identified two main groups. The first coordinate (24.9%) distinguished some Noronha individuals, separating them from a group comprising Noronha and Trindade individuals. The second coordinate (16.1%) indicated subtle differentiation between the populations within this group (Fig. 3).

Discussion

Genetic diversity indices

The red-footed booby population on Trindade exhibited higher genetic diversity than the population from Noronha. However, the H_E values for both Trindade and Noronha were lower than those reported for other *S. sula* populations in the Atlantic (Morris-Pocock et al. 2016) and for brown booby (*S. leucogaster*) colonies in the SW Atlantic Ocean

Fig. 3 Principal Coordinate Analysis (PCoA) for red-footed boobies (*Sula sula*) from the Fernando de Noronha Archipelago ($n=34$) and the extinct population of Trindade Island ($n=30$), based on eight microsatellite loci. The two principal axes are plotted, with their values shown



(Nunes and Bugoni 2017). This suggests that red-footed booby populations can persist despite low genetic diversity, as evidenced in other seabirds, such as albatrosses (Milot et al. 2007). Nevertheless, low genetic diversity poses a risk to species viability, underscoring the importance of continued monitoring (Canteri et al. 2021).

The high number of unique alleles and the elevated polymorphism in Trindade suggest a larger effective population size and greater genetic diversity than in Noronha. It is also possible that individuals from Trindade migrated to Noronha and established a population there, resulting in a founder effect. Consequently, Noronha may retain only a small fraction of the genetic variation from the original population (Hartl and Clark 2006).

Significant heterozygosity deficiencies in Trindade may indicate the immigration of birds introducing new alleles and potentially decreasing heterozygosity (Luikart et al. 1998; Piry et al. 1999). Migrations, despite the species' philopatric behavior, are plausible as evidenced by documented movements (Steeves et al. 2003). Migrating individuals could originate from other Atlantic colonies (e.g. Fernando de Noronha, Saint Helena, and Ascension). Population sub-structuring due to assortative mating could also contribute to heterozygote deficits. However, it is important to note that the Trindade samples were collected over different years, which could introduce temporal variation and potentially bias the conclusion of the presence of heterozygosity deficiencies in Trindade, as proposed by the Wahlund effect (Hartl and Clark 2006).

Genetic structure

Bayesian analyses indicated K = 2, representing two distinct populations, altough high levels of shared ancestry were observed. PCoA also revealed two groups: one exclusively composed of Noronha individuals and another with individuals from both populations, with some distinctions between them. The lack of clearer separation between populations may partly result from the quality of the DNA samples and allelic dropout (van Nieuwerburgh et al. 2009), which can hinder the detection of genetic variation between populations.

Four scenarios may explain the shared ancestry and relatedness between some Noronha and Trindade individuals:

i) Recent segregation of the two populations before the extinction of the Trindade colony, due to interrupted gene flow for unknown reasons (e.g. the influence of non-physical barriers) (Morris-Pocock et al. 2016);
ii) Colonies were segregated when both of them existed, but migrant individuals maintained gene flow (Steeves et al. 2003);
iii) Past panmictic populations with independent differentiation of Noronha after the extinction of Trindade;
iv) Founder effect from Trindade to Noronha leading to the subsequent independent diversification of the Noronha population.

These scenarios emphasize the importance of the Trindade colony for the genetic diversity of red-footed boobies in the SW Atlantic Ocean and its role in forming the Noronha population. Thus, the extinction of Trindade may have significantly affected Noronha's genetic pool by losing an essential allele source.

Conservation implications

The identification of allele sharing and ancestry between Trindade and Noronha suggests the potential for translocating chicks from Noronha to Trindade, especially through the recovery of local vegetation. Reintroducing the red-footed booby would restore its ecological role on Trindade and in the adjacent marine environments (e.g. Pacific Rim Conservation 2018). Additionally, it would benefit Trindade's ecosystem by transferring marine nutrients to the terrestrial environment (Anderson and Polis 1998), thereby supplying energy to various trophic levels on the island (McLoughlin et al. 2016). It could also support the conservation of other seabirds, such as the critically endangered endemic frigatebird of Trindade (MMA 2014).

Conclusion

The results offer valuable insights into the population structure of red-footed boobies in the SW Atlantic Ocean and enhance our understanding of the consequences of the extinction of the Trindade population for this threatened species on Brazilian islands. Evidence suggests subtle segregation between the Trindade and Noronha colonies, with shared ancestry. The extinction of the Trindade population has led to a loss of genetic diversity, supporting the study hypothesis.

The distinctiveness of populations within the same species emphasizes the importance of considering genetic diversity in conservation strategies (Canteri et al. 2021). In this context, molecular analyses enhance our understanding of the genetic structure and unique traits of each population, which are crucial for developing effective conservation plans (Taylor and Friesen 2012).

To our knowledge, this study is the first to analyze Sulidae using samples from an extinct population, overcoming the challenges of accessing genetic material (Schander and Halanych 2003). Additionally, using samples preserved in scientific museums highlights the significance of biodiversity collections, which are vital sources of knowledge for conservation and ecological restoration efforts.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10592-025-01683-5.

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Author contributions Conceptualization: V Muraro, AMCR Fregonezi, L Bugoni; Data curation: V Muraro, AMCR Fregonezi; Formal analysis: V Muraro, AMCR Fregonezi; Funding acquisition: L Bugoni; Investigation: V Muraro, AMCR Fregonezi, L Bugoni; Methodology: V Muraro, AMCR Fregonezi; Project administration: V Muraro; Resources: L Bugoni; Software: V Muraro, AMCR Fregonezi; Supervision: L Bugoni; Validation: V Muraro, AMCR Fregonezi, L Bugoni; Visualization: V Muraro; Writing – original draft: V Muraro; Writing – review & editing: V Muraro, AMCR Fregonezi, L Bugoni.

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Data availability DNA sequences are available at Zenodo https://doi.org/10.5281/zenodo.14722018.

Declarations

Ethical approval Sampling was conducted under the approval from Sistema de Autorização e Informação em Biodiversidade (license numbers 22697-7).

Competing interests The authors declare no competing interests.

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