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BIODIVERSITY RESEARCH

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When is a native species invasive? Incursion of a novel predatory marsupial detected using molecular and historical data

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Abstract

Aim: Range expansions facilitated by humans or in response to local biotic or abiotic stressors provide the opportunity for species to occupy novel environments. Classifying the status of newly expanded populations can be difficult, particularly when the timing and nature of the range expansion are unclear. Should native species in new habitats be considered invasive pests or actively conserved? Here, we present an analytical framework applied to an Australian marsupial, the sugar glider (*Petaurus breviceps*), a species that preys upon on an endangered parrot in Tasmania, and whose provenance was uncertain.

Location: Tasmania, Australia.

Methods: We conducted an extensive search of historical records for sugar glider occurrences in Tasmania. Source material included museum collection data, early European expedition logs, community observation records, and peer-reviewed and grey literature. To determine the provenance of the Tasmanian population, we sequenced two mitochondrial genes and one nuclear gene in Tasmanian animals (n = 27) and in individuals across the species' native range. We then estimated divergence times between Tasmania and southern Australian populations using phylogenetic and Bayesian analyses.

Results: We found no historical evidence of sugar gliders occurring in Tasmania prior to 1835. All Tasmanian individuals (n = 27) were genetically identical at the three genes surveyed here with those individuals being 0.125% divergent from individuals from a population in Victoria. Bayesian analysis of divergence between Tasmanian individuals and southern Australian individuals suggested a recent introduction of sugar gliders into Tasmania from southern Australia.

Main conclusions: Molecular and historical data demonstrate that Tasmanian sugar gliders are a recent, post-European, anthropogenic introduction from mainland Victoria. This result has implications for the management of the species in relation to their impact on an endangered parrot. The analytical framework outlined here can assist environmental managers with the complex task of assessing the status of recently expanded or introduced native species.

KEYWORDS
introduced species, invasive species, mtDNA, native species, range expansion, sugar glider

1 | INTRODUCTION

Human-induced range expansions are increasing through anthropogenic habitat change and purposeful introductions (Arthur, 1981; Ewel et al., 1999; McGeoch & Latombe, 2015; Wine, Gagné, & Meentemeyer, 2015), alongside natural range expansions through the onset of climate change (Hoegh-guldberg et al., 2008; Hoffmann & Sgrò, 2011; Parmesan & Yohe, 2003). Where a species expands its range, there is potential for that species to rapidly become abundant and pose risks for locally endemic species through competition and predation (Hoffmann et al., 2010; Huang, Davies, & Gittleman, 2012). Novel predators are particularly efficient at driving extinctions, owing to the naivety of prey and/or because they reduce the availability of critical prey items for other predators (Salo et al., 2007). The decision to control the negative impact of a species that is unambiguously alien to an area is relatively straightforward, but the decision is more difficult when that species has a natural distribution close to the area of concern or whose provenance is unclear. This conflict arises because native species are usually subject to protection under biodiversity legislation making their active control, or even eradication, difficult to prosecute. These "invasive native" species pose complex and potentially controversial challenges (Crees & Turvey, 2015), making the clarification of provenance fundamental to appropriate management.

The International Union for Conservation of Nature (IUCN) defines a native species as being "within its natural range or dispersal potential" (*IUCN*, 2015). However, other factors such as human-facilitated dispersal and the time frame for colonization (Webb, 1985) are also considered, making the very definition of "native" ambiguous. This ambiguity can be problematic when the impact of species management is controversial, for example in the case of dingo management in Australia (Allen et al., 2013; Burns & Howard, 2003; Fleming, Allen, & Ballard, 2013). A precise understanding of how and when a range extension may have occurred is required to accurately define the status of "invasive natives" and justify radical management options like eradication.

The introduction of species beyond their range will often generate a variety of evidence that enables reconstruction of the process. Historical evidence from the time of introduction such as eyewitness accounts and newspaper articles can provide reference points for inferring likely routes, sources, times and numbers of introductions. The use of such data has provided important evidence around the introduction of common brushtail possums (*Trichosurus vulpecula*) in New Zealand (Pracy, 1974) and red foxes (*Vulpes vulpes*) in Australia (Abbott, 2011). However, historical accounts are often incomplete. Molecular approaches can thus provide additional information to test the provenance of species and provide important additional information for matters of wildlife management. Molecular approaches can be used to identify potential sources of animals (Eldridge, Browning, & Close, 2001; Hogan, Campbell, Harrison, Milledge, & Cooke, 2013), detect wildlife trafficking from protected areas (Wasser et al., 2015), identify range expansions (Burridge et al., 2013; Taylor & Keller, 2007), and characterize invasion pathways and introductions (Estoup & Guillemaud, 2010; Weyl, Thum, Moody, Newman, & Coetzee, 2016). Thus, molecular data are a powerful tool to help resolve management conflicts where the introduced status of a pest is ambiguous.

Sugar gliders (*Petaurus breviceps*) are arboreal marsupials, native to continental Australia, as well as the island of New Guinea and some surrounding Indonesian islands (Smith, 1973). The sugar glider is thought to have been introduced from mainland Australia to the island state of Tasmania in the early 1800s. Like other regions, sugar gliders in Tasmania are found in rain forest, wet forest, dry forest and agricultural lands which harbour hollow-bearing trees. The species is dependent on hollows for breeding and nest in social groups (Koch, Munks, & Woehler, 2008). Recent ecological research has revealed that Tasmanian sugar gliders prey heavily upon tree cavity-nesting birds, (Stojanovic, Webb, Alderman, Porfirio, & Heinsohn, 2014). Sugar gliders are omnivores within their mainland Australian range, but the occurrence of direct and heavy predation upon bird populations is considered unusual behaviour for the species. This novel trophic interaction is unknown among gliders on mainland Australia, and its discovery precipitated recent questions about the provenance of sugar gliders in Tasmania. Predation pressure applied by the sugar glider in Tasmania is intense, and recently, the conservation status of the swift parrot (*Lathamus discolor*) was revised to critically endangered as a result of sugar glider predation-induced mortality of adult females and nestlings as well as issues around forestry in swift parrot habitat (Heinsohn et al., 2015). The initial discovery of predation by the sugar glider also highlighted the inability of other predators to access the small hollows used by swift parrots (Stojanovic et al., 2017). At least two other threatened bird species in Tasmania are also vulnerable to glider predation (Stojanovic et al., 2014). Currently, sugar gliders are protected in Tasmania under the *Nature Conservation Act 2002*, despite informally being considered introduced by the Department of Primary Industries, Parks Water and Environment (DPIPWE) (Mallick & Driessen, 2010). The inconsistency of this classification poses a serious obstacle to the protection of endangered prey species of the sugar glider by limiting management actions.

Here, we present an analytical framework for investigating recent introductions that uses a total evidence approach to test likely introduction scenarios. We apply our protocol to sugar gliders in Tasmania and test the four most likely scenarios (1) Invasive: a small number of individuals of the sugar glider comprised a recent "one-off" introduction from mainland Australia (severe bottle neck); (2) Invasive: the sugar glider was a recent introduction facilitated by European settlement, and there have been continuous contemporary introductions from mainland Australia; (3) Native: the sugar glider naturally dispersed

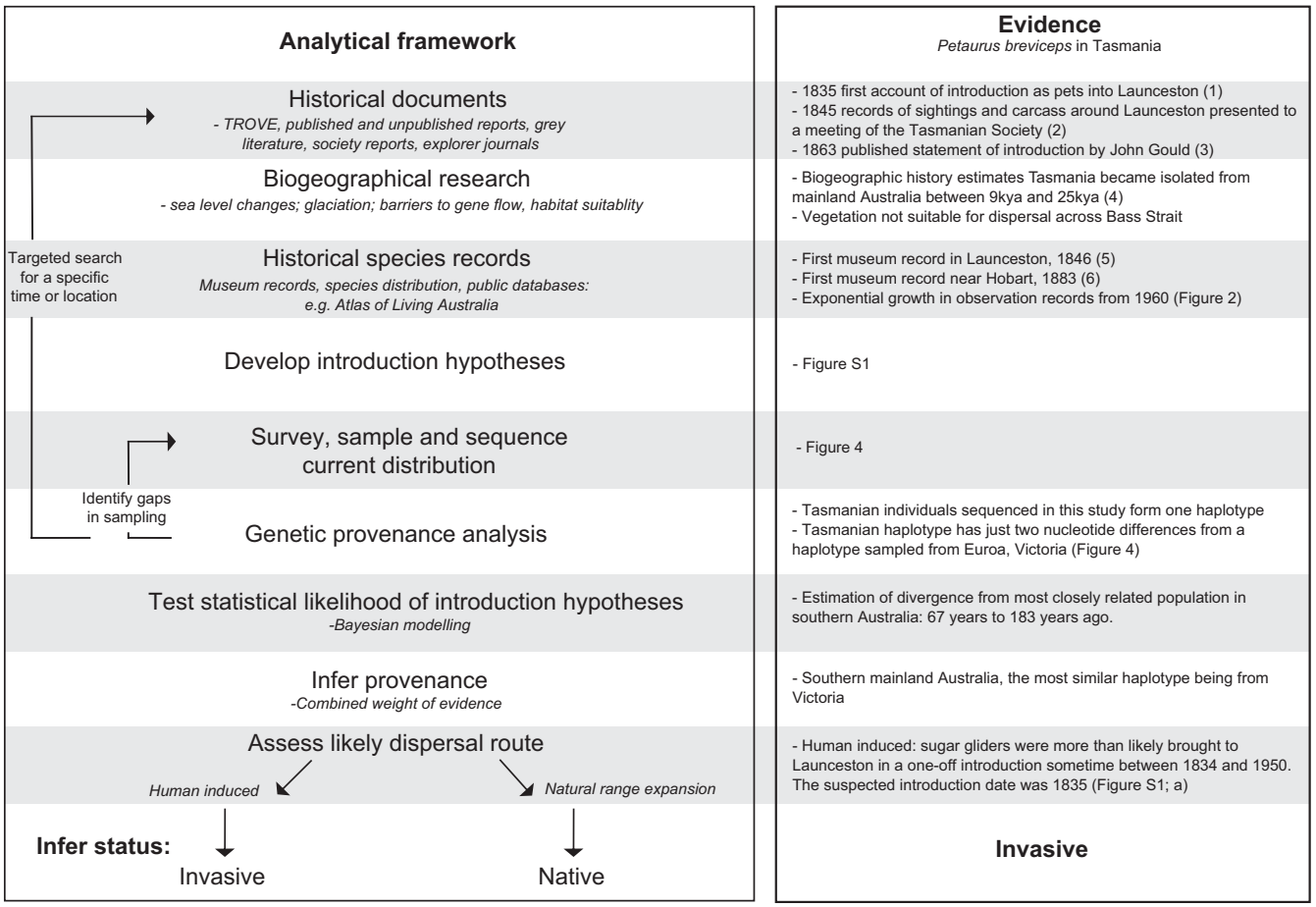

FIGURE 1 General framework for the detection of an invasive native species, and the application of this framework to an Australian marsupial, *Petaurus breviceps*. (1) Gunn (1851); (2) Gunn (1846); (3) Gould (1863); (4) Veevers (1991) and Allen and Kershaw (1996); (5) Gunn (1850); (6) Tasmanian Museum and Art Gallery, D Register of vertebrates

over the Australian-Tasmanian land bridge from mainland Australia, remained genetically isolated from the mainland since the Last Glacial Period (~10 kya) and its presence was undetected at European settlement; and (4) Native: the sugar glider naturally dispersed over the Australian-Tasmanian land bridge from mainland Australia and has experienced ongoing contemporary gene flow through repeated introductions after European settlement (Figure S1). We show that both historical collections and DNA analyses indicate that sugar gliders in Tasmania are the result of a recent post-European incursion from mainland Victoria.

2 | METHODS

2.1 | Developing and testing introduction scenarios

We developed an approach for formulating and testing invasion hypotheses (Figure 1). Published or unpublished written material was examined to identify the source and timings of introductions. Often fragmentary, these reports comprised unpublished journals or other historical documents, importation records, newspaper reports and museum records. First, historical and current distributional data were obtained from the literature, public databases and museum collection records. Next, we developed a database that encompasses DNA sequences from across the species' range with a view to pinpointing the origins of the Tasmanian population. The completed database was then subjected to phylogenetic analysis and Bayesian modelling and comparisons made with temporal occurrence data to identify the most likely provenance.

2.2 | Historical records

We searched for verified occurrences of the sugar glider from previously unpublished historical accounts, historical documents and museum records during the nineteenth and early twentieth century (n = 147) (Table S2). Museum specimens are particularly informative because they are vouchered anchors for a record. Tasmanian museums, Queen Victoria Museum and Art Gallery (QVMAG) in Launceston and Tasmanian Museum and Art Gallery (TMAG) in Hobart, did not actively collect sugar gliders but relied mostly on public donations of specimens (K Medlock, personal observation). Reliance on salvaged specimens can bias results towards donations of unfamiliar or new species (K Medlock, personal observation) which can be informative in tracking the front line of population expansions. Observational data from the Tasmanian Natural Values Atlas were used to supplement

these historical records along with samples collected within this study to compile the species distribution of the species in Tasmania (n = 68). The results of six collecting expeditions, undertaken by early European explorers such as John Gould, were also examined for records pertaining to collection of sugar gliders (Table S3).

2.3 | Tissue sample collection

Previously published mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) sequences for sugar gliders were sourced from Genbank and collated into a working database in Geneious 8.0.5 (Kearse et al., 2012). The mainland native range, not including Tasmania, has previously been surveyed in a study of *Petaurus* (mainland Australia, n = 71; Indonesia, n = 6; PNG, n = 28) (Malekian, Cooper, & Carthew, 2010; Malekian, Cooper, Norman, Christidis, & Carthew, 2010) (Table S1).

We supplemented these sequences with an additional 42 individuals sampled from museums, roadkills and by trapping. Trapping locations were selected using data from ongoing monitoring (Webb et al., 2017). Traps were deployed in trees for four nights during one trapping expedition to capture sugar gliders for DNA collection at three locations (1) Neika S: −42°57′, S: 147°13′; (2) Kermandie Divide S −43°13′, E 146°52′; (3) Tooms Lake S −42°13′, E:147°46′. Traps were deployed in grids of 20 spaced 50 m apart, baited with honey, oats and peanut butter, and cleared daily. These samples were collected from Tasmania (27) and other under-represented locations within the native range of sugar gliders (mainland Australia, 11; Indonesia, 2; PNG, 2) (Table S1). All tissue samples were stored in 99% ethanol and kept at −20°C, or stored on Whatman FTA cards at room temperature.

2.4 | DNA extraction and PCR amplification

DNA was extracted from 40 tissue samples (ear or liver) using the Qiagen Puregene® Tissue Kit following the manufacturer's protocols. A further two blood samples stored on Whatman classic FTA cards were amplified using the "punch in" method as per the Whatman FTA protocol BD01. Two mitochondrial genes (ND2 and ND4) and one nuclear gene (ω-globin) were amplified to complement previous phylogenetic studies of the sugar glider (Malekian, Cooper, & Carthew, 2010). A 700-bp fragment of the mtND2 gene was targeted using primers mmND2.1 (5′-GCACCATTCCACTTYTGAGT-3′) and mrND2c (5′-GATTTGCGTTCGAATGTAGCAAG-3′) (Osborne & Christidis, 2001). A 900-bp fragment of the mtND4 gene was targeted using primers mt10812H (5′-TGACTACCAAAAGCTCATGTAGAAGC-3′) and mt11769L (5′-TTTTACTTGGATTTGCACCA-3′) (Arevalo, Davis, & Sites, 1994) and a 700-bp fragment of the nuclear ω-globin gene was targeted using primers G314 (5′-GGAATCATGGCAAGAAGGTG-3′) and G424 (5′-CCGGAGGTGTTYAGTGGTATTTTC-3′) (Wheeler et al., 2001). PCR amplifications contained 50 ng of DNA, 1 × MyTaq HS Red (Bioline), 0.4 μM each forward and reverse primer and ddH_20 to a total volume of 25 μl. PCR conditions consisted of denaturation at 95°C for 1 min followed by 35 cycles of denaturation at 95°C for 15 s, 55°C for 15 s and 72°C for 30 s and finally an extension period of 72°C for 4 min. Some samples did not amplify under these conditions and so were repeated using the following cycling conditions, 95°C for 5 min followed by 15 cycles of 95°C for 20 s, 65–50°C for 20 s and 72°C for 60 s, followed by 30 cycles of 95°C for 20 s, 50°C for 20 s and 72°C for 60 s followed by a final extension period of 72°C for 4 min.

2.5 | Sequencing

PCR products were purified using Diffinity RapidTip® (Sigma) following the manufacturer's protocol. Sequencing reactions consisted of 1 μl of purified PCR product, 3.5 μl of BigDye 3.1 (Applied Biosystems), 1× sequencing buffer, 2 μM primer and ddH_20 to a total volume of 20 μl. Cycling conditions were 94°C for 5 min, 30 cycles of 96°C for 10 s, 50°C for 5 s followed by 60°C for 4 min. Sequencing reactions were purified using the ethanol/EDTA precipitation method (Applied Biosystems, 2009). Sequencing was performed on an AB 3730xl DNA Analyser at the ACRF Biomolecular Resource Facility within the John Curtin School of Medical Research, Australian National University.

2.6 | Phylogenetic analysis

Forward and reverse raw sequences were aligned in Geneious 8.0.5 (Biomatters) and subsequently checked and edited manually. The consensus sequences for all individuals were aligned in MUSCLE (Edgar, 2004). Mitochondrial data were concatenated to produce the main haplotype network. Haplotype networks were generated using median-joining network analysis (Bandelt, Forster, & Röhl, 1999) with software package POPART (Allan Wilson Centre Imaging Evolution Initiative). An appropriate mutation model was determined for each gene individually using MEGA v6.0 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013). Phylogenetic trees were prepared using GARLI v2.01 (Zwickl, 2006) with partitioned models. A clade only schematic was prepared using randomly selected individuals from each clade after the initial tree was generated. Gamma distribution, percentage of invariant sites and models were chosen using AIC calculations in MEGA v6.0. Number of haplotypes, number of variable sites, haplotype diversity, nucleotide diversity, Tajima's D (Tajima, 1989) and Fu's Fs (Fu, 1997) were calculated in DNASP v5.10.1(Librado & Rozas, 2009). Mismatch analysis of pairwise distance was run on individuals from the 11 most closely related haplotypes to the Tasmanian haplotype (Victoria and South Australia). A population growth–decline model using estimated theta and tau was run in DNASP v5.10.1 (Librado & Rozas, 2009). This analysis can explain recent population expansion or declines (Rogers, 1995; Rogers & Harpending, 1992).

2.7 | Bayesian analysis of population history

Population history was inferred through approximate Bayesian computations using DIYABC v2.1(Cornuet et al., 2014). This method compares different scenarios that could explain the observed data by including a historical model or models describing how the sampled

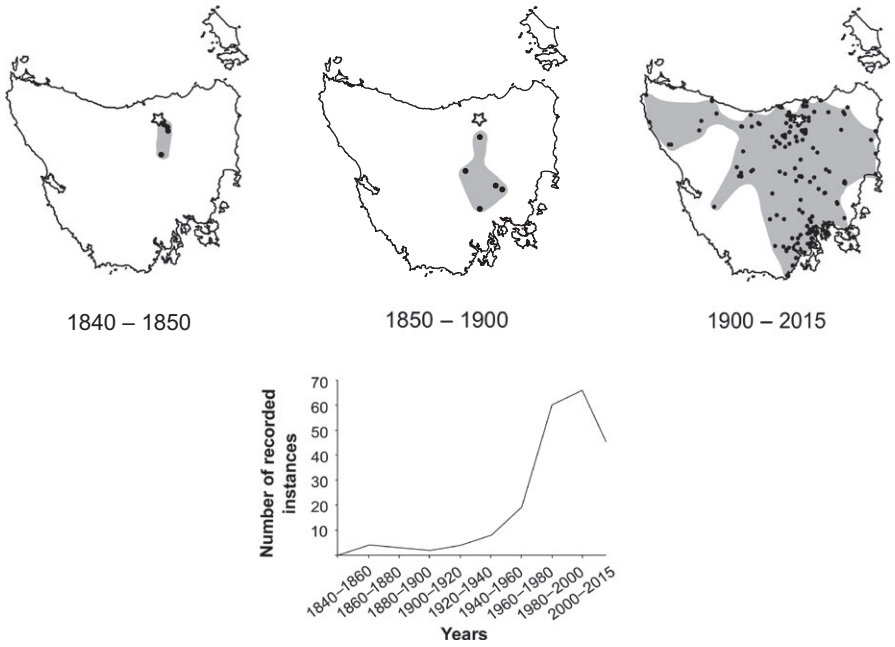

FIGURE 2 Historical species occurrences and observational records of *Petaurus breviceps* across Tasmania from 1840 to 2015. Black dots indicate museum records, sample collections, Tasmanian Natural Values records and trapping records from this study, and grey shading indicates the inferred species range; hollow star represents location of Launceston. The occurrence of *P. breviceps* museum records shows exponential growth from around 1960, which is likely to reflect an increase in the population size at that time

populations are connected to their common ancestor (Figure S10). Mutation models were predicted using MEGA v6.0 (Tamura et al., 2013) and were partitioned as per the phylogenetic analysis. No heterozygous sites were detected in the nuclear gene; therefore, globin sequences were analysed as a single haplotype. To test two of the four divergence hypotheses (Figure S1a,c), the data set was split into three populations, AUS1 clade (pop 1), AUS2 (pop 2) and Tasmania (pop 3); Papua New Guinea was removed for this analysis. Population size was estimated in DIYABC v2.1 using priors of up to 10 million individuals for both Australian clade populations and up to 1 million individuals for the Tasmanian population. Divergence times were predicted using the known biogeographical isolation times for Tasmania, up to 20 ky (Lambeck & Chappell, 2001). A burn-in of one million iterations was run before testing the fit of our data to the predicted model (Figure S11).

3 | RESULTS

3.1 | Historical records

The sugar glider is widely believed to have been introduced to Tasmania in 1835 (Gunn, 1851) decades after European human settlement in 1803 (Reynolds, 2012). We did not identify any reference to this species in Tasmania prior to 1835 and observed a complete lack of specimens in Tasmanian museum collections or published references until 1846 (Gould, 1863; Gunn, 1846, 1851; Heinsohn, 2004; Lord & Scott, 1924). Our historical data are consistent with Gunn (1851) that sugar gliders were introduced into Launceston in 1835 and suggest that the species spread rapidly south across Tasmania from the focal point of Launceston (Figure 2). The earliest records of sugar gliders north of Launceston are in 1845, and sugar gliders did not appear in museum records south of Launceston until approximately 40 years later (Table S2). No sugar gliders were collected by the six faunal expeditions conducted in Tasmania between 1838 and 1921. However, the absence of samples collected is not definitive evidence that the species did not occur in Tasmania as it is possible that they were already considered to be an introduced species (Table S3).

3.2 | Phylogenetic analysis

At the mitochondrial ND4 gene (n = 124), genetic diversity was limited in the southern population, representatives from all six geographic regions, including Tasmania, sharing the most common haplotype (H02) (Figures S2 and S3). At the nuclear ω-globin gene (n = 103), haplotype diversity (Hd) was very low and 76 individuals from all geographic regions had a single haplotype (H10, Figure S4). Very little differentiation was seen among all haplotypes (Figure S5). In contrast, at the mitochondrial ND2 gene (n = 140), haplotype diversity was high and 59 haplotypes were recognized (Figure S6). Tasmanian sequences all fall within one haplotype (H06) and have 98% sequence identity with a haplotype found in samples from South Australia and Victoria (H08) (Figure S6). Maximum likelihood analysis highlights the limited diversity in the southern region (Figure S7).

Of the 147 samples, 124 had complete data for both mitochondrial genes and 90 had complete data for all three genes. A maximum likelihood tree generated using samples across the entire geographic range showed a clear difference between the northern clades (all five PNG clades plus AUS1, AUS3 and AUS4; 100% bootstrap support) and the southern clade (AUS2); therefore, further analyses were among these two groups. Within the northern clades, we observed a total of 241 variable sites forming 34 haplotypes (Hd = 0.993; nucleotide diversity Pi = 0.05687) (Figure S8). The observed value of Tajima's D, 0.02711, was not significant (p = 0.01) and so provided no evidence for a population expansion. The southern clade, AUS2, had 54 variable sites forming 23 haplotypes (Hd = 0.8472; Pi = 0.00927). Tajima's

D was negative, −1.36355, which can be indicative of a rapid population expansion; however, this result was not significant (p = 0.10). The median-joining network for the south shows a cluster of closely related haplotypes all from Tasmania, Victoria and South Australia (Figure 3). The majority of the concatenated haplotypes in the south were observed in just one to four individuals. In contrast, a single haplotype (H06) was observed in all 20 Tasmanian individuals and one Victorian individual. The Tasmanian haplotype was most closely related to a haplotype found in Victoria and South Australia (H10). Mismatch analysis was unable to be run on the Tasmanian population as there was just one haplotype with no variation within the population; hence, the analysis was run on the Tasmanian population and the most closely related haplotypes from the mainland. Results showed a possible population bottleneck and subsequent expansion (Figure S9) with support from Fs (−4.412, p = .03) and Tajima D (−1.0, p = .10). Nucleotide diversity of this group was very low (0.003) suggesting very little divergence between Tasmanian animals and the Victorian and South Australian population.

The most appropriate mutation models chosen were HKY+G (Hasegawa, Kishino, & Taka-aki, 1989) for Intron2 of the nuclear gene ω-globin and HKY+I+G for mtDNA genes ND2 and ND4 (Hasegawa et al., 1989). We also used maximum likelihood estimation (using unique sequences only) to compare isolated island populations to their closest counterparts on the Australian mainland (Figure 4). We found that there was a 92.6% pairwise identity between the northern Australian haplotypes and the PNG and Indonesian haplotypes. In contrast, sequences from Tasmanian sugar gliders had higher sequence identity (98%) when compared to sequences from individuals from nearby southern mainland Australia. Malekian, Cooper, Norman, et al., 2010 identified five Papua New Guinean clades and two Australian clades. With more extensive sampling from the Northern Territory, we identified two additional Australian clades (AUS3 and AUS4) in the north.

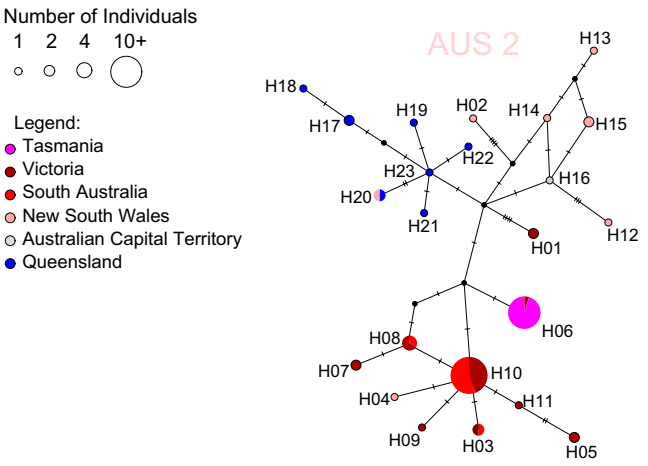

FIGURE 3 Median-joining network for concatenated ND2 and ND4 mitochondrial genes for the sugar glider in AUS2 clade. Haplotypes are shown by coloured circles, with number of individuals depicted using various sized circles (Bandelt et al., 1999). All Tasmanian individuals have sampled have identical sequences (H06) and have just two nucleotide substitutions difference from individuals from Victoria (H10)

3.3 | Bayesian analysis of population history

Our predictive modelling using approximate Bayesian computation analysis of two of the four hypotheses posed in Figure S1a,c estimated the time of divergence to be between 996 and 106 years for AUS2 clade and Tasmanian sugar gliders. This estimate is much more recent than the predicted period of isolation a native population would have experienced during the Last Glacial Maximum (9–6 kya) (Figure S12).

Collectively, our data suggest that the Tasmanian sugar gliders comprise a homogenous group consistent with a population founded recently from a very small number of individuals. As such, scenario a (Figure S1) comprising a recent introduction without subsequent immigration from the mainland is the most likely scenario. The close genetic similarity of the Tasmanian animals with those from South Australia and Victoria suggests that the founders of the Tasmanian population came from that region of continental Australia.

4 | DISCUSSION

Our combined approach using historical records and molecular analysis suggests strongly that the sugar glider is not native to the island state of Tasmania. Specifically, our data imply that there was a single contemporary introduction of a small number of individuals from the southernmost part of the Australian mainland to Launceston in Tasmania at or around European settlement (Figure S1: hypothesis a), the most likely source being the southern state of Victoria. All Tasmanian individuals sampled in this study were 0.125% divergent from a haplotype from southern Australia (H10). Our estimate of the genetic diversity in Tasmanian sugar gliders is zero for the three mitochondrial genes investigated (100% sequence identity, n = 27 individuals), indicating a severe bottleneck due to a recent introduction of a just a few individuals. Bayesian analysis also supports a contemporary introduction that occurred much more recently than the conditions expected for a native population that either dispersed into Tasmania prior to the last glacial maximum or was continuously distributed and then isolated since the Last Glacial Maximum.

We suggest that ongoing contemporary gene flow from mainland Australian populations is unlikely (Figure S1; hypothesis b) because only a single haplotype exists in Tasmania, whereas up to eight haplotypes exist in the immediate areas surrounding the putative source population. Bayesian analysis clearly rejects the possibility of sugar gliders existing in Tasmania since before the Last Glacial Maximum. Thus, we do not consider the species native to Tasmania (Figure S1; hypotheses c and d). There is very little genetic differentiation between clade AUS2 and Tasmania (0.125% divergence). Even if native Tasmanian populations had collapsed to very small numbers for a prolonged period of time, we would expect substantial differentiation between Tasmanian and Victorian haplotypes. If native sugar gliders did exist in Tasmania, we can detect no evidence that the populations

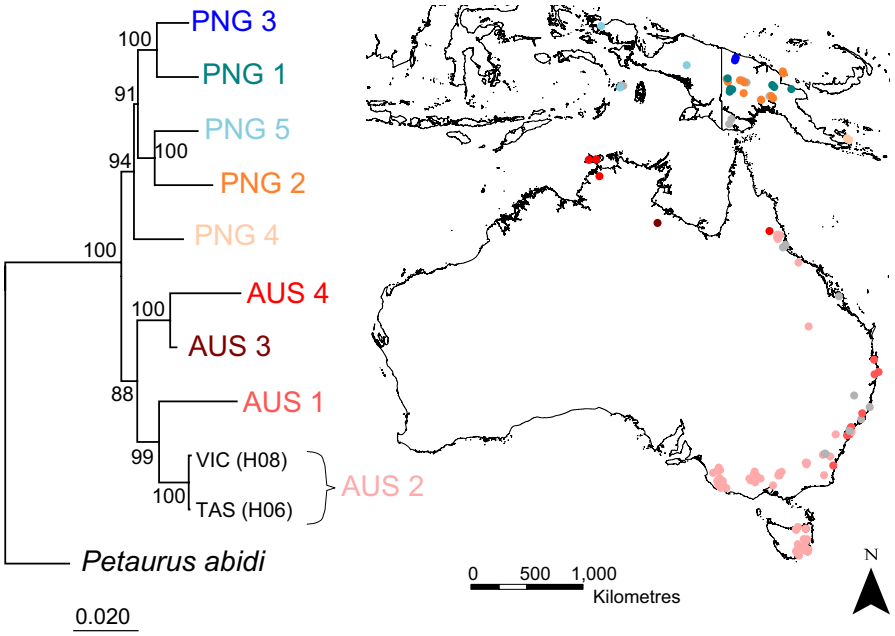

FIGURE 4 Schematic of sugar glider sample locations across the geographic distribution combined with the concatenated ND2 and ND4 mitochondrial genes and the nuclear ω-globin gene across the species geographic distribution (clades represented only). Evolutionary history was inferred using the maximum likelihood method based on the HKY+I+G model (Hasegawa et al., 1989) in Garli (Zwickl, 2006). All Tasmanian individuals have identical sequences with very little differentiation from southern Australian individuals. Grey dots represent individuals with missing data

remain there now or their detection has been obscured by significant recent introgression and/or mitochondrial capture.

Tasmania's biogeographical history further supports our genetic and historical evidence of a recent introduction. Predicted vegetation types for the land bridge that connected the island to the continent are considered unsuitable for natural dispersal by the sugar glider. The contemporary analogue for Late Pleistocene steppe vegetation across the land bridge is the shrubby grasslands in the Tasmanian highlands today (Hope, 1994). Sugar gliders require wet or dry sclerophyll forest to disperse and do not often come to ground for long periods (Smith, 1973); therefore, low lying shrubs and grasslands are unsuitable dispersal habitat over long distances. Thomas and Kirkpatrick (1996) used palynological evidence from a near coastal site in north-eastern Tasmania to show that prior to the end of the Last Glacial Period, the vegetation at that time comprised shrubby grasslands with sparse tree cover. This may indicate that the contiguous vegetation across most of the Bassian Plain was similar. The Bassian Plain was uniformly flat except where it rose towards the east in a broken chain of hills and mountains. Moreover, while fossil remains of sugar gliders have been found on mainland Australia (Smith, 1973), they are absent from similar fossil deposits searched in Tasmania (Hope, 1973; Rawlinson, 1974).

Comparative genomic analysis of other Tasmanian species, which are clearly documented as native species, supports the expectations arising anecdotally for an invasive population of sugar gliders. The flooding of the land bridge between 9kya and 6kya years ago (Blom, 1988 in Pardoe et al., 1991; Veevers, 1991; Allen & Kershaw, 1996) has affected genetic differentiation of a number of species that occurred both on Tasmania and on continental Australia pre-isolation. There are endemic Tasmanian species, and species which now only occur in Tasmania, which show very high haplotype diversity (Cliff, Wapstra, & Burridge, 2015; Macqueen, Goldizen, & Seddon, 2009). There are also species which show diversity within Tasmania and high haplotype diversity compared with mainland Australia, these species act as a baseline for what we would expect in the sugar glider if it was indeed a native to Tasmania (Chapman, 2001; Dubey & Shine, 2010; Frankham, Handasyde, & Eldridge, 2012; Gongora et al., 2012; Symula, Keogh, & Cannatella, 2008; Zenger, Eldridge, & Cooper, 2003). However, the ~10,000 years isolation from mainland Australia is relatively short in biogeographical terms and some species show a lack of haplotype diversity across Bass Strait despite it being a barrier to gene flow (Chapple, Hoskin, Chapple, & Thompson, 2011; Hughes, Baker, De Zylva, & Mather, 2001; Murphy, Joseph, Burbidge, & Austin, 2011) (Table S4, Figure S13). Further, there are species which show the same genetic signal as the sugar glider with zero diversity in Tasmania where the mainland individuals have a high diversity (Burridge et al., 2013). In general, we would expect a recent introduction, be it a natural range expansion or human-mediated translocation, to show the pattern of limited or no haplotype diversity in Tasmania and many on the mainland.

Currently, sugar gliders are listed as a protected native species in Tasmania under the *Nature Conservation Act 2002*. This poses a serious challenge to managing them effectively to protect endangered tree cavity-nesting birds from predation. Here, by removing doubt about the introduction history of the sugar glider, we have achieved a crucial step in preparing an updated management strategy for protecting the swift parrot and other threatened Tasmanian birds. This information is critical in dealing with community and stakeholder concerns about management activities that may suppress sugar glider populations. It also expands the range of intervention options available to conservation managers. We have successfully demonstrated how a framework combining molecular data and historical records can identify the provenance of species occupying new territory.

Our study highlights the complex issues concerning management action around cases involving species whose native status or provenance is uncertain. Range expansion of a species can have serious implications throughout multiple trophic levels in a new

habitat, possibly causing local extinctions and irreversible ecosystem changes. The sugar glider in Tasmania is an example of an introduced species fundamentally altering an endemic food web. The sugar glider appears to be occupying a new ecological niche, exploiting novel prey items that are inaccessible to native Tasmanian predators (Stojanovic et al., 2017). Our work highlights how recent introductions can create novel trophic interactions as the sugar glider has assumed the role of a highly effective and uncontested predator of endangered parrots and other hollow-nesting birds in the novel Tasmanian environment (Stojanovic et al., 2014). Tasmania's sugar gliders occur on an island which has long been isolated from mainland Australia, and our evidence provides robust support for amending their status to an introduced species. However, not all examples of invasive native species are so clear. For example, range expansion of species owing to favourable conditions and anthropogenic habitat changes (Moritz et al., 2008; Parmesan & Yohe, 2003) or reinvasion events in habitat once cleared of a species (Valière et al., 2003) poses serious economic, social and ecological challenges. There is no consistent or agreed approach in the management of the species and these challenges are heightened by inconsistencies in how to classify them, that is, pest native or introduced. The framework outlined here (Figure 1) can provide a pathway to remove doubt about the provenance of new populations, and management approaches can then be tailored to each individual case with confidence.

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DATA ACCESSIBILITY

All genetic data are available on Genbank, accession numbers KY352532–KY352636 and KY421780–KY421782. Table S1 includes accession numbers for samples collected in Malekian, Cooper, & Carthew, (2010); Malekian, Cooper, Norman, et al., (2010) and samples collected within this study. All historical occurrence records are listed in Table S2.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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