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RESEARCH PAPER

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Two speed invasion: assisted and intrinsic dispersal of common mynas over 150 years of colonization

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Abstract

Aim: Despite the common myna's widespread distribution, and the significant impact it has caused in parts of its non-native range, there have been no comprehensive genomic studies of its invasion of any region. We aimed to characterize the common myna invasion of the Australian continent to understand its population genetic landscape, introduction history, dispersal characteristics, and the interconnectedness between different source populations and invasive fronts.

Location: Common mynas from 26 geographical locations spanning the Australian continent were utilized in this study.

Taxon: Common myna (*Acridotheres tristis*).

Methods: We used a reduced genome representation method (DArTseq) to generate thousands of single nucleotide polymorphism markers in 462 common mynas. We then applied population genomic techniques to identify the common myna's population attributes such as gene flow, genetic diversity, and effective dispersal, all of which are critical for understanding geographical range expansion of pest species.

Results: We found significant genetic structuring across the common myna's Australian distribution, indicating limited levels of effective dispersal amongst the populations founded from historic introductions in the 19th century. The historic introduction points were found to be genetically distinct, such that in the region on the invasion front where admixture did occur, myna populations exhibited higher genetic diversity than in the source populations. Significant isolation by distance was evident amongst populations derived from the same founding population, with genetic diversity decreasing moving away from the point of colonization, and in general, higher levels of gene flow from source to front than vice versa.

Main conclusions: This study indicates that despite a 150-year colonization history of mynas in Australia, contemporary genetic structure still largely reflects human-mediated dispersal. However, expanding populations are now connecting and the consequent increased genetic diversity may improve evolutionary potential. These results suggest that more management focus should be directed towards the invasion fronts, rather than the large, historic source populations.

KEYWORDS

Acridotheres tristis, alien, effective dispersal, gene flow, invasion biology, population genomics, range expansion

1 | INTRODUCTION

Invasive species are considered to be the second greatest threat to biodiversity after habitat loss (Luque et al., 2014). They pose threats to both natural ecosystems and agricultural systems and can act as a vector for exotic diseases (Rollins, Woolnough, Wilton, Sinclair, & Sherwin, 2009; Shirley & Kark, 2011). Information on the origin of invasive species, their dispersal characteristics, and their population dynamics, particularly at the invasion front (i.e., the edge of the range expansion), is essential for monitoring and managing invasions and minimizing their impacts (Evans, Kumschick, Şekercioğlu, & Blackburn, 2018; Rollins et al., 2009; Sherwin et al., 2015). Population genetic methods, such as those commonly applied to describe evolution in wild populations and to inform conservation of threatened species/populations (Frankham, Ballou, & Briscoe, 2002), can be used to characterize invasion history, identify invasive fronts and examine population demographics (Kekkonen et al., 2011; Marrs, Sforza, & Hufbauer, 2008; Rollins, Woolnough, & Sherwin, 2006; Trumbo et al., 2016).

The common myna (*Acridotheres tristis*) ("myna" hereafter) is one of only three bird species listed in the 100 most invasive species globally (along with *Pycnonotus cafer*, red-vented bulbul, and *Sturnus vulgaris*, common starling), according to the International Union for the Conservation of Nature (GISD, 2015). The species inhabits urbanized areas, open agricultural land, and forest edges in its introduced range (Long, 1981). Mynas have the potential to spread disease (Baker, Harvey, & French, 2014), and in some parts of their geographical range mynas can compete with native species for tree hollows and other resources (Pell & Tidemann, 1997; Harper, McCarthy, & van der Ree, 2005; Tindall, Ralph, & Clout, 2007; Grarock, Tidemann, Wood, & Lindenmayer, 2012; Orchan, Chiron, Shwartz, & Kark, 2013; but see Crisp & Lill, 2006; Parsons, Major, & French, 2006; Lowe, Taylor, & Major, 2011; Davis, Major, & Taylor, 2013). They roost in large congregations in cities (Martin, 1996; Old, Spencer, & Wolfenden, 2014), which may cause disturbance to humans, and are considered one of the most unpopular feral animals in some areas of their introduced range (e.g., Thompson, Arthur, & Gilmour, 2005).

The myna is native to Asia, and has been introduced to Africa, New Zealand, North America, the Middle East, Europe, many oceanic island nations, and Australia (Holzapfel, Levin, Hatzofe, & Kark, 2006; Hone, 1978; Long, 1981; Saavedra, Maraver, Anadón, & Tella, 2015). The myna was first introduced into Australia in the early 1860s to control insect pests (McCoy, 1885–1890). It is reported to have been initially introduced to Melbourne and Sydney, then subsequently introduced to north Queensland (from Melbourne), southern Queensland (from north Queensland), and later to Canberra (multiple introductions from Sydney) via human-mediated translocations (Chisholm, 1919; Hone, 1978; Long, 1981; Walker, 1952) (Figure 1). By the 1880s, the Sydney and Melbourne myna populations had become well-established (Long, 1981). However, the birds remained at relatively low abundance at the points of introduction and expanded slowly over many decades. Since the 1940s their abundance and range has increased dramatically (Hone, 1978), and they are now one of the most commonly observed species in urban centres along the east coast of Australia (Long, 1981; Parsons et al., 2006; Sol, Bartomeus, & Griffin, 2012). The pathways used by mynas to invade from these introduction/translocation points remain unknown. Population genomics provides an opportunity to address how mynas are expanding their range.

A key element of any effective pest-control strategy is an understanding of the invasion pathways and characteristics of dispersal. The expansion rate and extent of the invasive front can be characterized by comparing the genetic composition of the "front" populations with those from the initial points of introduction (Marrs et al., 2008; Sakai et al., 2001). Generally, when an alien species disperses into a new region, the founder effect influences allelic variation (Baker & Moeed, 1987; Excoffier, Foll, & Petit, 2009; Peter & Satkin, 2013). Hence, identifying the invasive front and the order of colonization among different populations can be achieved by investigating changes in genetic diversity (Rollins et al., 2009). If connectivity is detected between the different invasive fronts this could indicate the presence of genetic admixture between the earliest documented introduction points. In the context of conservation biology, admixture between different source populations can be utilized to increase (or maintain) the genetic diversity of a population in a reintroduction program (White, Moseby, Thomson, Donnellan, & Austin, 2018). However, in the context of invasion biology, admixture should be avoided as it may increase the adaptive potential of an invasive population and will reduce the effects of inbreeding (Dlugosch, Anderson, Braasch, Cang, & Gillette, 2015; Frankham et al., 2002).

Additionally, the fine-scale genetic structure of different invasive populations and their patterns of gene flow may provide insights into their mode of effective dispersal (i.e., dispersing to a new location and subsequently producing offspring). Invasive species may expand their ranges via infrequent long-distance migration events with minimal gene flow between separate populations. If this is the case, it may be possible to block the dispersal of the birds and even eradicate satellite populations (Rollins et al., 2009). Alternatively, a species may expand its range via a simple advancing invasive front with high gene flow. If there are high levels of gene flow, and there is significant admixture, it may be more effective treating the population as a single unit and coordinating a management plan to minimize its expansion.

The aim of this study was to identify any patterns of population differentiation and genetic diversity of mynas across eastern Australia to provide a platform for population management. We addressed four main questions: (a) What is the population genetic landscape of the myna in Australia? (b) How accurate is our current literature-based understanding of historic colonization events of mynas in Australia? (c) What is the myna's mode and scale of effective dispersal? (d) Is there admixture between the colliding front populations? To answer these questions, we used a reduced genome representation method to generate a robust, high-resolution array of single nucleotide polymorphism markers (SNPs) to characterize 462 mynas from 26 geographical locations.

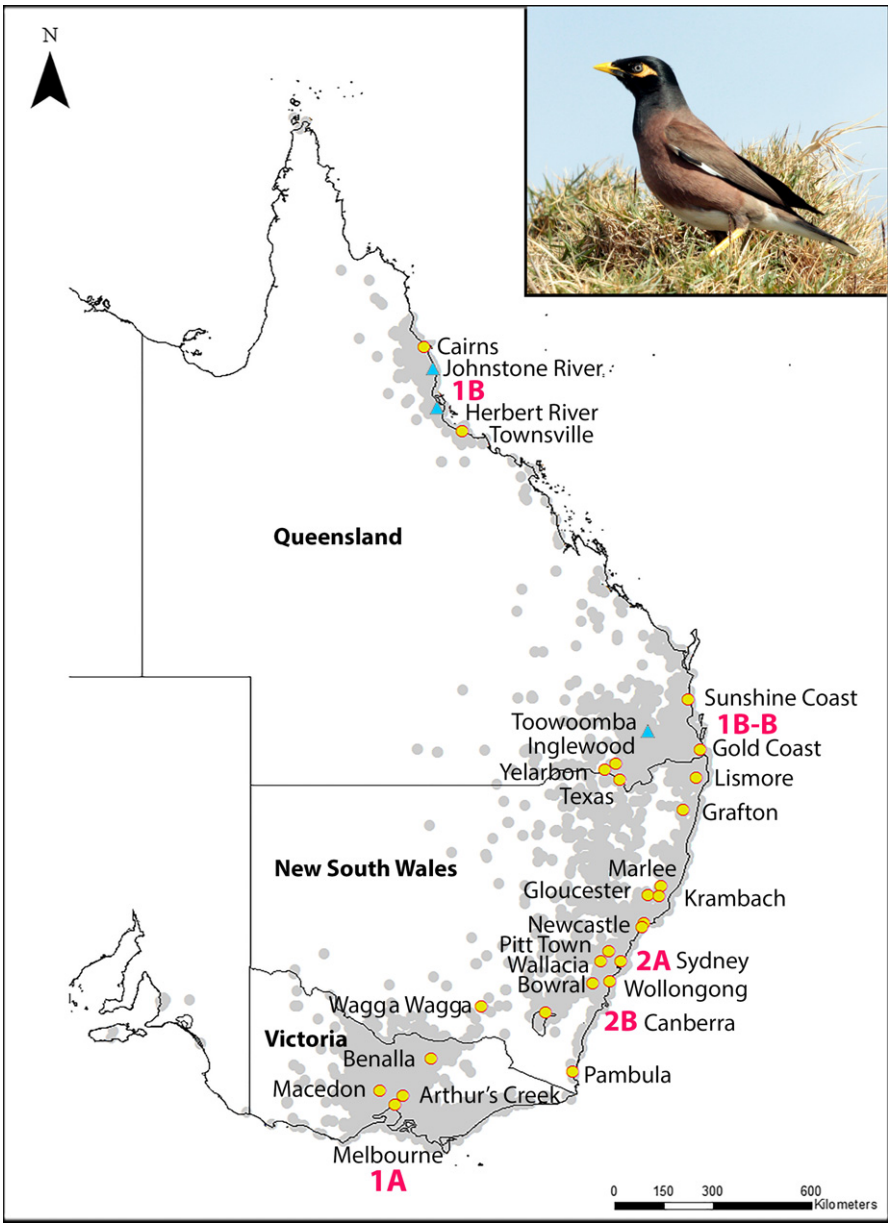

FIGURE 1 The current distribution of the common myna (inset) in Australia (grey dots), the localities of genotyped birds (yellow dots) and the putative introduction/translocation sites (pink "1" or "2" representing the two source populations). Original introductions are marked with the letter "A", while translocations from their source populations are marked with the letter "B". Localities marked with a blue triangle are discussed in this text but were not sampled. Distribution data from the Atlas of Living Australia https://www.ala.org.au/; introduction/translocations from Chisholm (1919), Walker (1952), Hone (1978) and Long (1981). The distribution is supported by Government websites/reports (e.g. PestSmart, 2014) and public databases. Photo: Corey Callaghan [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Sampling and DNA extraction

We contacted 115 local government and individual participants involved in myna control programs across eastern Australia, who provided frozen carcasses of culled mynas trapped from across their Australian range between 1/09/2014 and 30/06/2015 (Figure 1). Our target was 20 individuals per population but some volunteers had limited trapping success resulting in some populations with limited samples ($n < 10$). All birds were sexed anatomically by dissection, and liver and muscle samples were collected using sterile equipment for each specimen (for sample sizes and collection data, see Appendix S1, Table S1.1, in Supplementary Information).

Genomic DNA was extracted following the manufacturer's protocols for the "Bioline Isolate II Genomic DNA kit" Bioline (Australia), and DNA concentration was measured using a Qubit 2.0 Flurometer (Thermo Fisher Scientific). We performed dilutions to standardize the DNA at concentrations of 50–100 ng/μL, prior to sending 10 μL samples in 96-well plates to Diversity Arrays Technology (DArT) (Cruz, Kilian, & Dierig, 2013; Kilian et al., 2012) for further processing.

2.2 | SNP generation

SNPs were generated using DArTseq™, a combination of DArT complexity reduction methods and next generation sequencing platforms (Kilian et al., 2012; Cruz et al., 2013; see Appendix S2 for details). DArTseq is a restriction enzyme-based genome complexity reduction method that has previously been utilized to generate SNP data in a range of vertebrate species for phylogeographic, phylogenetic, and population genetic studies (Melville et al., 2017). The resultant short-read sequences were processed using proprietary DArTsoft14 SNP calling

pipeline and STACKS (Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011) (see Appendix S3 for details). Most analyses were run with SNP data from both the DArTsoft14 pipeline ("DArT dataset" hereafter) and STACKS pipeline ("STACKS dataset" hereafter) to ensure robust inference, as it has been demonstrated that different RADseq bioinformatics pipelines may produce dramatically different results (Shafer et al., 2016).

2.3 | SNP QC

We included 17 replicate samples to quantify pre- and postfiltering error rates of the DArTseq platform in combination with the two bioinformatics pipelines. Error rates and levels of missing data were calculated using R functions from Mastretta-Yanes et al. (2015) and the 'dartR' R package version 0.93 (Gruber & Georges, 2017; R Core Team, 2017).

2.4 | SNP filtering

The DArT dataset was filtered based on data quality, missing data, linkage, and neutrality. Three different filtering strategies were used depending on the analysis undertaken, as different analyses had different population genetic assumptions (such as loci being at Hardy–Weinberg equilibrium and/or linkage equilibrium). We utilized GENALEX version 6.503 (Peakall & Smouse, 2006, 2012), the 'dartR' R package and PGDSPIDER version 2.1.0.3 (Lischer & Excoffier, 2012) for data filtering and manipulation. The number of loci removed when applying the following SNP filtering methods differed depending on which populations were included in the analysis.

2.4.1 | SNP quality filtering method A

SNPs were filtered based on call rate and reproducibility. Loci that were not genotyped in 100% of individuals were removed from the dataset (i.e., call rate). DArTseq™ runs 30% of the samples in replicate in independent libraries and sequencing runs, and the consistency of each locus is measured across these replicates (i.e., reproducibility). Loci that were not 100% reproducible were removed from the dataset. Many RAD-seq studies use a minor allele frequency (MAF) filter, but we believe that given the stringent filters we have already used this filter was unnecessary for the DArT dataset. Before further downstream analysis, one of each of the replicate samples was removed from the dataset.

2.4.2 | SNP quality, linkage, and outlier filtering method B

Starting with the dataset from "filtering method A," we kept one SNP within a set of potentially linked SNPs, i.e., SNPs that were called within the same DArTseq marker (i.e., the same locus) that could show linkage disequilibrium. Outlier loci were identified using LOSITAN (Antao, Lopes, Lopes, Beja-Pereira, & Luikart, 2008; Beaumont & Nichols, 1996) and removed from the dataset. LOSITAN detects outlier loci that are potentially in directional or balancing selection using a F_{ST} outlier approach; i.e., loci with F_{ST} significantly different from neutral expectations. For this analysis, samples were divided into populations based on their geographic location, then 50,000 simulations were performed implementing the "infinite alleles" mutation model using a 0.95 confidence interval and a 0.1 false discovery rate. Monomorphic loci were also removed from the dataset.

2.4.3 | SNP quality, linkage, and neutrality filtering method C

Data from "filtering method B" were filtered to remove all further non-neutral loci by applying a Hardy–Weinberg equilibrium (HWE) filter. Departure from HWE was tested for each locus within each population (based on their geographical origin) using ARLEQUIN version 3.5 (Excoffier & Lischer, 2010). For this analysis, 1,000,000 Markov Chain steps and a burnin of 100,000 was used. Loci with a p-value < 0.01 were removed from the dataset.

For the STACKS dataset, all SNPs with any missing data were removed, linked SNPs were removed, a MAF of <0.05 was applied (as reproducibility scores were not calculated), and non-neutral SNPs were removed using the aforementioned LOSITAN F_{ST} outlier test and HWE test. One replicate sample was removed at random.

2.5 | Identifying population structure

To visualize genetic similarities and differences among individuals and populations, we conducted a principal coordinates analysis (PCoA) using the 'dartR' R package and the 'ade4' package version 1.7 (Chessel, Dufour, & Thioulouse, 2004), implementing filtering method A (as PCA is free of HWE and linkage equilibrium assumptions). To quantify interpopulation genetic similarity we generated pairwise F_{ST} values using ARLEQUIN (applying 1,000,000 permutations) for all population combinations, implementing filtering method C. Separate Mantel tests, using the Isolation by Distance function in the 'adegenet' R package version 2.1.1 (Jombart, 2008), were used to determine whether genetic variation between populations found to be derived from the same colonization point (see below) could be explained by geographical distance. Populations derived from the Sydney colonization included Sydney, Pitt Town, Wollongong, Bowral, Pambula, Wallacia, Newcastle, Williamtown, Gloucester, Krambach and Marlee, and populations derived from Melbourne included Melbourne, Arthur's Creek, Macedon and Benalla (also see Figure 1).

STRUCTURE version 2.3 (Pritchard, Stephens, & Donnelly, 2000) was used to investigate patterns of population structure and admixture among all populations. We ran STRUCTURE for 10^5 iterations with a burnin of 10^4 implementing filtering method C. We modelled up to 10 ancestral populations (i.e., K = 1–10), replicating each model 10 times. We assumed admixture, independent allele frequencies and did not use location information to establish priors. To assess the optimal K value (the number of genetic groups sampled to partition genotypes) we utilized the ΔK method (Evanno, Regnaut, & Goudet, 2005) using STRUCTURE HARVESTER web version 0.6.94 (Earl & von Holdt, 2012). Results of replicate runs were merged using CLUMPP version 1.1.2 (Jakobsson & Rosenberg, 2007), and bar plots were generated using DISTRUCT version 1.1 (Rosenberg, 2004). Additionally, we conducted a population assignment using GENECLASS2 version 2.0 (Piry et al., 2004),

with an assignment threshold of 0.01, to identify the most likely origin of a single individual from Wagga Wagga (no other mynas had been observed in the Wagga Wagga district).

2.6 | Measuring genetic diversity

Allelic richness (AR) with rarefaction was calculated using the 'PopGenReport' R package version 3.0 (Adamack & Gruber, 2014). The mean observed heterozygosity, mean expected heterozygosity and the percentage of polymorphic loci were calculated for each population using GenAlEx. For these analyses, some populations were merged based on the results of the population structure analyses (indicated in Table S5.5). A count of private alleles in populations at each putative introduction point (discussed below) was implemented with manual rarefaction, calculated using the 'poppr' R package version 2.6.1 (Kamvar, Brooks, & Grünwald, 2015; Kamvar, Tabima, & Grünwald, 2014). All of these genetic diversity analyses were performed implementing filtering method C.

2.7 | Determining the origin of a nonconcordant population

Based on the population structure analyses, we identified a distinct population cluster in the Gold Coast/Sunshine Coast region. The history of this population is not well-understood, both in terms of the literature (Walker, 1952) and in its genetic signature. Establishing the origin of this population based on the aforementioned population structure methods is problematic, as these analyses do not take into consideration the stochastic effects of more realistic demographic events, such as genetic drift in the source and derived populations, the effect of sampling founders that only constitute a fraction of the source population, and the genetic bottlenecks that occur after a founder event (Estoup & Guillemaud, 2010). We therefore utilized an approximate Bayesian computational approach (ABC) to identify the source of the Gold Coast population (Sunshine Coast samples were excluded to simplify the ABC modelling). Another benefit of ABC is that admixture and ghost populations (populations contributing to the scenario but that are not sampled) can be incorporated into the analysis (Estoup & Guillemaud, 2010). We tested six possible scenarios using DIYABC version 2.1 (Cornuet et al., 2014) (Figure 2). DIYABC utilizes coalescence and the resultant summary statistics to calculate the posterior distribution and probabilities of competing scenarios. The DIYABC analysis was run using both the DArT dataset implementing filtering method C and the Stacks dataset to ensure consistency. The prior distributions, summary statistics, confidence, and error statistics, and other settings used in this analysis can be found in Appendix S4 and Table S5.1.

2.8 | Measuring gene flow

Contemporary migration patterns among Victorian populations (Melbourne, Arthur's Creek, Macedon and Benalla) and selected New South Wales populations (Wollongong, Sydney, Pitt Town and Newcastle Figure 1) were estimated using BayesAss version 1.3 (Wilson & Rannala, 2003). These two sets of populations were chosen to represent "replicate" single-source population expansions as they occur at a similar geographical scale (Figure 1) and comprise adequate population sizes (≥20 individuals per population) to perform a BayesAss analysis. To eliminate sample-size bias, equal population sizes (n = 20) were achieved by randomly excluding individuals from populations with larger sample sizes, and filtering method B was implemented. BayesAss estimates the proportion of individuals that derive from the same population, and the proportion that have migrated from another population. Mixing parameters for the Victorian BayesAss analysis were optimized (ΔM [migration rate] = 0.30, ΔA [allele frequencies] = 0.75 and ΔF [inbreeding coefficients] = 0.12) to ensure an appropriate acceptance rate, and then run for 4×10^7 iterations, 4×10^6 burn-in and a sampling frequency of 1,000. Likewise, mixing parameters for the New South Wales BayesAss analysis were optimized (ΔM = 0.93, ΔA = 0.93 and ΔF = 0.87), and then run for 5×10^7 iterations, 2×10^7 burn-in, and a sampling frequency of 1,000. Both analyses were repeated ten times with different starting seeds. Consistency between the replicate runs was checked, and the best run was chosen based on the Bayesian deviance criterion calculated using R (R script from Meirmans, 2014).

3 | RESULTS

3.1 | SNP data generation

The DArTsoft14 pipeline called 23,709 SNPs including 10% missing data (with the DArTsoft14 preliminary filtering already implemented), while the Stacks pipeline called 82,276 catalogue SNPs including 60% missing data (after the Stacks populations script was run with no associated filters). The error rates (based on the 17 replicate samples) of the SNP datasets were reduced after filtering (Table S5.3). In downstream filtering (using the DArT dataset and incorporating all populations), 1,081 outlier SNPs (of 4,137) were identified (using the LOSITAN F_{ST} outlier approach) and subsequently removed, and 259 non-native SNPs (of 3,056) were identified (using a test for HWE) and subsequently removed. In the following, results are presented from the DArT dataset, with filtering criteria as indicated in the Methods, and depending on the analysis are based on between 2,756 and 4,156 SNPs. Results from the Stacks dataset are shown in the Supplementary Information.

3.2 | Population structuring

The PCoA revealed three distinct clusters (Figure 3): the populations derived from the Melbourne introduction clustered together (i.e., Victorian, north Queensland, and Wagga Wagga populations); the populations derived from the Sydney introduction clustered together (i.e., southern to mid New South Wales populations); and the Gold Coast and Sunshine Coast populations clustered together (although less tightly than the other two clusters). Five populations in northern New South Wales and southern Queensland clustered along an axis between the Gold Coast/Sunshine Coast cluster and the cluster of populations derived from the Sydney introduction.

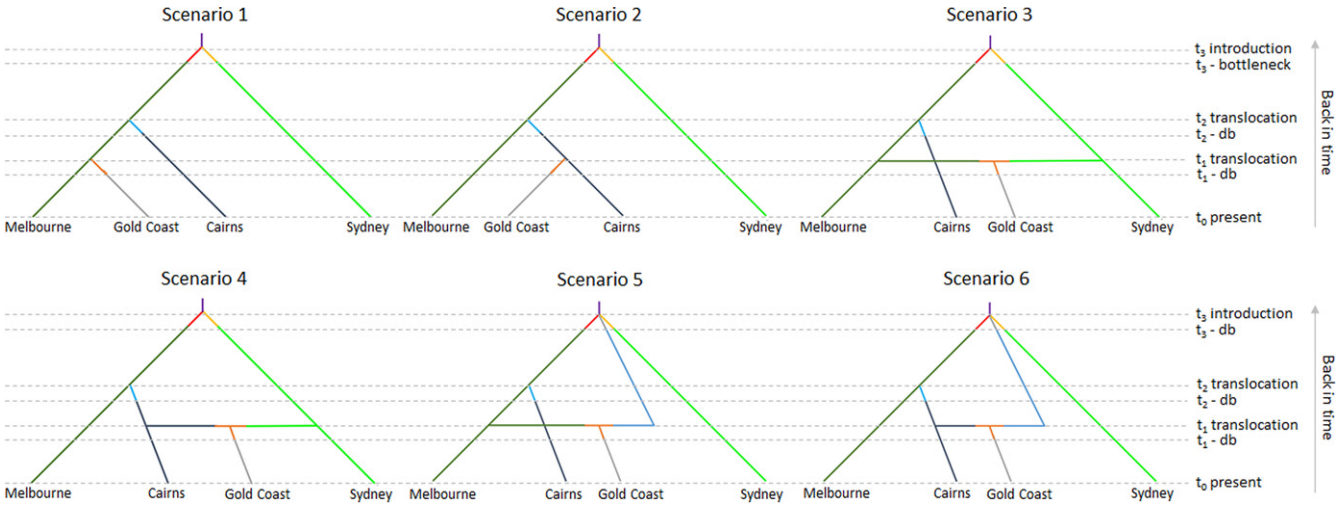

FIGURE 2 The six different colonization scenarios for mynas in the Gold Coast region, implemented in DIYABC. The different scenarios are as follows: Scenario 1—Gold Coast was colonized by birds from Melbourne. Scenario 2—Gold Coast was colonized by birds from Cairns. Scenario 3—Gold Coast was colonized by an admixed Melbourne and Sydney population. Scenario 4—Gold Coast was colonized by an admixed Cairns and Sydney population. Scenario 5—Gold Coast was colonized by an admixed Melbourne and "ghost" population. Scenario 6—Gold Coast was colonized by an admixed Cairns and "ghost" population. A ghost population is a population that contributes to the scenario but is not sampled. NB: "db" represents the duration of a population bottleneck after the founder event. Parameter priors are shown in Table S5.1 [Colour figure can be viewed at wileyonlinelibrary.com]

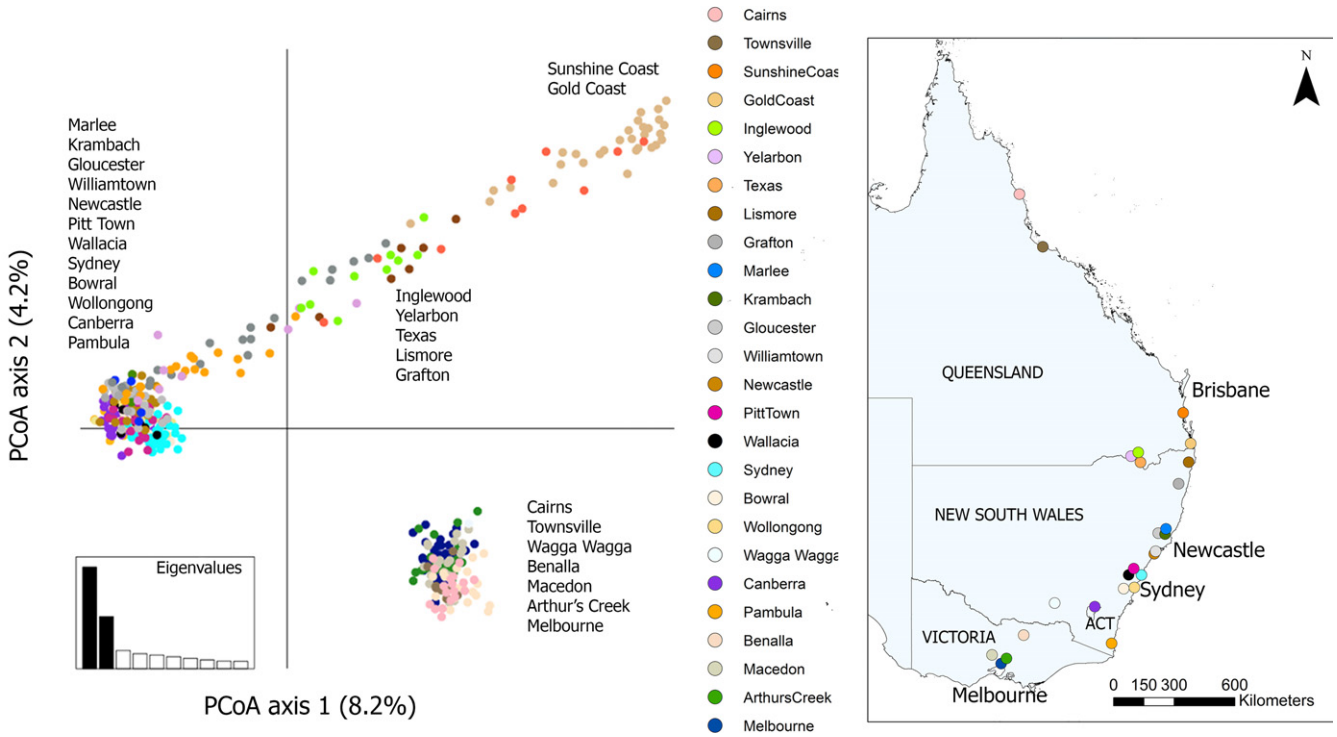

FIGURE 3 PCoA plot for 445 mynas using 4,156 SNPs. Individuals are coloured by their sampling locality (indicated in the legend and map). The three main clusters apparent in the figure are labelled (i.e., Victoria and north Queensland, southern to mid New South Wales, and Gold Coast and Sunshine Coast). The PCoA axes are labelled with the percentage of total variance that they represent, and a scree plot of eigenvalues (bottom left) indicates the variation explained by additional axes (relative to the first two) [Colour figure can be viewed at wileyonlinelibrary.com]

Moderate population differentiation between the three main clusters was evident in the pairwise F_{ST} values (Table S5.4). Within the main clusters there was lower but in general significant genetic differentiation. The Mantel tests revealed significant isolation by distance in both the New South Wales region (r = 0.9114, p = 0.001) and the Victoria region (r = 0.9797, p = 0.042) (Figure 4).

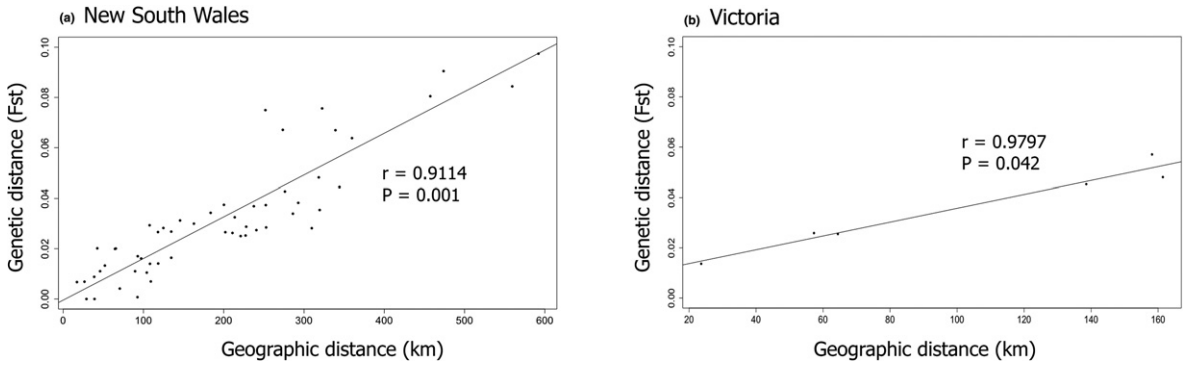

FIGURE 4 Mantel test for mynas in (a) the New South Wales region comprising the Sydney, Pitt Town, Wollongong, Bowral, Pambula, Wallacia, Newcastle, Marlee, Krambach and Gloucester populations; and (b) the Victoria region comprising the Melbourne, Arthur's Creek, Macedon and Benalla populations

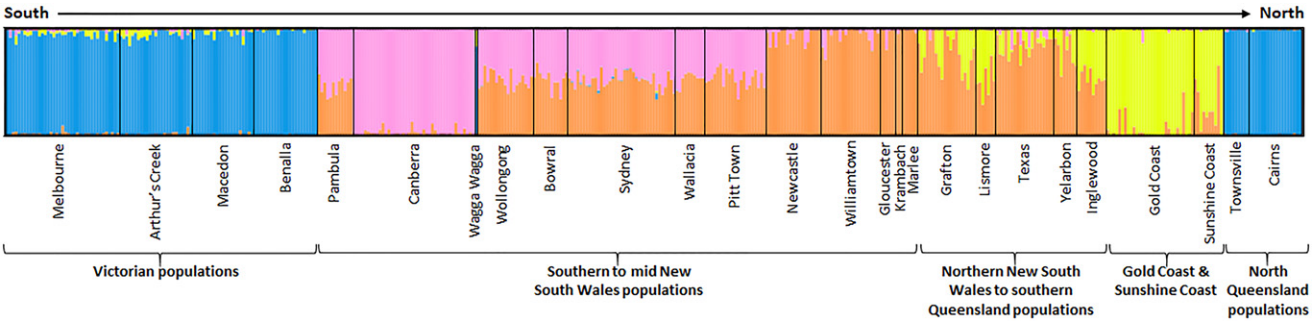

FIGURE 5 STRUCTURE plot for 445 mynas across 26 populations, using $K = 4$. Each individual is represented by a vertical bar showing the percentage ancestry that is attributable to each of the four genetic groups, identified by different colours [Colour figure can be viewed at wileyonlinelibrary.com]

The STRUCTURE analysis determined that the genetic variability observed in the complete dataset was best explained using $K = 4$, and identified the same three major genetic clusters as the PCoA; some admixture and fine-scale structuring was also evident within these genetic clusters (Figure 5). The single bird obtained from Wagga Wagga was assigned to the Melbourne population (with an assignment score of 100%) using GENECLASS2.

3.3 | Patterns of genetic diversity

The Melbourne population was more diverse than the Sydney population (AR = 4,789 and AR = 4,374, respectively) and variation in levels of genetic diversity of other populations were mostly consistent with the distance from these introduction points (Table S5.5). The exception to this pattern was in some northern New South Wales and southern Queensland populations which exhibited higher genetic diversity (e.g. Grafton/Lismore AR = 4,418) than the Sydney populations, suggesting an admixture event (Table S5.5). The average numbers of private alleles after rarefaction in Sydney, Melbourne and the Gold Coast (representing three putative introduction points—see below) were 140.4 ± 2.3 (SE), 466.8 ± 5.74 (SE), and 45.8 ± 1.6 (SE) respectively.

3.4 | Determining population origin with ABC

The scenario in which the Gold Coast population was derived from admixture between the Melbourne population and a ghost population (scenario five, see Figure 2) received the strongest statistical support in the ABC analysis (Table 1). The error and additional confidence statistics of the alternative scenarios can be found in Appendix S4 and Appendix S5 (Table S5.2 & Figure S5.1).

3.5 | Gene Flow

Estimations of gene flow using BAYESASS generally supported the prediction that migration was higher from long-established populations to recent ones than in the reverse direction (Figure 6). Amongst Victorian populations, Melbourne was the primary source of immigrants for the three satellite populations, with negligible reverse migration. However, amongst New South Wales populations, the population on the fringe of Sydney (Pitt Town) appeared to be the primary source for NSW satellite populations, rather than the Sydney population (Figure 6). The ten replicate BAYESASS runs were mostly consistent, and all showed the same migration patterns.

4 | DISCUSSION

Demographic processes following the introduction of an invasive species may leave a genetic footprint in the invasive populations across the landscape. We have utilized genome-wide data in 462 mynas and population genomic techniques to map myna invasion history at a continental scale for the first time. This is the most comprehensive study to date

TABLE 1 Posterior probabilities for the six scenarios (Figure 2) based on logistic regression on the 0.5% (n = 30,000) and 1% (n = 60,000) closest simulated datasets to the empirical data. The highest posterior probabilities are indicated with bold type

Scenario	Posterior probabilities calculated using 0.05% of the closest simulated datasets (95% confidence intervals)	Posterior probabilities calculated using 1% of the closest simulated datasets (95% confidence intervals)
1	0.0531 (0.0217, 0.0845)	0.0464 (0.0292, 0.0636)
2	0.0001 (0.0000, 0.0105)	0.0001 (0.0000, 0.0108)
3	0.0000 (0.0000, 0.0104)	0.0000 (0.0000, 0.0107)
4	0.0000 (0.0000, 0.0104)	0.0000 (0.0000, 0.0107)
5	**0.7459 (0.7003, 0.7915)**	**0.7072 (0.6744, 0.7400)**
6	0.2009 (0.1603, 0.2415)	0.2463 (0.2139, 0.2787)

that investigates the genetic landscape of the common myna, one of the world's most invasive bird species (GISD, 2015). This dataset has provided insights into the myna's introduction history, its effective dispersal, and the dynamics of the invasive front, all of which will have important management implications. Through this work we found a surprising amount of genetic structure across the myna's Australian distribution indicating limited effective dispersal, which is unexpected for an invasive bird species undergoing range expansion (Sakai et al., 2001).

4.1 | Introduction history of the common myna in Australia

The major genetic clusters identified in this study indicate that the Australian myna distribution is derived from three ancestral introduction points. These ancestral populations are consistent with contemporary populations in New South Wales, Victoria/north Queensland and southern Queensland. The results confirm most of the historical accounts of the species introduction and movements around Australia (Figure 1), but raise questions about reported translocations to southern Queensland.

The myna was first introduced into Australia in 1862, where more than 100 birds were released in Melbourne to control insect populations (Gregory-Smith, 1985; McCoy, 1885–1890), followed by additional Melbourne introductions in 1863, 1864, 1866, and 1872 (Long, 1981). Mynas are thought to have been introduced to Sydney at a similar time (Hone, 1978; Long, 1981), but no historical information is available on whether this was a separate introduction from Asia, or a translocation from Melbourne (Chisholm, 1919; Long, 1981). The underlying population structure of the Australian distribution is indicative of these two introduction points (Figures 3 & 5), as birds in the Melbourne region are clearly distinct from birds in the Sydney region. However, without genetic data on potential source populations from the mynas' native range we cannot resolve the endemic population origins of these initial introductions.

Melbourne mynas were translocated to two cane fields in north Queensland (on the Herbert and Johnstone rivers, between Cairns and Townsville) and in Townsville in 1883, to combat locusts and cane beetles (Chisholm, 1919; Long, 1981). The genetic data corroborate this translocation event, since Townsville birds cluster with Melbourne birds (Figures 3 & 5). Mynas were documented to have been taken to Cairns in 1918 (Long, 1981) from Townsville (or the northern cane fields) (Blakers, Davies, & Reilly, 1984). However, the Cairns population is much more closely related to the Melbourne population (pairwise F_{ST} = 0.071) than the Townsville population (pairwise F_{ST} = 0.162). Additionally, the genetic diversity in Cairns (AR = 4,404) is significantly higher than in Townsville (AR = 3,951), which contradicts the historical belief that the Cairns population was founded by Townsville birds. We believe that the most likely scenario is that the birds released in the Herbert and Johnstone River regions (Figure 1) in 1883 from Melbourne migrated north to establish the Cairns population, and that the founder size was larger in the Cairns region than in Townsville. Alternatively, a separate translocation from Melbourne may have taken place, or possibly both scenarios occurred. Therefore, we believe that Long (1981) and Blakers et al. (1984) have misinterpreted Walker's (1952) initial observations about the Cairns birds; Walker (1952) reports that birds were taken from Cairns in 1918 (and taken to Toowoomba), rather than birds taken to Cairns in 1918.

Between 1968 and 1971, 110 myna birds were translocated from Sydney to Canberra (Hone, 1978). Their range and abundance in this region has increased significantly since introduction (Long, 1981; Pell & Tidemann, 1997), and, as expected, the Canberra population clusters with the Sydney population (Figures 3 & 5), but has lower genetic diversity (Table S5.5), having been founded by a subset of Sydney birds.

Along with the two main clusters representing the two primary introduction points (i.e.. Melbourne and Sydney), a third cluster in the Gold Coast and Sunshine Coast region is very apparent. Some historical evidence suggests that mynas were introduced to the Toowoomba (Darling Downs) region in southern Queensland (Figure 1) in 1918 (Walker, 1952). Walker (1952) suggests that eight birds were translocated from Cairns, but also reports contrary claims of a separate introduction, just south west of Toowoomba. The coastal Gold Coast and Sunshine Coast populations are the best representative populations for the more inland Toowoomba region based on their locality and their genetic signature. These three locations are part of a south-eastern Queensland distribution that has been continuous since the 1950s (Blakers et al., 1984) and it is likely that they all have a similar origin. If this population was derived from a single source, as suggested by Walker (1952), we would expect the population to broadly cluster within the source population (similar to the Townsville, Cairns, and Canberra translocation events). However, this population forms a distinct cluster indicating that this population either represents a separate introduction or is the result of admixture between multiple sources. By comparing six possible introduction scenarios for the Gold Coast population using an ABC approach (Figure 2), we found that the Gold Coast population most likely derived from admixture between a ghost population and Melbourne (i.e., scenario five, see Figure 2) (Table 1). Because the Gold Coast population contains many private alleles (46), one possibility is that this ghost population is from an overseas source, although it is unlikely this would have occurred within the last ~100 years due to Australia's strict biosecurity laws. The mixed results obtained when using the STACKS dataset (Appendix S4) are

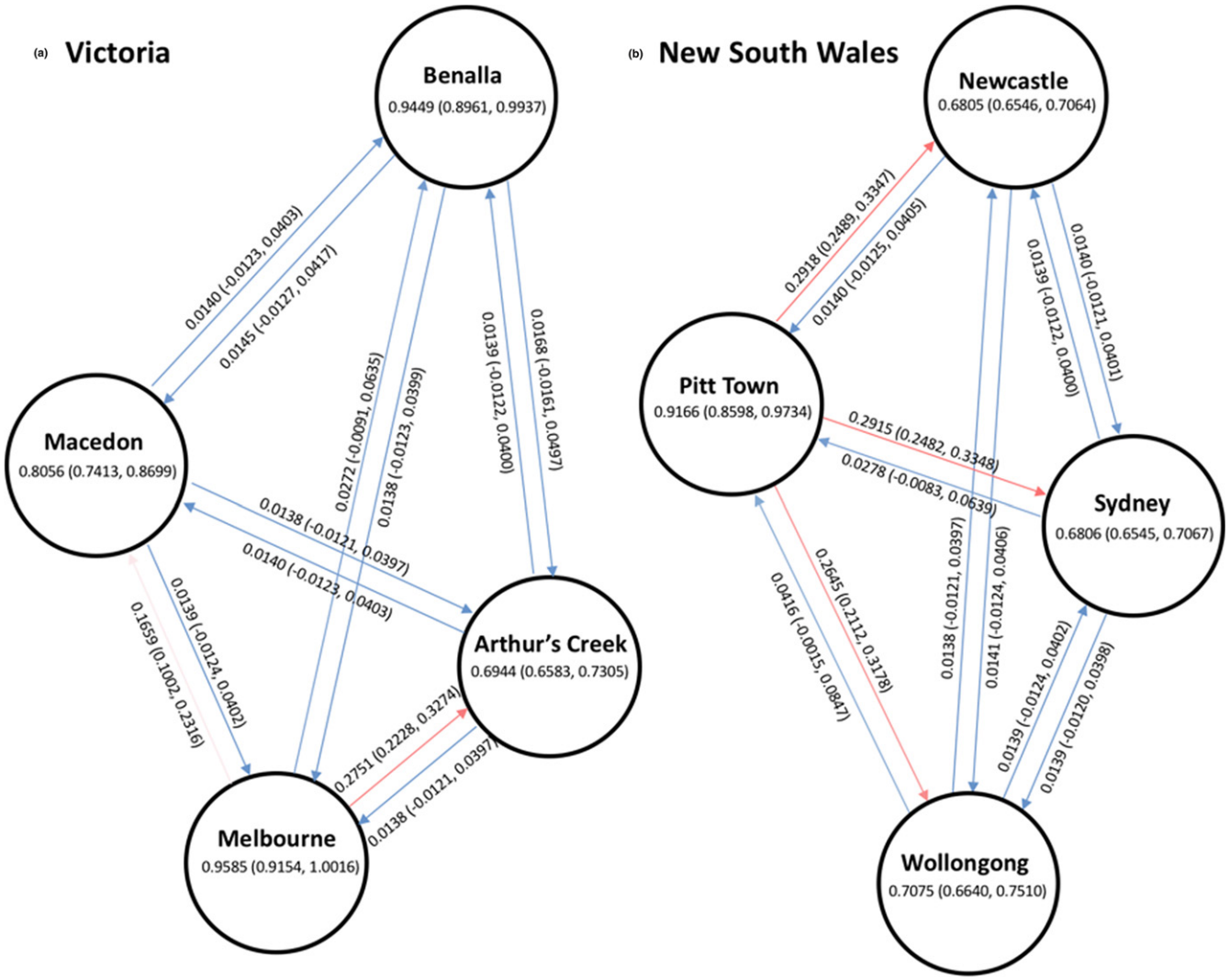

FIGURE 6 Posterior mean estimates (95% credible intervals) of the proportion of migrants for populations within the Victorian (a) and New South Wales (b) regions estimated from SNP data using Bayesass (Wilson & Rannala, 2003). The arrows represent the direction of migration, and are colour-coded from high migration (red) to low migration (blue). The estimates within the population circles represent the proportion of individuals in each generation that are non-migrants. The run with the lowest Bayesian deviance is reported (out of the 10 replicate runs). Distances between population circles are not to scale [Colour figure can be viewed at wileyonlinelibrary.com]

likely due to the similarity between scenarios five and six (i.e., scenario five: Gold Coast mynas derived from admixture between a ghost population and the Melbourne population, and scenario six: Gold Coast mynas derived from admixture between a ghost population and the Cairns population), as Cairns and Melbourne populations belong to the same genetic cluster (Figures 3 & 5).

4.2 | Levels of effective dispersal

The considerable population differentiation between the main genetic clusters indicates that there is little to no gene flow between these primary introduction points (Figure 3, Figure 5, & Table S5.4). Mynas therefore do not appear to be effectively dispersing among the Melbourne, Sydney, and Queensland regions, even 150 years post introduction. The exception to this pattern is in the north New South Wales/south Queensland region, where admixture is now occurring.

Even within the Sydney and Victoria regions over relatively small spatial scales, there is significant genetic structuring (Table S5.4), indicating restricted gene flow between most of these populations. For example, there is clear genetic differentiation between individuals from Sydney and Canberra (Figure 5). Since the translocation of Sydney birds to Canberra it appears that there has been very little subsequent gene flow (if any) into Canberra from the other sampled NSW populations, as it is still more genetically similar to Sydney than any other population (Table S5.4).

This low level of effective dispersal over small spatial scales contrasts with similar studies on other invasive bird species (Kekkonen et al., 2011; Low et al., 2018; Rollins et al., 2009). For example, the closely related common starling exhibits significantly lower levels of population differentiation across its range. There is no significant genetic differentiation in starling populations within the South Australian region (mean pairwise F_{ST} = 0.003; *SE* ± 0.001), even between

populations that are >800 km apart (e.g. the pairwise F_{ST} between Nullarbor, South Australia, and Mallala, South Australia, which are ~842 km apart, is 0.002) (Rollins et al., 2009).

Mantel tests support a significant relationship between genetic distance (F_{ST}) and geographical distance between myna populations within both Victoria and New South Wales (Figure 4). Genetic isolation by distance is therefore a significant explanation for the differentiation between populations within each region. Tracking studies have demonstrated that mynas travel relatively small distances compared to other bird species, with dispersal distances <16 km (Berthouly-Salazar, van Rensburg, Le Roux, van Vuuren, & Hui, 2012; Kang, 1992), although there are reports of individual mynas travelling far greater distances (Dhami & Nagle, 2009; Parkes & Avarua, 2006; Peneaux & Griffin, 2016). Based on significant population structuring (Table S5.4) and significant isolation by distance (Figure 4) however, these longer dispersal events generally do not lead to gene flow (i.e., effective dispersal) in Australian myna populations, although they do suggest that mynas might be capable of occasional long-distance dispersal events (i.e., jump-dispersal) to expand their range. Transport infrastructure can facilitate jump-dispersal along roads, railways, and other corridors that connect towns (Martin, 1996; Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009). This is a possible explanation for the bird from Wagga Wagga, which was assigned to the Melbourne population (473 km away) despite the closer proximity of this population to other Victorian (i.e., Macedon and Benalla) and New South Wales populations (i.e., Canberra and Pambula).

4.3 | Invasion dynamics

Populations undergo genetic bottlenecks as founders establish in new areas. Measures of genetic diversity can therefore be used to identify the order of colonization events (Rollins et al., 2009). In the Victorian region, Arthur's Creek has the highest level of genetic diversity (AR = 4,791). However, based on the STRUCTURE analysis (Figure 5) and pairwise population differences (Table S5.4), Melbourne and Arthur's Creek are genetically very similar. Genetic diversity then decreases moving away from the Melbourne/Arthur's Creek region, from Macedon (AR = 4,633) to Benalla (AR = 4,503). Therefore, the invasive front for the Melbourne range expansion is likely in the Benalla region (based on the sampled populations), an area that is north/inland from the coastal city of Melbourne (Figure 1).

As expected, the most diverse population among those proximal to Sydney is Sydney itself. Similar to the scenario in Victoria, the genetic diversity decreases in populations further from Sydney in all directions. However, the diversity increases in the Grafton/Lismore region in far north New South Wales (AR = 4,418), which is even more diverse than the Sydney population (AR = 4,374). This is likely due to an admixture event. The pattern at the third introduction point in the Gold Coast/Sunshine Coast region mirrors the Sydney expansion scenario, with genetic diversity increasing south of the Gold Coast (Table S5.5). Based on the direction of these founder effects and the patterns in the STRUCTURE analysis (Figure 5), there has been admixture between the Sydney and Gold Coast/Sunshine Coast introduction points as their invasion fronts have collided at these intermediate populations. The STRUCTURE analysis demonstrates this shared ancestry, with intermediate populations such as Grafton, Lismore, Texas, Yelarbon, and Inglewood containing a significant proportion of their genetic composition from both the Sydney and Gold Coast/Sunshine Coast populations. Admixture has introduced new genetic diversity into the northern New South Wales/southern Queensland region which will likely counteract founder effects and increase the potential for the population to evolve local adaptations and/or enhance invasive characteristics (Dlugosch et al., 2015; Lee, 2002).

Several studies have demonstrated that mynas prefer urban environments (Old et al., 2014; Peacock, van Rensburg, & Robertson, 2007; Sol et al., 2012). Therefore, we would expect city centres, such as Melbourne and Sydney, to act as source populations, and surrounding populations to act as sinks under a model of population saturation across a heterogeneous landscape (Dias, 1996). The gene flow patterns in Victoria support this hypothesis, as the contemporary gene flow from Melbourne to Arthur's Creek and Macedon is considerably higher than the contemporary gene flow to Melbourne (Figure 6). A similar, but less clear trend was found in the New South Wales region. A suburb at the fringe of Sydney (Pitt Town) now appears to be acting as a source population to the surrounding populations and to the Sydney population. We assume that the original source population was at the introduction point (i.e., Sydney), but it is conceivable that the population density on the urban fringes in New South Wales has increased, resulting in a change in source.

4.4 | Data QC

This study is comprehensive in both the number of samples (and their geographical coverage) and the number of genetic markers we have utilized. The abundance of SNP markers that were generated using the DArTseq platform allowed us to implement stringent filters whilst maintaining ample numbers of SNPs to produce high-resolution population genetic estimates. Our SNP filtering methods improved the quality of our datasets (Table S5.3), and importantly, both of our SNP datasets (from two different bioinformatic pipelines) produced qualitatively consistent results for the demographic analyses (Appendix S4).

5 | CONCLUSION

Biological invasions are among the greatest threats to biodiversity, causing immense ecological, economic, and social effects worldwide (Luque et al., 2014; Marbuah, Gren, & McKie, 2014). As one of the world's most invasive birds (GISD, 2015), the myna has significantly impacted the environments of countries where it has been introduced (Grarock et al., 2012; Lowe, Browne, Boudjelas, & De Poorter, 2000; Tindall et al., 2007). We have detected significant genetic differentiation between myna populations across their Australian range, even at small spatial scales (Figures 3, 5 & Table S5.4). These results suggest that, following introductions/translocations to multiple sites across eastern Australia, the myna has largely retained historical population structure, with restricted gene flow between many populations due to the myna's limited effective dispersal capabilities. Limited effective dispersal and highly structured populations (which are isolated by distance; Figure 4) lends support to the strategy of

eradicating mynas in localized regional areas, rather than treating the population as a whole. Particular attention should be paid to the invasive front populations to prevent admixture between the gene pools of the original introduction sites which may lead to high diversity populations. Additionally, the contemporary gene flow patterns support source/sink population dynamics in both Victoria and New South Wales. Knowledge of the source of new myna incursions will assist control programs that are attempting to minimize the connectivity between populations.

The methods in this study can be applied to other alien species or to native species that have undergone a recent range expansion. The identification of the colonization points, subsequent admixture events, population dynamics and the invasive front/s is vital information to inform management strategies to mitigate invasive species, a fundamental threat to natural ecosystems.

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CONFLICTS OF INTEREST

None.

DATA ACCESSIBILITY

Title: Data from: Two speed invasion: assisted and intrinsic dispersal of common mynas over 150-years of colonization

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.670716m

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BIOSKETCH

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SUPPORTING INFORMATION

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

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