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Genetic analyses reveal complex introduction histories for the invasive tree *Acacia dealbata* Link around the world

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Abstract

Aim: To compare genetic diversity and structure between *Acacia dealbata* populations sampled across the species' native range in Australia and from its non-native ranges in Chile, Madagascar, New Zealand, Portugal, La Réunion island, South Africa and the United States, and to investigate the most likely introduction scenarios to non-native ranges.

Location: Global.

Taxon: *Acacia dealbata*, Fabaceae.

Methods: Our dataset comprised 1615 samples representing 92 populations sampled in the species' native and non-native ranges. We employed a combination of genetic fingerprinting (microsatellite markers) and genetic modelling approaches. We calculated genetic diversity for each population and tested for genetic isolation by distance within each range. A combination of Bayesian assignment tests and multivariate ordination was applied to identify genetic structure among populations. Approximate Bayesian Computation (ABC) analyses were conducted to test different competing introduction scenarios for each non-native range.

Results: The majority of the species' non-native ranges was characterized by high genetic diversity and low levels of genetic structure. With regard to introduction histories, however, our results supported different introduction scenarios for different non-native ranges. We did not find strong support for any of tested introduction scenarios for populations in Chile and Madagascar, but these likely originated from multiple introductions followed by admixture. Populations in New Zealand and La Réunion most likely originated directly from Tasmania, possibly through multiple introductions. Similar to previous findings for South African populations, no clear introduction history could be identified for populations in Portugal and the United States.

Main conclusions: Our study shows that global introductions of *A. dealbata* were complex and one scenario does not fit the invasion history of the species in different regions. We discuss how this complexity needs to be considered when formulating strategies for the effective management of the species. Future research needs to help bridge persisting knowledge gaps are discussed.

KEYWORDS
Australian acacias, biological invasions, Fabaceae, genetic diversity, genetic structure, introduction history, microsatellite markers, tree invasions, wattles

1 | INTRODUCTION

Invasive species are a major threat to biodiversity and human livelihoods, and recent estimates show that one-sixth of the world's land surface is highly vulnerable to invasion (Early et al., 2016). Knowledge of the routes of introduction and propagule pressure is important for understanding a species' introduction history, spread, evolutionary responses during invasion, to explore management options (e.g. identification of suitable biological control agents) and to develop biosecurity strategies (Cristescu, 2015; Le Roux & Wieczorek, 2009; Pyšek et al., 2013). In a few cases, precise information on the invasion history of a species can be found in historical records, but for many species such records are lacking, incomplete or misleading (e.g. Fischer et al., 2015; Hirsch et al., 2011). The application of molecular genetics is therefore valuable for reconstructing the introduction histories of invasive species for which little is known about where they were introduced from, how often and in what quantities (Cristescu, 2015; Fischer et al., 2015).

Among invasive plants, trees present special challenges for researchers (Richardson et al., 2014). While they share many characteristics with other plant taxa, they have key features (e.g. unique architecture, longevity, mostly intentionally introduced and subject to artificial selection, etc.) that clearly distinguish them from most other invasive plants (Hirsch et al., 2017; Richardson & Rejmánek, 2011). Also, many invasive trees remain valuable resources and economic commodities and their invasion dynamics and suitable management options are therefore often complicated by socio-political issues (Richardson & Rejmánek, 2011; van Wilgen et al., 2011). Australian acacias are one of the most important and widely studied invasive tree groups globally (Richardson & Rejmánek, 2011; Souza-Alonso et al., 2017). Features commonly related to the invasiveness of acacias include their ability to form symbiosis with nitrogen-fixing bacteria, allelopathy, fast growth, ability to re-sprout after cutting, massive seed production, long seed viability and high intraspecific variability (Gibson et al., 2011; Le Roux et al., 2011; Morris et al., 2011; Souza-Alonso et al., 2017; Yannelli et al., 2020). These and other factors, such as the commercial value and extensive planting of acacias, can greatly complicate the management of invasive populations. Moreover, invasive acacias may cause changes in (a)biotic conditions, such as elevated soil nutrients, that may persist after the removal of biomass of invasive trees (Morris et al., 2011; Nsikani et al., 2018), posing major challenges for restoration (Holmes et al., 2020).

This study focuses on *Acacia dealbata* Link (silver wattle) and, more specifically, the reconstruction of the history of human-mediated movement of this species around the globe. The species, native to south-western Australia (i.e. Australian Capital Territory, New South Wales, Victoria and eastern Tasmania), has been introduced to many parts of the world for multiple purposes (e.g. forestry, horticulture, perfume production, railway fuel, shade and shelter) (Kull et al., 2008; Lorenzo et al., 2010; Poynton, 2009; Richardson & Rejmánek, 2011). For example, according to the Global Biodiversity Information Facility (GBIF), *A. dealbata* is currently present in 29 countries and islands outside Australia (GBIF Secretariat, 2019). In many of these areas, the species has escaped cultivation and is now considered an aggressive invasive species (Richardson et al., 2011; Richardson & Rejmánek, 2011). In these regions, dense mono-specific populations of *A. dealbata* replace or radically alter native vegetation and change soil characteristics through the release of allelopathic compounds and the fixation of atmospheric nitrogen (Poynton, 2009; Lorenzo, Pereira, & Rodríguez-Echeverría, 2013).

Acacia dealbata has a short generation time and can reach reproductive maturity at four to five years of age (Stelling, 1998). The species also has generalist pollination requirements and seed-dispersal syndromes (Carr, 2001). Based on morphology and environmental requirements, it was previously thought that *A. dealbata* consisted of two subspecies (Kodela & Tindale, 2001). However, recent studies based on a combination of ecological niche modelling, DNA sequencing analyses and microsatellite genotyping questioned this taxonomic division (Hirsch et al., 2017, 2018). Instead, across the species' native range, two geographically structured genetic lineages, corresponding roughly to Australian mainland populations and Tasmanian populations, have been described (Hirsch et al., 2018). In our latest work, we compared the genetic makeup of these native lineages to invasive populations from South Africa where the species was introduced in the mid-19th century (Hirsch et al., 2019; Poynton, 2009). Surprisingly, South African populations were genetically distinct from native populations, and modelling approaches indicated that these populations originated from an unknown or "ghost" source (Hirsch et al., 2019). To gain a more comprehensive understanding of the species' introduction history around the world, this study aims to compare the two native lineages of *A. dealbata* with invasive populations from Chile, Madagascar, New Zealand, Portugal, La Réunion and the United States—countries that represent some of the species most prominent invasive ranges (Lorenzo et al., 2010; Richardson et al., 2011). Historical records documenting the introduction histories of *A. dealbata* to these countries are largely lacking, in particular with regard to the origin of invasive populations.

In Europe, *A. dealbata* was first introduced in 1816 for horticultural and floricultural purposes and is now considered a highly invasive species in south-western parts of the continent (Adair, 2008; Cavanagh, 2006; Martins et al., 2016). In Portugal, the first record of the species is from 1850, when it was introduced for the cut-flower, tannin and timber industries (Alves, 1858; Martins et al., 2016). Although the species already established invasive populations during the 19th century, it was only in 1999 that it was officially listed as

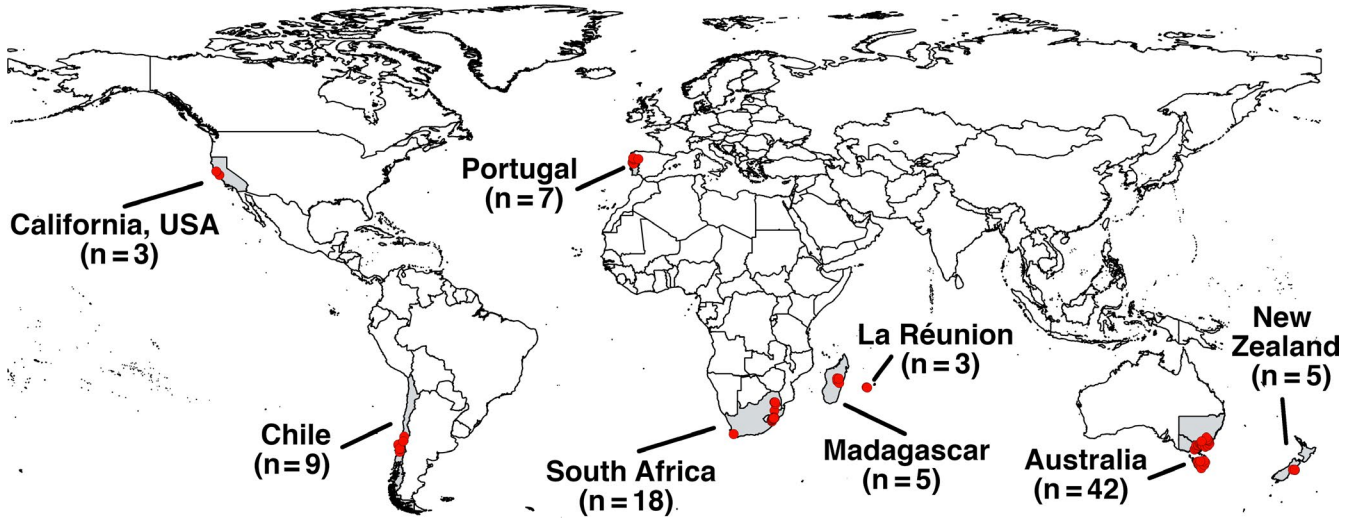

FIGURE 1 Regions where *Acacia dealbata* samples were collected for this study. Red circles indicate exact sampling locations (see Table 1) and numbers in parentheses give the number of individual populations sampled in each country/region

invasive (Marchante et al., 2005; Martins et al., 2016). *Acacia dealbata* now occurs throughout Portugal (Marchante et al., 2005), and it is considered one of the top 20 target species for biological control programs in Europe (Sheppard et al., 2006). *Acacia dealbata* is also considered invasive on the two western Indian Ocean islands of Madagascar and La Réunion, where it was introduced in 1898 and 1841, respectively (Kull et al., 2008, 2011). In La Réunion, the species was primarily introduced to control soil erosion, while in Madagascar, its main uses were afforestation, railway fuel and shading (Kull et al., 2008). Around the mid 1900s, aircraft were used to disseminate *A. dealbata* seed over large parts of Madagascar; by the end of the 1960s, the species occurred over more than 30,000 ha (Chauvet, 1968; Roche, 1956). Although *A. dealbata* is clearly invasive, some policymakers in Madagascar downplay this status and laud its value for reforestation (Kull et al., 2007, 2008). In Chile, after being introduced in 1869, the wider dissemination of *A. dealbata* started in the early 1900s for erosion control and as a source of fuel wood (Fuentes et al., 2014; Kull et al., 2011). The species currently has vast invasive populations along rivers, roads and in disturbed habitats across central Chile from Valparaiso to Los Lagos (including Juan Fernandez Island and Easter Island (Langdon et al., 2019)). In the Bío-Bío region alone, it is estimated that the species may cover as much as 100,000 ha (Fuentes-Ramírez et al., 2010). Another country where *A. dealbata* is listed as invasive species is New Zealand (CABI, 2020). According the New Zealand Conservation Network (http://www.nzpcn.org.nz), the species became naturalized in the country in 1870, although the date of introduction remains unknown. The species is valued for its attractive flowers, coppicing ability, quality timber and shelter, and is still available for sale in New Zealand (e.g. https://www.southernwoods.co.nz/shop/acacia-dealbata/). Unlike many regions around the globe, growth trials in New Zealand used seed material of *A. dealbata* sourced from Tasmania, mainland Australia and from non-native ranges of the species, such as India (Shelbourne et al., 2000). In the United States, *A. dealbata* occurs almost exclusively in California (USDA & NRCS, 2020) and is not considered invasive (CABI, 2020). It was one of the first Australian acacias to be introduced to California in the early 1850s, and subsequent introductions are thought to have occurred (Butterfield, 1938). The species did not fare well in California, and many individuals died within a few years after their introduction (M. Rejmánek, pers. comm.; Hastings & Heintz, 1976).

By comparing the genetic characteristics (i.e. genetic diversity and structure) of *A. dealbata* populations collected across the native range and introduced ranges discussed above, and by applying state-of-the-art genetic modelling, our study aims to shed more light on the historical movement of the species and its global biogeography. Such information may benefit ongoing initiatives to develop effective management options for the species (e.g. biological control) and improve biosecurity strategies.

2 | MATERIALS AND METHODS

2.1 | Sampling, DNA extraction and genotyping

In addition to available data for native *A. dealbata* populations (Hirsch et al., 2018) and invasive South African populations (Hirsch et al., 2019), we also generated microsatellite genotyping data for non-native populations in Chile, Madagascar, New Zealand, Portugal, La Réunion and the United States of America (USA) (Figure 1; Table 1). In each country, fresh healthy leaves were sampled from 20 randomly chosen individuals per population. Care was taken to sample individuals across the distribution of each population (i.e. sampling of only one part of a population was avoided) and the minimum distance between sampled individuals was 5 m. The collected plant material was dehydrated and stored on silica gel until DNA extraction. DNA extractions were carried out using the cetyltrimethylammonium bromide (CTAB)

TABLE 1 Population information and genetic diversity measures for *Acacia dealbata* populations included in this study. Lat = Latitude (decimal degrees); Long = Longitude (decimal degrees); Year = sampling year; *N* = number of sampled trees; MLG = Number of unique multi-locus genotypes (MLG) observed; PD = percent distinguishable genotypes (i.e. MLG/N); A_R = Allelic richness calculated using rarefaction to account for different sample sizes within populations, H_O = Observed heterozygosity, H_E = Expected heterozygosity, F_{IS} = Inbreeding coefficient. The column "RangeID" shows the range abbreviations used in Figures 2, 3 and 4, and differentiates the native populations according to the two genetic lineages as defined in Hirsch et al. (2018). Genetic diversity measures for native and South African populations were previously published by Hirsch et al. (2019) and are shown here for the sake of comparison. *SD* = standard deviation

PopID	Range	RangeID	Lat	Long	Year	Collector[a]	*N*	MLG	PD	A_R	H_O	H_E	F_{IS}
Native populations													
TAS1	Australia (Tasmania)	NAT1	−41.51	146.08	2013	FI; CK	19	17	0.89	3.35	0.458	0.463	−0.010
TAS2	Australia (Tasmania)	NAT1	−41.47	146.13	2013	FI; CK	18	18	1.00	3.54	0.441	0.451	0.052
TAS3	Australia (Tasmania)	NAT1	−41.40	146.42	2013	FI; CK	18	17	0.94	3.32	0.488	0.463	−0.074
TAS4	Australia (Tasmania)	NAT1	−41.57	146.82	2013	FI; CK	18	18	1.00	3.25	0.402	0.467	0.137
TAS5	Australia (Tasmania)	NAT1	−41.78	147.33	2013	FI; CK	14	12	0.86	3.19	0.473	0.489	0.056
TAS6	Australia (Tasmania)	NAT1	−42.27	147.41	2013	FI; CK	20	8	0.40	2.76	0.596	0.507	−0.211
TAS7	Australia (Tasmania)	NAT1	−42.52	146.95	2013	FI; CK	19	7	0.37	1.64	0.474	0.265	−0.556
TAS8	Australia (Tasmania)	NAT1	−42.47	146.70	2013	FI; CK	17	8	0.47	2.82	0.492	0.423	−0.115
TAS9	Australia (Tasmania)	NAT1	−42.39	146.59	2013	FI; CK	17	17	1.00	3.76	0.511	0.530	0.031
TAS10	Australia (Tasmania)	NAT1	−42.73	146.92	2013	FI; CK	19	8	0.42	2.99	0.510	0.415	−0.156
TAS11	Australia (Tasmania)	NAT1	−43.24	147.15	2013	FI; CK	19	19	1.00	3.49	0.491	0.534	0.054
TAS12	Australia (Tasmania)	NAT1	−42.40	147.93	2013	FI; CK	20	10	0.50	2.40	0.417	0.339	−0.181
TAS13	Australia (Tasmania)	NAT1	−41.65	148.24	2013	FI; CK	17	15	0.88	3.54	0.529	0.522	−0.002
TAS14	Australia (Tasmania)	NAT1	−41.20	147.91	2013	FI; CK	17	17	1.00	3.72	0.524	0.557	0.079
TAS15	Australia (Tasmania)	NAT1	−41.34	146.87	2013	FI; CK	20	17	0.85	3.29	0.472	0.493	0.037
AUS1	Australia (mainland)	NAT1	−38.13	145.28	2013	FI; CK	18	17	0.94	3.29	0.497	0.513	0.039
AUS2	Australia (mainland)	NAT1	−37.75	145.55	2013	FI; CK	20	19	0.95	3.39	0.530	0.510	−0.051
AUS3	Australia (mainland)	NAT1	−37.56	145.89	2013	FI; CK	19	19	1.00	4.01	0.558	0.566	0.015
AUS4	Australia (mainland)	NAT2	−36.99	145.74	2013	FI; CK	19	6	0.32	2.22	0.485	0.335	−0.362
AUS5	Australia (mainland)	NAT2	−37.14	146.46	2013	FI; CK	18	18	1.00	4.02	0.529	0.562	0.095
AUS6	Australia (mainland)	NAT2	−37.11	146.30	2013	FI; CK	19	11	0.58	2.50	0.495	0.435	−0.130
AUS7	Australia (mainland)	NAT2	−36.91	146.30	2013	FI; CK	19	14	0.74	3.04	0.533	0.466	−0.124
AUS8	Australia (mainland)	NAT2	−36.55	146.71	2013	FI; CK	18	18	1.00	3.83	0.549	0.593	0.055
AUS9	Australia (mainland)	NAT2	−36.34	147.17	2013	FI; CK	18	15	0.83	2.90	0.415	0.425	0.008
AUS10	Australia (mainland)	NAT2	−36.51	147.44	2013	FI; CK	19	8	0.42	3.01	0.489	0.450	−0.014
AUS11	Australia (mainland)	NAT2	−36.56	146.97	2013	FI; CK	18	17	0.94	3.54	0.528	0.517	−0.012
AUS12	Australia (mainland)	NAT2	−36.80	147.22	2013	FI; CK	17	8	0.47	2.71	0.518	0.408	−0.194

(Continues)

TABLE 1 (Continued)

PopID	Range	RangeID	Lat	Long	Year	Collector[a]	*N*	MLG	PD	A_R	H_O	H_E	F_{IS}
AUS13	Australia (mainland)	NAT2	−36.95	147.40	2013	FI; CK	18	7	0.39	2.95	0.526	0.432	−0.185
AUS14	Australia (mainland)	NAT2	−37.04	147.58	2013	FI; CK	19	12	0.63	3.05	0.489	0.466	0.001
AUS15	Australia (mainland)	NAT2	−37.39	148.26	2013	FI; CK	17	12	0.71	3.62	0.499	0.506	0.012
AUS16	Australia (mainland)	NAT2	−35.89	148.41	2013	FI; CK	19	4	0.21	1.98	0.603	0.371	−0.581
AUS17	Australia (mainland)	NAT2	−36.07	148.87	2013	FI; CK	17	4	0.24	1.92	0.400	0.279	−0.214
AUS18	Australia (mainland)	NAT2	−36.40	148.65	2013	FI; CK	18	15	0.83	3.22	0.454	0.464	0.029
AUS19	Australia (mainland)	NAT2	−37.11	148.90	2013	FI; CK	20	6	0.30	2.10	0.481	0.403	−0.202
AUS20	Australia (mainland)	NAT2	−37.11	148.91	2013	FI; CK	17	10	0.59	2.47	0.290	0.320	0.128
AUS21	Australia (mainland)	NAT2	−36.54	149.38	2013	FI; CK	19	10	0.53	3.27	0.484	0.509	0.000
AUS22	Australia (mainland)	NAT2	−35.78	149.26	2013	FI; CK	18	12	0.67	3.19	0.585	0.518	−0.109
AUS23	Australia (mainland)	NAT2	−35.59	149.09	2013	FI; CK	19	7	0.37	2.81	0.558	0.469	−0.098
AUS24	Australia (mainland)	NAT2	−35.32	148.95	2013	FI; CK	18	10	0.56	2.66	0.556	0.460	−0.224
AUS25	Australia (mainland)	NAT2	−35.37	148.80	2013	FI; CK	18	14	0.78	3.27	0.443	0.478	0.067
AUS26	Australia (mainland)	NAT2	−34.80	148.53	2013	FI; CK	17	14	0.82	3.40	0.473	0.524	0.095
AUS27	Australia (mainland)	NAT2	−35.83	147.22	2013	FI; CK	17	16	0.94	2.70	0.486	0.442	−0.111
						Mean	**18.21**	**12.64**	**0.70**	**3.05**	**0.494**	**0.460**	**−0.070**
						SD	**1.18**	**4.62**	**0.26**	**0.57**	**0.058**	**0.075**	**0.160**
Non-native populations													
RSA1	South Africa	RSA	−33.91	18.95	2014	HH	19	13	0.68	2.31	0.368	0.353	−0.030
RSA2	South Africa	RSA	−27.50	30.13	2010	CGS	18	18	1.00	2.59	0.418	0.435	0.021
RSA3	South Africa	RSA	−25.70	30.42	2010	CGS	9	9	1.00	3.00	0.488	0.474	−0.014
RSA4	South Africa	RSA	−30.45	29.46	2014	FI; HH; JH	10	8	0.80	2.32	0.410	0.341	−0.159
RSA5	South Africa	RSA	−30.17	29.31	2014	FI; HH; JH	11	6	0.55	2.35	0.705	0.458	−0.484
RSA6	South Africa	RSA	−30.02	29.36	2014	FI; HH; JH	16	16	1.00	2.34	0.493	0.446	−0.098
RSA7	South Africa	RSA	−29.92	29.39	2014	FI; HH; JH	11	4	0.36	1.99	0.627	0.363	−0.658
RSA8	South Africa	RSA	−29.70	29.49	2014	FI; HH; JH	20	18	0.90	2.58	0.405	0.415	0.085
RSA9	South Africa	RSA	−29.65	29.58	2014	FI; HH; JH	17	9	0.53	2.08	0.457	0.362	−0.230
RSA10	South Africa	RSA	−29.52	29.66	2014	FI; HH; JH	20	20	1.00	2.65	0.479	0.451	−0.039
RSA11	South Africa	RSA	−29.43	29.79	2014	FI; HH; JH	19	17	0.89	2.40	0.326	0.354	0.065
RSA12	South Africa	RSA	−29.38	29.89	2014	FI; HH; JH	20	20	1.00	2.83	0.418	0.418	0.021
RSA13	South Africa	RSA	−29.48	30.18	2014	FI; HH; JH	18	12	0.67	2.73	0.407	0.462	0.179
RSA14	South Africa	RSA	−29.37	30.12	2014	FI; HH; JH	12	12	1.00	2.42	0.485	0.416	−0.145

(Continues)

TABLE 1 (Continued)

PopID	Range	RangeID	Lat	Long	Year	Collector[a]	*N*	MLG	PD	A_R	H_O	H_E	F_{IS}
RSA15	South Africa	RSA	−29.53	29.93	2014	FI; HH; JH	18	15	0.83	2.28	0.447	0.429	−0.025
RSA16	South Africa	RSA	−25.13	30.08	2014	FI	20	19	0.95	2.32	0.389	0.390	0.000
RSA17	South Africa	RSA	−25.14	30.23	2014	FI	18	3	0.17	1.76	0.506	0.277	−0.521
RSA18	South Africa	RSA	−25.16	30.30	2014	FI	16	13	0.81	2.52	0.441	0.404	−0.022
						Mean	**16.22**	**12.89**	**0.79**	**2.41**	**0.459**	**0.403**	**−0.114**
						SD	**3.83**	**5.43**	**0.25**	**0.30**	**0.090**	**0.052**	**0.225**
CHL1	Chile	CHL	−36.97	−72.97	2015	AP	20	20	1.00	2.96	0.517	0.469	−0.098
CHL2	Chile	CHL	−36.66	−72.45	2015	AP	17	16	0.94	2.83	0.438	0.440	−0.010
CHL3	Chile	CHL	−36.67	−72.50	2015	AP	20	16	0.80	3.05	0.507	0.466	−0.043
CHL4	Chile	CHL	−36.75	−72.99	2015	AP	20	18	0.90	3.05	0.465	0.484	0.016
CHL5	Chile	CHL	−38.75	−72.59	2015	AP	20	19	0.95	2.82	0.457	0.440	−0.035
CHL6	Chile	CHL	−37.98	−72.43	2015	AP	20	17	0.85	2.82	0.449	0.421	−0.049
CHL7	Chile	CHL	−37.87	−72.60	2015	AP	19	17	0.89	2.84	0.342	0.398	0.102
CHL8	Chile	CHL	−34.59	−71.36	2015	AP	16	15	0.94	2.66	0.381	0.412	0.046
CHL9	Chile	CHL	−35.86	−71.61	2015	AP	18	18	1.00	3.06	0.478	0.471	−0.039
						Mean	**18.89**	**17.33**	**0.92**	**2.90**	**0.448**	**0.445**	**−0.012**
						SD	**1.54**	**1.58**	**0.07**	**0.14**	**0.056**	**0.030**	**0.059**
MG1	Madagascar	MG	−19.38	47.39	2014	PL	16	13	0.81	2.94	0.497	0.492	−0.011
MG2	Madagascar	MG	−19.38	47.36	2014	PL	19	15	0.79	2.91	0.591	0.491	−0.182
MG3	Madagascar	MG	−19.92	47.89	2014	PL	14	9	0.64	2.82	0.493	0.449	−0.101
MG4	Madagascar	MG	−18.65	47.28	2014	PL	19	7	0.37	2.45	0.632	0.455	−0.358
MG5	Madagascar	MG	−18.71	47.79	2014	PL	17	14	0.82	2.96	0.560	0.479	−0.170
						Mean	**17.00**	**11.60**	**0.69**	**2.82**	**0.555**	**0.473**	**−0.164**
						SD	**2.12**	**3.44**	**0.19**	**0.21**	**0.060**	**0.020**	**0.128**
NZ1	New Zealand	NZ	−43.66	172.71	2014	JP; RP	18	16	0.89	3.11	0.494	0.462	0.015
NZ2	New Zealand	NZ	−43.64	172.65	2014	JP; RP	20	6	0.30	2.73	0.615	0.453	−0.298
NZ3	New Zealand	NZ	−43.75	172.80	2014	JP; RP	20	20	1.00	3.68	0.516	0.536	0.050
NZ4	New Zealand	NZ	−43.64	172.25	2014	JP; RP	15	4	0.27	2.09	0.567	0.379	−0.493
NZ5	New Zealand	NZ	−43.63	172.74	2014	JP; RP	15	7	0.47	2.04	0.567	0.337	−0.602
						Mean	**17.60**	**10.60**	**0.58**	**2.73**	**0.552**	**0.433**	**−0.266**
						SD	**2.51**	**6.99**	**0.34**	**0.69**	**0.048**	**0.077**	**0.293**
POR1	Portugal	POR	40.74	−8.70	2014	EM	11	8	0.73	2.47	0.475	0.349	−0.286

(Continues)

TABLE 1 (Continued)

PopID	Range	RangeID	Lat	Long	Year	Collector[a]	*N*	MLG	PD	A_R	H_O	H_E	F_{IS}
POR2	Portugal	POR	40.45	−8.78	2014	EM	15	11	0.73	2.76	0.320	0.421	0.262
POR3	Portugal	POR	40.22	−8.45	2014	EM	18	16	0.89	3.48	0.492	0.495	−0.004
POR4	Portugal	POR	41.30	−8.55	2014	JV	14	14	1.00	2.87	0.517	0.446	−0.131
POR5	Portugal	POR	41.55	−8.47	2014	JV	16	15	0.94	3.25	0.545	0.504	−0.072
POR6	Portugal	POR	41.77	−8.61	2014	JV	19	16	0.84	2.96	0.569	0.501	−0.138
POR7	Portugal	POR	41.45	−7.17	2014	JV	16	9	0.56	2.26	0.406	0.308	−0.249
						Mean	**15.57**	**12.71**	**0.81**	**2.86**	**0.475**	**0.432**	**−0.088**
						SD	**2.64**	**3.35**	**0.15**	**0.42**	**0.086**	**0.078**	**0.182**
RE1	La Réunion	RE	−21.13	55.47	2014	SB	19	12	0.63	2.26	0.511	0.369	−0.209
RE2	La Réunion	RE	−21.07	55.37	2014	SB	18	14	0.78	2.39	0.369	0.415	0.100
RE3	La Réunion	RE	−21.20	55.56	2015	JLR	11	4	0.36	1.64	0.345	0.205	−0.509
						Mean	**16.00**	**10.00**	**0.59**	**2.10**	**0.408**	**0.330**	**−0.206**
						SD	**4.36**	**5.29**	**0.21**	**0.40**	**0.090**	**0.110**	**0.305**
USA1	USA	USA	37.07	−122.00	2015	MR	19	17	0.89	3.19	0.585	0.520	−0.042
USA2	USA	USA	38.09	−122.85	2015	MR	20	17	0.85	2.75	0.494	0.444	−0.104
USA3	USA	USA	38.11	−122.88	2015	MR	19	13	0.68	2.75	0.488	0.450	−0.056
						Mean	**19.33**	**15.67**	**0.81**	**2.90**	**0.522**	**0.471**	**−0.067**
						SD	**0.58**	**2.31**	**0.11**	**0.26**	**0.054**	**0.042**	**0.033**

[a]Collector(s): AP = A. Pauchard; CGS = C. Gairifo Santos; CK = C. Kleinjan; EM = E. Marchante; FI = F. Impson; HH = H. Hirsch; JH = J. Hoffman; JLR = J. Le Roux; JP = J. Pannell; JV = J. Vicente; MR = M. Rejmánek; PL = P. Lammers; RP = R. Pearson; SB = S. Baret.

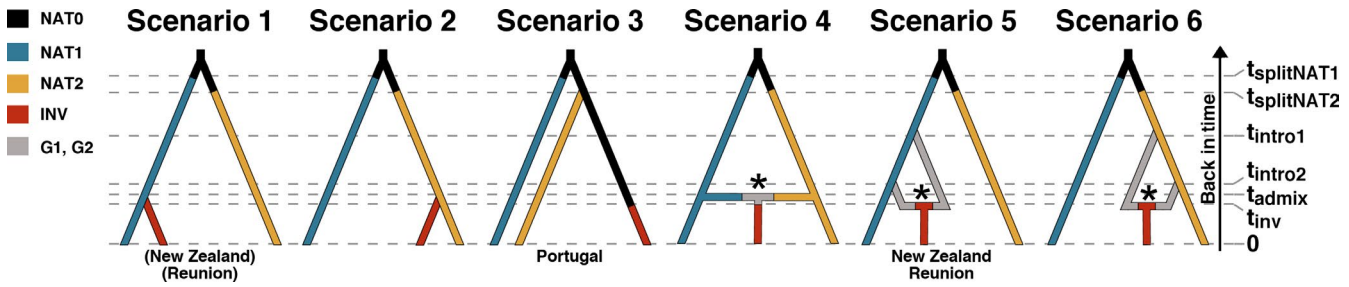

FIGURE 2 Diagrams of the competing introduction scenarios tested in the individual approximate Bayesian computation approaches (ABC) for each non-native range (excluding South Africa). The same scenarios were tested for the invasion history of South Africa populations by Hirsch et al. (2019). A change of colour along the scenario pathways represents a founding event of a new population for which potential bottleneck effects were considered. In cases where populations merge in the scenario (highlighted with an asterisk), admixture rates were implemented in the scenario code (for details see Table S2, Appendix S2). NAT0 = overarching native population; NAT1 = Tasmanian populations and Australian mainland populations AUS_1, AUS_2 and AUS_3; NAT2 = Australian mainland populations (except AUS_1, AUS_2 and AUS_3); INV = populations from corresponding non-native range; G1, G2 = two unsampled ("ghost") populations. Further details on the model parameters (i.e. tsplitNAT1, tsplitNAT2, etc.) are provided in Table S2, Appendix S2. The non-native range names underneath the diagrams indicate for which non-native populations the corresponding scenario was the most likely one (Figure S6, Appendix S1)

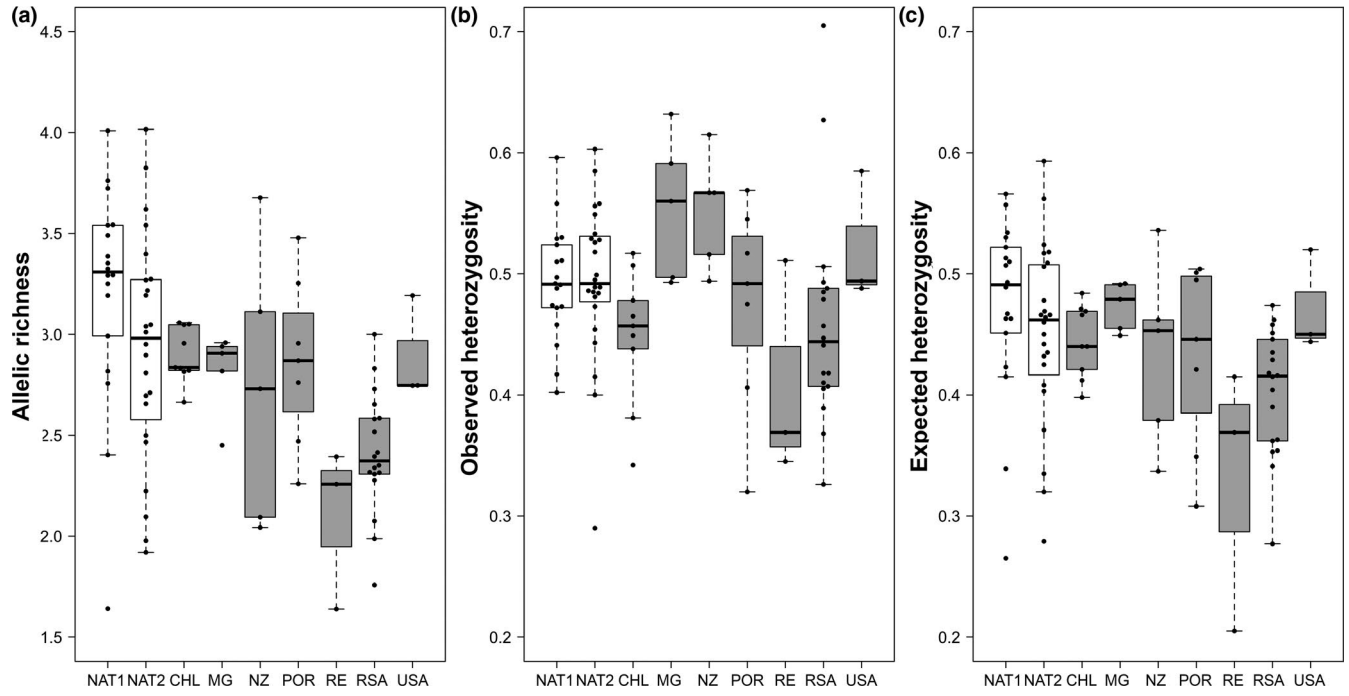

FIGURE 3 Comparison of the genetic diversity measures between the native (white) and non-native (grey) ranges of *Acacia dealbata*. (a) allelic richness, (b) observed heterozygosity and (c) expected heterozygosity. Native populations were grouped into two genetic lineages according to Hirsch et al. (2018) (NAT1 = Tasmanian populations and southern most mainland population; NAT2 = main Australian mainland population). Boxplots are combined with beeswarm plots (black points) to displays the distribution of individual measurements. Range abbreviations correspond to the "range IDs" in Table 1

method (Doyle & Doyle, 1990) with some modifications (see Hirsch et al., 2018, 2019). All DNA extractions were diluted to a concentration of 100 ng/μl. Ten nuclear microsatellites loci were amplified using a set-up of two multiplex PCRs (for PCR conditions and further details see Hirsch et al., 2018, 2019). Each 96-well PCR plate contained *A. dealbata* 92 samples plus three randomly selected technical replicate samples and one negative control (H_2O). Amplification products were separated via gel capillary electrophoresis at the Central Analytical Facility, Stellenbosch University, Stellenbosch, South Africa. Genotype scoring of samples was performed using the GeneMarker software (version 2.6.4; Genetics LLC, State College, Pennsylvania, USA) by applying customized marker panels to each locus to call alleles. This scoring was followed by manual checking of all scored alleles. Genotypes were obtained for a total of 558 individuals from populations sampled in Chile (170 individuals), Madagascar (85), New Zealand (88), Portugal (109), La Réunion (48) and the USA (58). These genotypes were combined with the 765 native range genotypes from Hirsch et al. (2018) and the 292 South African genotypes from Hirsch et al. (2019), resulting in a dataset consisting of 1615 genotypes,

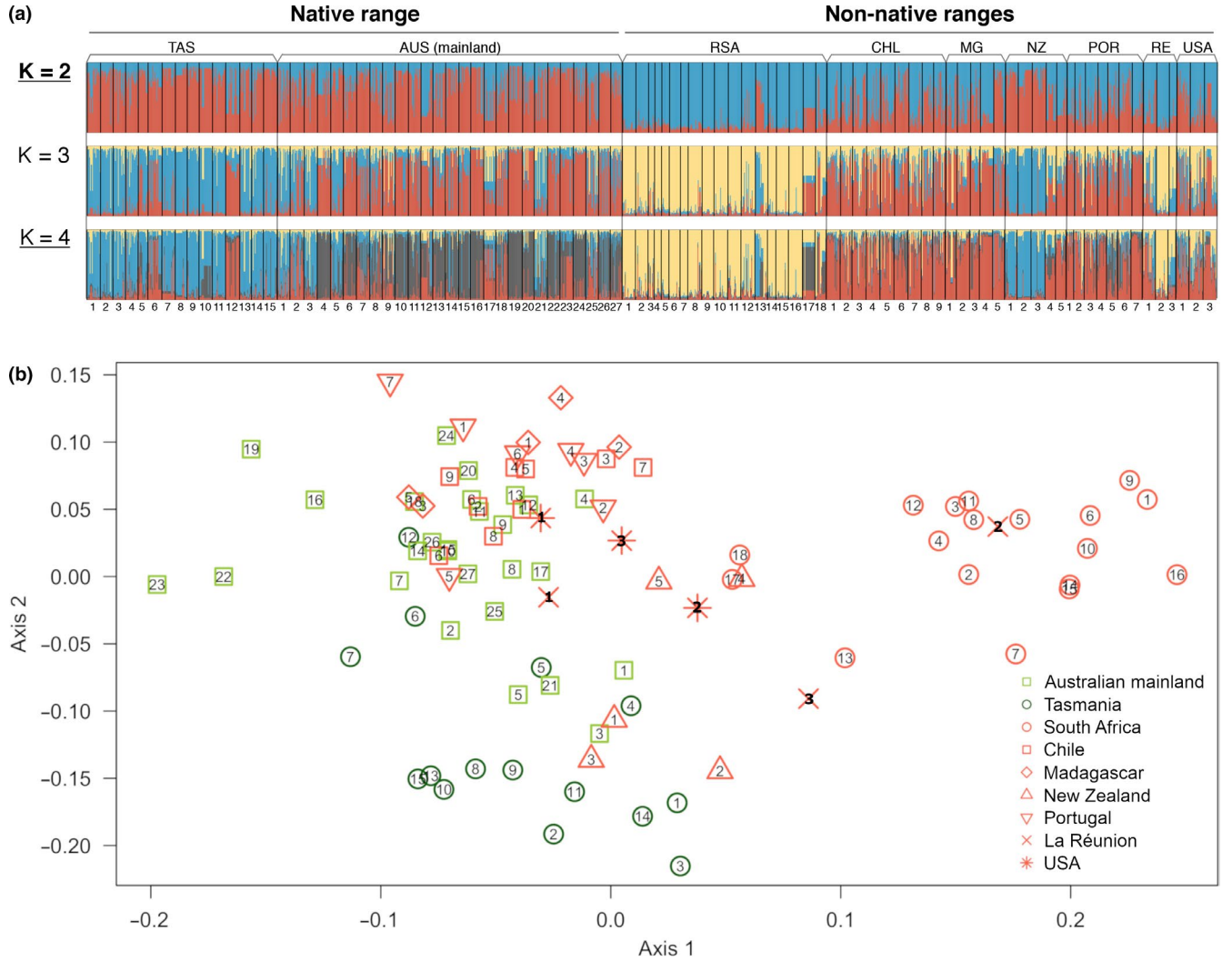

FIGURE 4 Genetic structure results for the native and non-native populations of *Acacia dealbata*. (a) STRUCTURE bar plots. The delta K method following Evanno et al. (2005) revealed $K = 2$ as optimal genetic structure but also showed a strong signal for $K = 4$. Range abbreviations above and numbers underneath the bar plots refer to the population ID's and range information provided in Table 1. (b) Principal coordinates analysis for the native and non-native populations of *A. dealbata*. The analysis was based on genetic distances (following Cavalli-Sforza and Edwards 1967) between populations and the first three axes explained 14.9%, 10.4% and 8.7% of the variation, respectively. Populations are indicated with different colours and symbols according to their geographic origin (see plot legend). The numbers within the symbols refer to the population IDs (without prefix "TAS," "AUS," etc.) provided in Table 1. Numbers for La Réunion and the USA are highlighted in bold for better readability

representing 42 native and 50 non-native populations (Table 1). It is worth noting that the microsatellite data reported in our previous studies (Hirsch et al., 2018, 2019) and the new data of this study were generated and scored at the same time.

2.2 | Dataset characteristics and genetic diversity

Our genotype dataset was initially checked for the presence of scoring errors and null alleles using the software Micro-Checker version 2.2 (Van Oosterhout et al., 2004). This software applies a Monte Carlo simulation method to calculate expected homozygote and heterozygote allele size difference by assuming Hardy–Weinberg equilibrium (HWE) conditions and generating the frequency of expected and detected null alleles (Van Oosterhout et al., 2004). Null alleles are identified at a given locus when HWE conditions among genotypes are rejected and if excess homozygote genotypes are evenly distributed among allele size classes. The presence of null alleles can bias calculations of F_{ST} values and may lead to overestimation of population differentiation (Kim & Sappington, 2013). Therefore, for more detailed estimates of null allele frequencies at each locus and population, the expected maximization method as implemented in the software FreeNA (Chapuis & Estoup, 2007) was also applied. FreeNA was also used to calculate uncorrected and corrected (i.e. excluding null alleles; so-called ENA method as described in Chapuis & Estoup, 2007) pairwise F_{ST} values (Weir, 1996). For all loci, allele frequency departures from HWE expectations were

tested using the packages *adegenet* version 2.1.1 (Jombart, 2008) and *pegas* version 0.11 (Paradis, 2010) in R version 3.5.3 (R Core Team, 2019).

For each population, we calculated the number of observed unique multi-locus genotypes (MLG) and the per cent of distinguishable genotypes (PD = MLG/N) to determine whether clones were present within our collected populations. As genetic diversity measures per population, we calculated allelic richness (A_R), observed and expected heterozygosity (H_O and H_E). To account for different sample numbers among populations, a rarefaction correction based on the smallest sample size (i.e. population RSA3 with nine samples; Table 1) was applied. Further, we calculated the inbreeding coefficient (F_{IS}) for each population. All genetic diversity-related calculations were performed using the *diveRsity* R package version 1.9.90 (Keenan et al., 2013).

2.3 | Genetic structure and variation

For the complete dataset (i.e. including all native and non-native populations), and for each non-native range separately, Bayesian assignment tests as implemented in STRUCTURE version 2.3.4 (Pritchard et al., 2000) were performed to investigate the genetic structure among populations of *A. dealbata*. The sub–datasets for native range and the South African range were previously analysed using the same approach (Hirsch et al., 2018, 2019), and these analyses were therefore not repeated in this study. For each dataset, a range of possible genetic clusters (*K* values; Table S1, Appendix S1) was evaluated by using an admixture model with correlated allele frequencies, 100,000 burn-in iterations, 500,000 Markov Chain Monte Carlo repetitions and 20 iterations for each value of *K*. To evaluate the optimum number of genetic clusters in each dataset, we used the online software STRUCTURE HARVESTER (version 0.6.94; Earl & vonHoldt, 2012) to apply the delta *K* method described by Evanno et al. (2005). To compile graphical displays of the STRUCTURE results, the software packages CLUMPP (version 1.1.2; Jakobsson & Rosenberg, 2007) and DISTRUCT (version 1.1; Rosenberg, 2004) were used. However, the delta *K* method cannot test whether populations represent a single genetic cluster (i.e. $K = 1$), but can only test for $K \geq 2$. Therefore, for each separate non-native range STRUCTURE model, we also tested the possibility no genetic structure ($K = 1$). For this, we compared the raw model probabilities from the $K = 1$ STRUCTURE iterations to the probabilities of the optimal *K* value (identified using the delta *K* method) for each non-native range using a Wilcoxon rank sum test.

We used the *vegan* R package (version 2.5-4; Oksanen et al., 2019) to perform a principal coordinate analysis (PCoA) which was based on the uncorrected genetic distances (Cavalli-Sforza & Edwards, 1967) calculated with FreeNA. Further, we tested whether the extent of genetic differentiation between pairs of populations (i.e. pairwise F_{ST} values) differed between native range and non-native ranges using a Kruskal–Wallis rank sum tests. Pairwise F_{ST} values were further used to test for isolation by distance (IBD) among *A. dealbata* populations within individual non-native ranges using a Mantel tests (Mantel, 1967). This was previously done for native and South African populations (Hirsch et al., 2018, 2019). For these tests, genetic distances between populations were represented as linearized pairwise F_{ST} values (i.e. $F_{ST}/1-F_{ST}$). GPS coordinates for each population (Table 1) were used to calculate geographic distances with the software Geographic Distance Matrix Generator (version 1.2.3; Erst, 2017). IBD tests were carried out in the *vegan* R package with 9,999 permutations.

2.4 | Inferring the introduction histories of *Acacia dealbata*

To test different introduction scenarios to each of the different non-native ranges of *A. dealbata* included here, we applied Approximate Bayesian Computation (ABC) analyses (Beaumont, 2010; Beaumont et al., 2002) using the software DIYABC (version 2.1.0; Cornuet et al., 2015). With this approach, a large number of genetic datasets can be simulated for a set of potential introduction scenarios which are then compared to the observed data to determine the most likely scenario (Barker et al., 2017; Beaumont, 2010; Chau et al., 2015). We specified different introduction scenarios for each non-native range using the approach of Hirsch et al. (2019). However, for each non-native range, slight modifications in introduction times were implemented as described below. In detail, Australian populations were grouped into the two genetic lineages (i.e. NAT1 and NAT2; Table 1) identified by Hirsch et al. (2018) using microsatellite markers and DNA sequencing. These two genetic groups served as potential native source regions in all analyses. For each introduction scenario, we allowed these two lineages to be linked by an overarching native population (NAT0) which also enabled us to account for the possibility that unsampled native genetic diversity acted as the sources for non-native populations. Further, non-native populations were pooled as single genetic clusters defined by non-native countries, that is each non-native country equalled a genetic cluster. In the construction of potential introduction scenarios, we also considered the possibility that non-native populations might represent admixed populations derived from both native genetic lineages, and the possibility of multiple introductions. For each non-native range (i.e. country), the following competing introduction scenarios were tested: (a) non-native populations have direct ancestral origin from genetic lineage NAT1; (b) non-native populations have direct ancestral origin from genetic lineage NAT2; (c) non-native populations have direct ancestral origin from an unknown source (NAT0) which is related to genetic lineages NAT1 and NAT2; (d) non-native populations originated from an unsampled non-native population (i.e. ghost population) with admixed ancestry of both NAT1 and NAT2 genetic lineages; (e) non-native populations originated from multiple introductions from genetic lineage NAT1; and (f) non-native populations have ancestral origin from genetic lineage NAT2 that stemmed from multiple introductions (Figure 2).

Before running all simulations, the performance of prior estimates was tested for each dataset following the recommendations by Bertorelle et al. (2010). For the final analysis of each non-native range

dataset, 1×10^6 datasets were simulated for each scenario using the high-performance computation cluster at Stellenbosch University's Central Analytical Facilities' (http://www.sun.ac.za/hpc). The prior distributions of parameters and parameter rules applied for these analyses are specified in Table S2, Appendix S2. As an initial step, these prior settings were optimized in preliminary DIY ABC runs as recommended by Bertorelle et al. (2010). For each simulation, we used information from the primary literature to infer the time of introduction of *A. dealbata* (i.e. residence time) to corresponding non-native ranges (see Introduction section for details) and the species' minimum generation time of four to five years (Stelling, 1998). This provided us with the maximum number of generations within each non-native range (Table S2, Appendix S2). For each ABC analysis, we applied a generalized stepwise mutation model and the following summary statistics were used: mean number of alleles, mean genetic diversity (Nei, 1987), mean allele size variance, mean Garza-Williamson's *M* (Excoffier et al., 2005; Garza & Williamson, 2001), F_{ST} (Weir & Cockerham, 1984), shared allele distance (Chakraborty & Jin, 1993) and genetic distance ($\delta\mu^2$; Goldstein et al., 1995). The posterior probabilities of competing scenarios were compared using logistic regression on the 1% of simulated datasets that were closest to the observed dataset (Cornuet et al., 2010). Under the best scenario (see Results) of each analysis, posterior distributions of each parameter were estimated by applying a local linear regression with logit transformation on the 1% closest simulated datasets (i.e. 10,000 datasets per scenario). The median of the absolute deviation (RMedAD) and the median relative bias (MedRB) on 500 test datasets for the most likely scenario were calculated to assess the precision of parameter estimations (Cornuet et al., 2010).

For the scenario with the highest posterior probability in each ABC analysis (see Results), we estimated type I errors (i.e. false negatives) and type II errors (i.e. false positives) by using the "confidence in scenario choice" function implemented in DIYABC and following the protocol described by Cornuet et al. (2010). For these calculations, a set of 100 independent datasets and logistic regression approaches were used. For the most likely scenarios, we also applied the "model checking" option of the DIYABC software to test the ability (i.e. adequacy) of these scenarios to simulate datasets similar to the observed datasets (Cornuet et al., 2010). For this approach, 1,000 datasets were simulated from the parameter posterior distributions of the corresponding scenario and different summary statistics as for previous steps were used to avoid overestimating the fit of a scenario (Cornuet et al., 2010).

3 | RESULTS

3.1 | Dataset characteristics and genetic diversity

We found no evidence for scoring errors due to band stuttering in our genotype dataset. All loci were polymorphic and the number of alleles per locus ranged between 5 and 17 (mean: 9.2). All loci were also characterized by significant departures from HWE expectations (Figure S1, Appendix S1). However, there was no consistent pattern of significant HWE departure for a specific locus across all populations. Overall, allele frequency departure from HWE was due to a bias towards an excess of heterozygous genotypes (data not shown).

We detected a low average null allele frequency of 0.023 in our dataset but did not find a significant difference between ENA-corrected and uncorrected pairwise F_{ST} values (Kruskal–Wallis chi-square = 1.39, $p = .24$). Null allele correction was therefore not considered for all further analyses.

Non-native populations of *A. dealbata* in La Réunion harboured lower genetic diversity than native range populations (Table 1, Figure 3). South African populations also had much lower allelic richness than native populations (Hirsch et al., 2019; Table 1, Figure 3). Populations from all other non-native ranges had similar, or even slightly higher, genetic diversity measures compared to native populations (Table 1, Figure 3). In all cases, inbreeding coefficients were very low or showed no evidence of inbreeding (Table 1).

We found evidence for clones in the majority (i.e. 80.4%) of the 92 investigated *A. dealbata* populations (Table 1). Native populations had a mean PD of 0.70, while the mean PD varied between 0.58 and 0.92 in non-native populations (Table 1). We did not find any significant differences in PD or MLG between the native range and non-native ranges (Kruskal–Wallis chi-squared = 10.85, $p = .15$ and Kruskal–Wallis chi-squared = 12.49, $p = .09$, respectively). We also found allelic richness, regardless if calculated with the full dataset (Table 1) or the clone-corrected dataset (Table S3, Appendix S1), to be significantly and positively correlation with MLG (Spearman's rho = 0.59, $p < .001$ and Spearman's rho = 0.36, $p < .001$, respectively). Overall, the presence of clones did not influence the overall genetic diversity results (Figure S2 and Table S3, Appendix S1) and we therefore report all further results on the full dataset.

3.2 | Genetic structure

The STRUCTURE analysis of the complete dataset (i.e. all native and non-native populations) revealed the highest delta *K* values for $K = 2$ (delta $K = 65.9$) and $K = 4$ (delta $K = 42.3$) (Figure S3, Appendix S1). When visualizing two genetic clusters (i.e. $K = 2$), South African populations separated from the other populations, similar to previous findings (Hirsch et al., 2019; Figure 4a). When considering four genetic clusters (i.e. $K = 4$), South African populations, and one population from La Réunion, formed a separate cluster (Figure 4a), a pattern that also emerged in the PCoA (Figure 4b). The STRUCTURE results for $K = 4$ further implied that populations from the remaining non-native ranges seem to be more closely related to some native populations from Tasmania (i.e. TAS6 and TAS12) than those from the Australian mainland (Figure 4a). In contrast, the PCoA results showed that the majority of populations from Chile, Madagascar and Portugal to be more similar to Australian mainland populations than to Tasmanian populations (Figure 4b). Among the populations from the United States, only one clustered with Australian mainland populations while the other two populations did not show any clear association with any native *A. dealbata* populations (Figure 4b). A

similar lack of association was observed for two New Zealand populations, while the remaining three populations from this country clustered with Tasmanian populations (Figure 4b).

When considering the separate STRUCTURE analyses for each of the non-native ranges, we identified two genetic clusters in New Zealand (delta $K = 8.8$), in Portugal (delta $K = 25.4$), in La Réunion (delta $K = 196.2$), and in the United States (delta $K = 20.4$) (Figures S3 and S4, Appendix S1). Within Chile and Madagascar, three genetic clusters were identified (delta $K = 23.0$ and 39.3, respectively) (Figures S3 and S4, Appendix S1). However, for Chile, Madagascar, Portugal and the United States, the graphical representation of these groups (Figure S4, Appendix S1), as well as significantly lower pairwise F_{ST} values between pairs of populations *within* each non-native range compared to native populations (Figure S5 and Table S4, Appendix S1), rather suggest a lack of biologically meaningful genetic structure in these ranges. In contrast, pairwise F_{ST} values between pairs of populations within New Zealand and La Réunion were significantly higher than those between native populations (Figure S5 and Table S4, Appendix S1). However, in the case of New Zealand, the extremely low delta K value (i.e. 8.8; Figure S3, Appendix S1) provides only very weak support for two genetic structures. The lack of genetic structure in Chile was further supported by the fact that raw model probabilities from the $K = 1$ STRUCTURE runs did not differ significantly from those for the $K = 3$ (i.e. the optimal K found in this non-native range) (Wilcoxon rank sum test; $W = 241.5$, $p = .260$). For all other non-native ranges, the probabilities of their optimal K were significantly higher than those for $K = 1$ (in all cases: $W = 400$, $p < .001$). Further, no evidence for IBD was found within any of the non-native ranges (Table S5, Appendix S1).

3.3 | Introduction histories

The DIYABC results showed that scenario 4 had the highest probability for Chile ($p = .403$; 95% CI = 0.391–0.414) and Madagascar ($p = .456$; 95% CI = 0.429–0.483), and scenario 3 for the United States ($p = .325$; 95% CI = 0.313–0.337). However, the low probability levels in both these cases, as well as the high similarity to probabilities of the other scenarios tested (Figure S6, Appendix S1), indicate a lack of power in these models. Consequently, all further discussion around the introduction history of *A. dealbata* in these ranges does not rely on DIYABC results (see Discussion section below).

For the remaining non-native ranges, the analyses resulted in higher support for likely introduction scenarios. First, non-native populations originating from an unknown source, rather than from the genetic lineages in the species' native range (scenario 3), was the most likely scenario for populations from Portugal ($p = .829$; 95% CI = 0.816–0.842) (Figure S6, Appendix S1). Second, non-native populations originating from multiple introductions from lineage NAT1 (i.e. predominantly Tasmanian populations) was the most supported scenario (scenario 5, Figure 2) for New Zealand ($p = .519$; 95% CI = 0.512–0.526) and La Réunion ($p = .370$; 95% CI = 0.354–0.387) (Figure S6, Appendix S1). Further, these two non-native ranges also had high probabilities for scenario 1 ($p = .456$, 95% CI = 0.449–0.4630 and $p = .3486$, 95% CI = 0.333–0.365, respectively) (Figure S6, Appendix S1). This scenario also implies and further strengthens the likelihood of a direct Tasmanian origin, but not involving multiple introductions (Figure 2). However, in contrast to La Réunion, confidence intervals for these two scenarios in New Zealand did not overlap which points to a higher likelihood for the multiple introduction scenario than for the single introduction scenario. The overlapping confidence intervals for La Réunion, on the other hand, do not allow a clear distinction between scenario 1 and 5. Confidence intervals of the most likely scenarios for all other non-native ranges did not overlap with any of the five alternative scenarios tested.

Based on the posterior distributions of parameters estimated under the corresponding most likely scenario, the mean time since (first) introduction to New Zealand, Portugal and La Réunion was 20.2, 21.3 and 23.4 generations ago, respectively (Table S2, Appendix S2). Introduction estimates for the non-native ranges were associated with short (i.e. 2.9 to 3.2 generations) and strong to moderate (mean effective founder population size: 105 to 782 individuals) bottleneck events (Table S2, Appendix S2). The majority of the bias values (i.e. RMedAD and MedRB) were estimated with high confidence implying model estimates are plausible (Table S2, Appendix S2).

Our likely introduction scenario for Portugal inferred from the DIYABC analysis was characterized by low Type I (0.03) and Type II (0) errors. The scenario with the highest probability for New Zealand and La Réunion (i.e. scenario 5) showed in both cases high Type I errors (Table S6, Appendix S1). In these two cases, the high Type I error was mainly due to the fact that scenario 1 was "mis-identified" as the scenario with the highest probability (i.e. for New Zealand in 69 out of 100 cases and for La Réunion in 76 out of 100 cases). For each non-native range, however, results of the adequacy tests via the model checking function in DIYABC showed no significant deviation between observed and simulated summary statistics for the corresponding most likely introduction scenario. This indicates that the posterior distributions of these scenarios are well corroborated by the observed data and they sufficiently explain the "real" observed data (Table S7, Appendix S1).

According to our STRUCTURE analyses that included only populations from La Réunion (i.e. identification of two genetic clusters), we also ran DIYABC models for each cluster separately. Although the quality of the parameter performance was not affected by these models, they produced no meaningful outcomes (i.e. nearly all posterior probabilities for the tested scenarios had similar and low values). We therefore considered only the DIYABC model for which the non-native populations were pooled.

4 | DISCUSSION

Our results show that the global history of *A. dealbata* introductions and invasions is complex and that the native sources of many invasive populations around the globe remain unknown, despite our comprehensive sampling in Australia.

While our ABC modelling approach did not clearly support a specific introduction scenario for Chile and Madagascar, our Bayesian

assignment analyses suggest that these populations exhibit patterns consistent with admixture between different sources following multiple introductions. Such a geographic reshuffling of genetic diversity is generally considered as being beneficial for maintaining high diversity levels and can contribute to a lack of clear genetic structure (Cristescu, 2015; Smith et al., 2020), as was evident in both ranges. Admixture between previously isolated populations can have an important influence on the invasion success of a species (Dlugosch et al., 2015). High genetic diversity can help the introduced species to overcome negative effects of genetic bottlenecks and to decrease its sensitivity to genetic drift (Lavergne & Molofsky, 2007). Genetic admixture can also create novel genotypes which may promote rapid adaptation to novel environmental conditions or is often characterized by increased performance (Lavergne & Molofsky, 2007). Such increased performance is also known as "heterosis" (i.e. hybrid vigour) which is the phenotypic superiority that is often evident for first generation hybrid genotypes compared to their parental genotypes (Ellstrand & Schierenbeck, 2000; Li et al., 2017). A recent study by Li et al. (2017) showed that heterosis effects due to admixture can persist beyond the first generation in invasive plants. We also detected instances of clonality in populations from both the native and non-native ranges of *A. dealbata*. Whether these clones represent individual trees or coppicing stems from the same individual remains unknown. However, since we sampled trees at least 5m apart, it is likely these represent different individuals.

Our ABC models showed that a direct origin, after multiple introductions, from only one of the two native lineages (i.e. Tasmania) seemed to be the most likely for *A. dealbata* populations in New Zealand and La Réunion. Populations in these two regions, however, show differences in genetic diversity and structure. New Zealand populations had similar genetic diversity levels to native and other non-native ranges and showed no clear genetic structure. We assume that high propagule pressure due to the multiple introductions helped to maintain high levels of genetic diversity in this range (Thompson et al., 2016). As discussed above, such a boost of genetic diversity can be beneficial for the invasion success of an introduced species by providing sufficient genetic variation to overcome founder effects and to cope with environmental conditions in the new range (Dlugosch et al., 2015; Lavergne & Molofsky, 2007). Moreover, although genetic structure had weak support in New Zealand, the STRUCTURE analysis indicated gene flow between putative genetic clusters (Figure S4, Appendix S1) which is likely to sustain the genetic diversity in this range. In contrast, populations from La Réunion have very low genetic diversity (even lower than South African populations; see Hirsch et al., 2019) and showed genetic structure. Such extremely low genetic diversity levels are likely due to very low propagule pressure (number and size of introduction events) and genetic drift (Thompson et al., 2016; Ward et al., 2008), a notion supported by our ABC model estimates which showed that La Réunion had the lowest estimated introduced population size of all non-native ranges we considered (i.e. 105 individuals; Table S2, Appendix S2). We cannot exclude the possibility that there might have been a single introduction event only (i.e. scenario 1 and 5 had similar posterior probabilities for La Réunion with overlapping confidence intervals). Moreover, low levels of gene flow between populations in La Réunion (i.e. high pairwise F_{ST} values) probably prevented the dilution of founder effects. Similarly, Hagenblad et al. (2015) found very low genetic diversity despite multiple introductions of *Impatiens glandulifera* to Europe. These authors argued that the invasion success of *I. glandulifera* seems to be largely attributable to high phenotypic plasticity. Such an explanation may also be appropriate for *A. dealbata* in La Réunion. Testing this hypothesis will require experiments to compare the growth performance under different biotic and/or abiotic conditions in common gardens (e.g. Lamarque et al., 2013; Peperkorn et al., 2005).

The ABC analysis also showed that populations of *A. dealbata* in Portugal originated from an unknown "ghost" population. Although not sufficiently supported by our DIYABC models, multivariate ordination (PCoA) indicated that such unknown origin scenario is also likely for the majority of populations from the United States. This is similar to the results found by Hirsch et al. (2019) for the South African populations of *A. dealbata*. While this finding might suggest insufficient sampling of populations in the native range, we think that this is unlikely given our very comprehensive sampling in Australia (Hirsch et al., 2019). However, we cannot exclude the possibility that the "ghost" population might represent a native source population that has gone extinct at the time of our sampling. Including material from herbarium samples in future genetic studies would help to assess the likelihood of this being the case (Besnard et al., 2018). Another explanation for a "ghost" population could be that the unknown source represents an unsampled population from another non-native range that was not included in this study (e.g. Italy, France). Such a phenomenon is called a "bridgehead effect" in which a particular invasive population serves as source for introductions into other areas (Lombaert et al., 2010). The unknown population, however, might also represent a cultivated source as was shown for *A. saligna* in several parts of its non-native range (Thompson et al., 2012, 2015). Further studies on the global invasion history of *A. dealbata* should sample invasive populations from other parts of the world and should also include samples from herbarium specimens and commercially distributed seed lots.

Some of our results should be interpreted with caution. For instance, for La Réunion and the United States, the small number of populations (i.e. three in each case) may bias the outcomes of the genetic analyses and modelling. Future studies on the genetic characteristics of non-native populations from these ranges should include more populations to allow for more generalizable conclusions. An increased sampling might also help to achieve better supported models in the ABC approach for Chile, Madagascar and the United States, as this would not only increase the power of the overall dataset but would also allow to define additional potential introduction scenarios in more detail.

Another aspect shown by our results is that, specifically in the case of populations from La Réunion, discrepancies can occur between ABC approaches and more traditional genetic methods (i.e. STRUCTURE and PCoA). To elucidate, if only the traditional methods had been considered in drawing conclusions about the introduction history, the interpretation would most likely have been that these populations originated from an unknown source (Figure 4). The ABC

approach, however, predicted a Tasmanian origin for the populations in La Réunion. Similar inconsistencies between these different methodologies were observed by Mallez et al. (2018). As far as we know, the study by Mallez et al. (2018) is the only study before ours where such different outcomes were observed. Reasons for such discrepancies remain to be determined. However, as discussed by Mallez et al. (2018), a potential explanation could be that very low genetic diversity levels bias the reliability of traditional genetic approaches. In invasive populations, low genetic diversity is usually the result of strong genetic drift following founder events. In contrast to traditional methods, the ABC approach is able to take the stochasticity and therefore random consequences of genetic drift, into account; it is therefore a more reliable approach for drawing conclusions about introduction histories (Guillemaud et al., 2010; Mallez et al., 2018).

Our results have several implications for the management of invasive populations of *A. dealbata*. Although there are important benefits to be gained from transferring insights on, and lessons from, management strategies for invasive species between regions (Richardson et al., 2015; Wilson et al., 2011), the clear differences in the introduction histories for different parts of the non-native range must be considered. This applies especially for the evaluation of biological control agents which should ideally be highly co-evolved and locally adapted to achieve the best results (Müller-Schärer et al., 2004). In cases like New Zealand and La Réunion, where invasive populations originated directly from one of the native clusters (i.e. Tasmania), the search for co-evolved control agents could be restricted to these source areas. For the other investigated ranges where non-native populations originated from admixture or even from unknown source areas, the selection of biological control agents will be more challenging. Further, to improve management strategies in ranges for which our approach revealed a "ghost" population as source of introduction, further studies are needed to determine the identity of the unknown source(s). For example, if a "ghost" population resembles a bridgehead population from another non-native range, it would be important to focus management (i.e. vigilance) against the corresponding source populations (Lombaert et al., 2010). If the unknown source resembles cultivated populations, management should focus on preventing the further (commercial) distribution of seed material or other propagative material from such sources. In general, care needs also to be taken when applying niche-model approaches to predict the species potential ranges. Such approaches are likely to produce inaccurate outcomes when models do not consider detailed information on the origins of invasive populations (Thompson et al., 2012).

5 | CONCLUSION

Our study shows that globally invasive *A. dealbata* populations have complex and contrasting introduction histories which need to be taken in account for when planning management approaches. While our data comprised a comprehensive global sample set, intensified sampling is still required to unravel the introduction histories for some ranges in more detail. Consequently, it is also important to recognize that current programs aiming to import and breed new genetic material of *A. dealbata* should be halted until we can fully understand how that new genetic material could affect the invasiveness of the species.

We also showed that it is important to combine traditional genetic methodologies with newly developed approaches. They can be complementary, although in some cases traditional genetic tools can be misleading.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this article.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data used in this study are available from the authors upon request.

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BIOSKETCH

Our research focuses on the understanding of biological invasions and includes invasion genetics, investigating the drivers of invasions as well as the impacts of invasive species on biological diversity and ecosystems. With our research, we aim to assist policymakers and invasive species managers with options for rational decision making.

Author contributions: J.J.L.R., H.H. and D.M.R. designed the study. J.J.L.R., H.H. and A.P. collected samples part of the analysed data. H.H. did the molecular analysis and performed the statistical analyses. H.H. drafted the manuscript with substantial inputs from J.J.L.R, D.M.R and A.P.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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