Diversity and Distributions, (Diversity Distrib.) (2017) 23, 41–52

BIODIVERSITY RESEARCH

Genetic diversity and structure of the Australian flora

Linda Broadhurst[1]*, Martin Breed[2], Andrew Lowe[2], Jason Bragg[3], Renee Catullo[4], David Coates[5], Francisco Encinas-Viso[1], Nick Gellie[2], Elizabeth James[6], Siegfried Krauss[7,8], Brad Potts[9], Maurizio Rossetto[3], Mervyn Shepherd[10] and Margaret Byrne[5]

[1]*Centre for Australian National Biodiversity Research, CSIRO National Research Collections Australia, PO Box 1600, Canberra, ACT 2601, Australia,* [2]*Environment Institute, School of Biological Sciences, University of Adelaide, North Terrace, SA 5005, Australia,* [3]*National Herbarium of NSW, Royal Botanic Gardens & Domain Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia,* [4]*School of Science and Health, Western Sydney University, Sydney, NSW 2751, Australia,* [5]*Science and Conservation Division, Department of Parks and Wildlife, Locked Bag 104, Bentley Delivery Centre, Perth, WA 6983, Australia,* [6]*Royal Botanic Gardens Victoria, Private Bag 2000, Melbourne, Vic. 3141, Australia,* [7]*Science Directorate, Botanic Gardens and Parks Authority, Fraser Avenue, West Perth, WA 6005, Australia,* [8]*School of Plant Biology, The University of Western Australia, Crawley, WA 6907, Australia,* [9]*School of Biological Sciences, University of Tasmania, Hobart, Tas. 7001, Australia,* [10]*Southern Cross Plant Science, Southern Cross University, Lismore, NSW 2480, Australia*

*Correspondence: Linda Broadhurst, Centre for Australian National Biodiversity Research, CSIRO National Research Collections and Facilities, PO Box 1600 Canberra, ACT 2601, Australia.
E-mail: Linda.Broadhurst@csiro.au

ABSTRACT

Aim To investigate the relationships between species attributes and genetic parameters in Australian plant species and to determine the associations in relation to predictions from population theory and previous global analyses.

Location Continent of Australia.

Methods We assembled a dataset of all known population genetic analyses of Australian plants based on neutral markers and catalogued them according to key species attributes, including range, abundance, range disjunction, biome and growth form; and genetic parameters, mean number of alleles per locus, observed and expected heterozygosity and population differentiation. We determined relationships between species attributes and genetic parameters using a maximum-likelihood, multimodel inference approach.

Results We found many associations that were consistent with predictions. Species attributes with greatest effect on genetic diversity were range size, growth form, abundance and biome. The most important attributes influencing genetic differentiation were range disjunction and abundance. We found unexpected results in the effects of biome and growth form on genetic diversity, with greater diversity in the eastern biome of Australia, and lower diversity in shrubs compared to trees.

Main conclusions Our analysis of genetic diversity of Australian plants showed associations consistent with predictions based on population genetics theory, with strong effects of range size, abundance and growth form. We identified a striking effect of range disjunction on population genetic differentiation, an effect that has received little attention in the literature. We also found some notable differences to global predictions, which were most likely explained by confounding effects across variables. This highlights that caution is needed when extrapolating trends from global analyses to regional floras. Identifying associations between species attributes and patterns of genetic diversity enables broadscale predictions to facilitate the inclusion of genetic considerations into conservation decision-making.

Keywords

biome, conservation, disjunction, genetic differentiation, genetic diversity, life history.

INTRODUCTION

Levels of genetic diversity within and among populations have important consequences for the evolutionary trajectories of species and for the function and composition of ecological communities (Hughes *et al.*, 2008). Genetic diversity influences functional trait variation, recovery of populations following disturbance, species interactions, community structure and nutrient and energy fluxes (Whitham *et al.*, 2006; Hughes *et al.*, 2008; Bell & Gonzalez, 2009).

DOI: 10.1111/ddi.12505
http://wileyonlinelibrary.com/journal/ddi

Diversity and Distributions
A Journal of Conservation Biogeography

Consequently, understanding how genetic diversity is distributed in time and space is critical for managing biodiversity over broad spatial scales (e.g. responses to climate change) within biologically realistic time frames (i.e. decadal and longer) and helping to guide investments into on-ground actions (e.g. restoration). A major goal of multi-species meta-analyses in conservation biology is the identification of predictable biological patterns that can be used to guide the development of conservation and restoration frameworks. Identifying predictive associations between genetic diversity and explanatory variables that are easily measured is highly advantageous, given that the resources available for studying genetic diversity are finite.

Both adaptive and neutral evolutionary processes shape the distribution of genetic variation within species. While knowledge of the genetic variation underlying past adaptation and potentially available for future adaptation is an ideal for conservation and restoration biology, assessing this variation is both time-consuming and resource intensive (e.g. common garden or transplant studies). Such assessments often require large-scale and often long-term quantitative genetic studies, with the validation of associations between functional traits and fitness being challenging (Rockman, 2012). Consequently, for the majority of species of interest in conservation, we must continue to largely rely on putatively neutral genetic variation to link molecular variants with functional traits. In plants, neutral genetic variation is influenced by a range of life-history, geographic and demographic attributes, such as growth form, range size and abundance (Hamrick & Godt, 1996). Understanding associations between these species attributes and the level and structuring of neutral genetic diversity can help build generalizations to guide conservation and restoration decisions, especially for plant species where little or no information exists. These generalizations would be useful in several areas of conservation biology including: (1) informing the current debate in restoration genetics on the importance of genetic diversity in seed sources and the genetic connectivity of restored and remnant populations (Broadhurst *et al.*, 2008; Breed *et al.*, 2013); (2) providing guidance for the application of risk and management frameworks in conservation and restoration (Byrne *et al.*, 2011a; Ottewell *et al.*, 2016); (3) planning to meet the enormous global scale of restoration in the coming decades (Perring *et al.*, 2015; Suding *et al.*, 2015); (4) facilitating the inclusion of demographic processes (e.g. source–sink dynamics, refugia) into the next generation of species distribution models (Bellard *et al.*, 2012; Pauls *et al.*, 2013; Catullo *et al.*, 2015); (5) the incorporation of genetic factors into population viability modelling (Pierson *et al.*, 2015); (6) identifying groups of species to be prioritized for assisted management strategies (Rossetto *et al.*, 2015; Christmas *et al.*, 2016); and (7) developing guidelines for the management of small populations of threatened species (Frankham, 2015).

Developing broad principles to meet any or all of these objectives is complex and rests on the premise that generalized patterns of genetic diversity actually exist. Several studies have examined the partitioning of neutral genetic variation by species attributes to produce generalized findings that have been argued to be globally relevant (Hamrick *et al.*, 1979; Loveless & Hamrick, 1984; Hamrick & Godt, 1989, 1996; Gitzendanner & Soltis, 2000; Nybom & Bartish, 2000; Nybom, 2004; Duminil *et al.*, 2007). These studies have indicated that range size, growth form and mating system are some of the most important predictors of species' genetic diversity. Widespread species presumably maintain more diversity due to lower genetic drift in large, stable meta-populations than species with narrower distributions (Hamrick & Godt, 1989). Range size has also been found to be correlated with plant mating systems, with the distribution of self-pollinating species being up to two times larger than their outcrossed sister species (Grossenbacher *et al.*, 2015). Self-pollinating species are predicted to be better colonizers than those that outcross as reproductive assurance can facilitate geographic range expansion (Baker, 1955; Stebbins, 1957; Pannell, 2015). Plant form and generation time are predicted to influence genetic diversity because species with shorter generation times are expected to have smaller neighbourhoods, which promotes population isolation, whereas genetic diversity should decay more slowly in longer-lived species (Loveless & Hamrick, 1984), although annuals with large population sizes may not experience this effect. Age-related fecundity and overlapping generations also homogenize long-lived populations (Kuparinen *et al.*, 2010). Reproductive strategy may influence genetic diversity as inbreeding tends to homogenize genotypes and increase population differentiation, while outcrossing enforces pollen dispersal, increasing the likelihood that long-distance gene flow will reduce population divergence. Many plant species have a mixed mating system, although this may include a preference for outcrossed pollen [e.g. eucalypts (Griffin *et al.*, 1987; Byrne, 2008)], while low genotype diversity is often characteristic of clonal species (Millar *et al.*, 2010; Binks *et al.*, 2015). Short dispersal distances should promote differentiation, whereas regular, long-distance dispersal should promote population homogenization (Loveless & Hamrick, 1984).

The importance of identifying associations between species attributes and their genetic diversity is highlighted by the strong influence of population size, genetic variation and inbreeding on plant population fitness and future viability (Spielman *et al.*, 2004; Leimu *et al.*, 2006). While previous reviews (Hamrick *et al.*, 1979; Loveless & Hamrick, 1984; Hamrick & Godt, 1989, 1996; Gitzendanner & Soltis, 2000; Nybom & Bartish, 2000; Nybom, 2004; Duminil *et al.*, 2007) provide insights that could help guide conservation and restoration actions, their relevance in the Australian context has not been explored. These previous reviews focussed largely on northern temperate and Neotropical species, as relatively few Southern Hemisphere species were available for inclusion at the time. Distinct taxonomic and compositional differences in vegetation also exist between the Northern and Southern Hemispheres. Many of the genetic diversity

analyses to date for longer-lived species such as trees are focussed on boreal forests and montane coniferous forests that are common in the Northern Hemisphere, but less so in the Southern Hemisphere where other vegetation types and plant genera (e.g. *Eucalyptus*) dominate (Box, 2002). Consequently, it is unclear how well these previous findings reflect patterns in other regional floras such as Australia. The Australian continent is old, large (~7.74 M km^2, 2.99 M sq. miles), relatively flat, and has had a long and isolated history with few perturbations associated with volcanic activity or glaciation (Specht, 1981; Braithwaite, 1990). These characteristics have helped to drive the evolution of a phylogenetically diverse and rich flora with high levels of endemism that are distributed across 89 bioregions (419 subregions) including the south-western Australia global biodiversity hotspot (Myers *et al.*, 2000). Some 20,000 vascular plant species (*ca.* 7% of the world's flora; https://www.anbg.gov.au/aust-veg/australian-flora-statistics.html; B. Lepschi pers. comm.) occur in Australia with Myrtaceae, Proteaceae, Fabaceae, Mimosoideae and Asteraceae being the most dominant and species-rich plant families (Mast *et al.*, 2015).

As a large species-rich continent, supporting a broad range of biomes (e.g. alpine, temperate, tropical rain forest, arid and mediterranean-climate ecosystems), Australia provides an opportunity to evaluate the applicability of global predictions regarding genetic diversity and structuring. In this study, we compiled published and unpublished population genetic data for Australian plant species to examine associations between genetic diversity and species attributes. We were primarily interested in determining the influence of range size, growth form, abundance, biome and range disjunction on patterns of genetic diversity to assess how well the Australian data fit previous global predictions. Exploring the effects of mating system, pollination syndrome and seed dispersal were not possible in our dataset due to our study taxa primarily having small, gravity-dispersed seed and being insect-pollinated. We first made *a priori* predictions of the associations between species attributes and neutral genetic variation based on population genetic theory (Table 1). We then used a maximum-likelihood, multivariable approach that enabled comparisons of the relative importance of species attributes on neutral genetic variation for Australian plant taxa, while controlling for correlations among species attributes, to explore the following questions: (1) How do species attributes predict the level and structuring of population genetic diversity in Australian plants? and (2) How and why do these Australian patterns differ from previously published global patterns?

METHODS

Data gathering

An inventory of genetic data of Australian plant species was gathered from published and submitted papers as well as reports and unpublished datasets where we were confident of data integrity (Table S1 in Supporting Information). More than 300 microsatellite, allozyme, amplified fragment length polymorphism (AFLP) and restriction fragment length polymorphism (RFLP) studies were identified. Each was study evaluated as to how well it sampled the species distribution and whether there was sufficient sampling within and among populations (i.e. > 10 individuals per population sampled from across more than 70% of a species distribution). Nomenclature was clarified according to the Australian Plant Name Index (APNI, https://www.anbg.gov.au/apni/) to ensure that taxonomic boundaries were as current as possible. This recovered a total of 290 datasets from which the AFLP and RFLP studies were subsequently excluded due to insufficient representation (AFLP = 23, RFLP = 32) for

Table 1 Our predictions and observed trends of how species attributes influence levels and structuring of genetic diversity in the Australian flora. Observed trends matching expectations are italics, trends differing from expectations are in bold.

		H_E			F_{ST}/G_{ST}		
Plant attributes	Category	Prediction	Microsatellite obs.	Allozyme obs.	Prediction	Microsatellite obs.	Allozyme obs.
Abundance	Patchy	Low	*Low*	NS	High	*High*	NS
	Semi-continuous	High	*High*	NS	Low	*Low*	NS
Biome	West	No pred.	**Low**	NS	High	NS	NS
	Tropical	No pred.	**Low**	NS	Low	NS	NS
	East	No pred.	**High**	NS	Low	NS	NS
Disjunction	Yes	No pred.	NS	NS	High	*High*	*High*
	No	No pred.	NS	NS	Low	*Low*	*Low*
Form	Tree	High	*High*	NS	Low	NS	**High**
	Shrub	Mid	**Low**	NS	Mid	NS	**High**
	Herb	Low	*Low*	NS	High	NS	**Low**
Range	Widespread	High	*High*	NS	High	NS	NS
	Regional	Mid	*Mid*	NS	Mid	NS	NS
	Localized	Low	*Low*	NS	Low	NS	NS

NS, not significant.

meaningful analysis. There were few studies of polyploid species, and so, these were removed as the genetic values were not directly comparable with those of diploid species. Multiple studies of the same species were retained if different markers were used or if recognized subspecies or ecotypes were examined. A similar number of microsatellite (n = 118) and allozyme (n = 117) studies were retained for analysis across 235 taxa. The compiled dataset highlighted some pronounced imbalances in studies of Australian plants. For example, there was a significant bias towards eucalypts (25% of the studies) and the Myrtaceae more generally (35%) that subsequently influenced data associated with pollination syndromes and seed dispersal. In addition, studies from the western biome were dominated by rare and disjunct species reflecting the evolutionary drivers associated with this biodiversity hotspot (Hopper, 2009), and the largely conservation-orientated focus of researchers in this region.

We classified species according to several attributes using agreed data standards (Table 2). Species were classified according to the total size of their range area (Range); how populations were distributed within the species range (Abundance); the level of disjunction in the distribution of populations across the range (Disjunction); the predominant biome within which the species occurred (Biome); and growth form (Form), with the class 'Herb' referring to herbaceous perennials only as there were no data for annual species, as these are not common in the Australian flora due to its evolutionary history (Byrne *et al.*, 2008b, 2011b). We also characterized the mating system, pollination syndrome and seed dispersal mechanism of the species as these variables have been shown to significantly influence patterns of genetic diversity (Hamrick & Godt, 1996). However, we were unable to analyse the influence of these variables on genetic parameters due to the biased and non-balanced expression of traits exhibited in the species investigated, where the vast majority of species in the dataset were animal-pollinated with a mixed mating system. Most species were also characterized by gravity-dispersed seed, with other classes of seed dispersal having sample sizes too small for effective analysis.

For each species, we collected species-level genetic summary statistics from each study including the mean number of alleles per locus (A, n = 225), expected and observed heterozygosity (H_E, n = 219; H_O, n = 202) and population differentiation (G_{ST} and F_{ST}, n = 155), which were used as the response variables for our data analysis. We treated all microsatellite studies in one class, although genetic diversity levels in microsatellite studies based on species specific loci have been found to be higher than those on based on cross-species amplification (Primmer *et al.*, 1996; Barbará *et al.*, 2007). While F_{ST} describes the amount of genetic variation that can be explained by population structure and G_{ST} quantifies the genetic divergence among populations, there are similarities between the two measures (Hartl & Clark, 2007) and in practice G_{ST} is equal to F_{ST} (Nei, 1977). Consequently, we included both of these measures as estimates of differentiation, herein denoted as 'F_{ST}', as has been carried out elsewhere (Gitzendanner & Soltis, 2000).

Data analysis

To explore the redundancy and structure among the variables, we used principal component analysis (PCA) for the continuous genetic response variables and multiple correspondence analysis (MCA) for the categorical species attributes in the FACTOMINER package (Husson *et al.*, 2014) in R v.3.0.2 (R Core Team, 2015). We then used general linear models in a maximum-likelihood, multimodel inference framework in R to test for our hypothesized relationships between the predictor variables (i.e. species attributes; Range, Distribution, Abundance, Biome, Form) and the genetic

Table 2 Species attributes and genetic parameters assessed in this study.

Variables	Category	Classification	Description	Reference
Plant attributes	Range	Predictor	Widespread = > 600 km in one direction; regional = 150–600 km; localized = small, localized, < 100 km	Moran & Hopper (1987)
	Abundance	Predictor	Semi-continuous or patchy. Describes the pattern of population distribution within the species range	
	Disjunction	Predictor	Yes or No. Describes whether populations in species with semi-continuous distributions are very discrete and unlikely to be interacting, that is whether divergent lineages are likely to have evolved	
	Biome	Predictor	Eastern, western or tropical Australia	Olson *et al.* (2001)
	Form	Predictor	Tree, shrub, herb (perennial)	
Genetic parameters	Marker	Covariate	Microsatellite, allozyme	
	A	Response	Mean number of alleles	Hartl & Clark (2007)
	H_E	Response	Expected heterozygosity	Hartl & Clark (2007)
	F_{ST}	Response	Population differentiation	Wright (1951), Nei (1973)

response variables (A, H_O, H_E, F_{ST}). Firstly, we ran an exhaustive set of additive models for each response variable to determine which predictor variables were most important in explaining variation in the response variables. We estimated Akaike information criterion corrected for small sample sizes (AIC_c) and Akaike weights ($_wAIC$) for each model (Burnham & Andersen, 2002). To select predictor variables of greatest importance to each response variable, we derived the index of the relative importance of predictor variable i (AIC_i), the sum of Akaike weights for all models that included parameter i (Burnham & Anderson, 2002). A high AIC_i implies parameter i was more important in predicting variation in the response variable j than parameters with a lower AIC_i (i.e. a predictor variable with AIC_i approaching 1 suggests that this parameter has great importance).

We conducted nested ANOVAs to explore the phylogenetic signal in each genetic response variable using the LME4 package (Bates *et al.*, 2014) in R. Taxonomic levels (order, family, genus) were nested random effects within higher levels. Unlike previous studies (e.g. Duminil *et al.*, 2007), we detected only a weak phylogenetic signal in the genetic response variables [Table 3; sum of phylogenetic effects in our case was ≤ 40%, whereas it was > 75% in Duminil *et al.* (2007)]. Indeed, when genetic marker type was included in these models, marker type explained much more variance than the sum of taxonomic levels in all analyses (Table 3). The higher allelic diversity detected with microsatellites compared to allozymes is likely to strongly influence diversity parameters, but would not be as strong an effect on values of differentiation, although Hedrick (1999) has shown that differentiation will be underestimated in loci, such as microsatellites, with very high H_E values. To maintain statistical power and to avoid overparameterization of models predicting genetic variables, we chose to include genetic marker type as a covariate in all models to avoid any confounding effects.

In all linear models, we used Box–Cox transformations (Box & Cox, 1964) of the response variables to meet the assumption of normality of residuals, testing the normality of residuals of models with Shapiro–Wilk tests (Shapiro & Wilk, 1965).

RESULTS

As in previous studies (e.g. Barrett *et al.*, 2005), we found great redundancy in the three genetic diversity response variables (A, H_O and H_E; Fig. 1a) and therefore chose to explore variation in expected heterozygosity (H_E) only as it had the weakest phylogenetic signal (Table 3). Life-history predictor variables had more complex structure. The first two dimensions of a PCA explained 35% of the variation among these variables (Fig. 1b), and therefore, all were included in subsequent analyses.

We found differences for population genetic diversity (H_E) in microsatellite-based studies with Abundance (semi-continuous versus patchy: mean H_E = 0.73 vs. 0.58; Table 4; AIC_i = 0.98; Tables 6 and 7), Form (tree versus shrub versus herb: mean H_E = 0.69 vs. 0.60 vs. 0.63; Table 4; AIC_i = 0.86; Tables 6 and 7), Range (widespread versus regional versus localized: mean H_E = 0.70 vs. 0.64 vs. 0.59; Table 4; AIC_i = 0.91; Tables 6 and 7) and Biome (east versus west versus tropical: mean H_E = 0.72 vs. 0.60 vs. 0.60; Table 4; AIC_i = 0.99; Tables 6 and 7). Despite a similar number of allozyme studies, no trends were detectable for this marker type. Disjunction also had no detectable effect on genetic diversity for either marker class. Differences in genetic diversity were observed among the three Australian biomes for microsatellite studies, with greater H_E in the eastern biome than either the western or tropical biomes.

Comparisons of our genetic diversity (H_E) data to estimates derived from global analysis revealed that for most categories, allozyme-derived values were generally higher or similar for Australian species. The exception to this finding

Table 3 Variance explained by taxonomic levels and genetic marker on the genetic response variables.

Taxonomic level	A (%)	H_E (%)	F_{ST} (%)
Marker	78.95	88.25	14.56
Order	2.26	1.43	35.33
Family nested in order	0.00	0.00	0.00
Genus nested in family	6.39	2.32	0.00

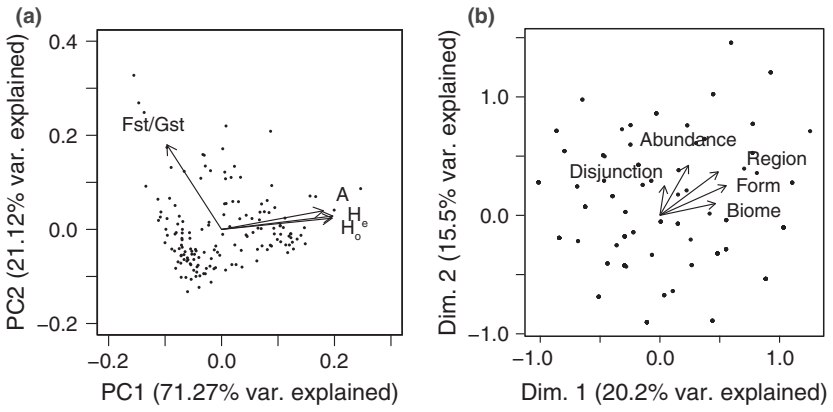

Figure 1 Variation explained in the datasets by the response variables. (a) Principal components analysis of genetic response variables from 155 Australian plant studies and (b) multiple correspondence analysis of life-history predictor variables from 254 Australian plant studies. Species with missing data were excluded from both analyses. Arrows represent the eigenvectors of the different variables included in the analyses.

Table 4 Summary of species-level mean gene diversity (H_E) from our study and from comparable studies based on global analysis of species.SE, standard error; *n*, sample size. Means of categories of the most important variables for predicting response are italics (see Tables 6 and 7 for details of this process). Footnotes indicate the most relevant category reported in previous reviews.

	This study				Hamrick & Godt (1989)		Hamrick *et al.* (1992)		Nybom (2004)	
	Allozymes		Microsatellite		Allozymes		Allozymes		Microsatellite	
Variable	*n*	H_E (SE)	*n*	H_E (SE)	*n*	H_E (SE)	*n*	H_E (SE)	*n*	H_E
Range size										
Widespread	37	0.20 (0.01)	48	*0.70 (0.02)*	105	0.16 (0.01)*	11	0.26 (0.04)*	31	0.62*
Regional	31	0.18 (0.01)	39	*0.64 (0.03)*	193	0.12 (0.01)†	115	0.17 (0.01)†	41	0.65†
Localized	49	0.21 (0.01)	31	*0.59 (0.02)*	101	0.14 (0.01)‡	45	0.17 (0.01)‡	16	0.56‡
Form										
Tree	41	0.17 (0.01)	63	*0.69 (0.03)*	110	0.18 (0.01)§	191	0.18 (0.01)§	59	0.68§
Shrub	48	0.20 (0.01)	47	*0.60 (0.02)*						
Herb	28	0.22 (0.02)	8	*0.63 (0.02)*	152	0.12 (0.01)¶	185	0.13 (0.01)¶		
Abundance										
Patchy	64	0.20 (0.01)	65	*0.58 (0.02)*						
Semi-continuous	53	0.19 (0.01)	53	*0.73 (0.02)*						
Biome										
East	47	0.22 (0.01)	45	*0.72 (0.02)*	348	0.15 (0.01)**	122	0.17 (0.01)**		
Tropical	7	0.13 (0.04)	20	*0.60 (0.04)*	76	0.15 (0.02)††	38	0.19 (0.02)††		
West	62	0.19 (0.01)	53	*0.60 (0.02)*	348	0.15 (0.01)**	122	0.17 (0.01)**		
Disjunction										
Yes	29	0.17 (0.02)	34	0.66 (0.03)						
No	88	0.21 (0.01)	84	0.65 (0.02)						

*'Widespread' (Hamrick & Godt, 1989; Nybom, 2004), 'widespread' woody plants only (Hamrick *et al.*, 1992).
†'Regional' (Hamrick & Godt, 1989; Nybom, 2004), 'regional' woody plants only (Hamrick *et al.*, 1992).
‡'Narrow' (Hamrick & Godt, 1989; Nybom, 2004), 'narrow' woody plants only (Hamrick *et al.*, 1992).
§'Long-lived perennial Woody' (Hamrick & Godt, 1989; Hamrick *et al.*, 1992), long-lived perennial (Nybom, 2004).
¶'Short-lived perennial Herbaceous' (Hamrick & Godt, 1989; Hamrick *et al.*, 1992), 'short-lived perennial' (Nybom, 2004).
**'Temperate' (Hamrick & Godt, 1989), 'temperate' woody plants only (Hamrick *et al.*, 1992).
††'Tropical' (Hamrick & Godt, 1989), 'tropical' woody plants only (Hamrick *et al.*, 1992).

was for widespread Australian species where the estimate was lower than that for widespread woody taxa in the global analyses, and for tropical Australian species that had lower estimates than global tropical species (Table 4). Comparisons of the data derived from microsatellites indicate that H_E was generally similar between Australian and global estimates with the exception of widespread Australian taxa where H_E was higher (0.70) than global estimates (0.62; Table 4).

Our analysis showed that population differentiation was strongly influenced by Abundance (semi-continuous versus patchy: microsatellite mean F_{ST} = 0.09 vs. 0.16; Table 5; allozyme mean F_{ST} not significant; AIC_i = 0.98; Tables 6 and 7), Disjunction (disjunction versus no disjunction: microsatellite mean F_{ST} = 0.15 vs. 0.12; Table 5; allozyme mean F_{ST} = 0.21 vs. 0.14; Table 5; AIC_i = 0.85; Tables 6 and 7) and Form (tree versus shrub versus herb: microsatellite mean F_{ST} not significant; allozyme mean F_{ST} = 0.18 vs. 0.17 vs. 0.11; Table 5; AIC_i = 0.83; Tables 6 and 7). Range and Biome were not strongly associated with population differentiation for either marker type. We note that mean differentiation values are generally lower in microsatellite studies than in allozyme studies (Table 5), consistent with the effect of high heterozygosity on differentiation values (Hedrick, 1999).

Comparisons of genetic differentiation in Australian allozyme data with global estimates indicate that widespread, regional and localized Australian species were less differentiated than expected based on global predictions (Table 5). However, comparison between Australian trees and long-lived woody perennials from the global analysis showed Australian trees had greater genetic differentiation. In contrast, Australian herbs were less differentiated than global estimates. Taxa in both eastern and western Australian biomes exhibited weaker differentiation than expected based on global estimates from temperate plants. Tropical Australian species had greater genetic differentiation than the global estimates (although this effect has been noted for other tropical flora (Newton *et al.*, 1999; Dick *et al.*, 2008) and may be influenced by the small sample size in this category along with the patchy contemporary and historical distribution of many tropical species studied in the Wet Tropics.

DISCUSSION

This analysis of the association of genetic diversity and differentiation with key species attributes for the Australia flora presents a novel evaluation of this biologically diverse

Table 5 Summary of species-level mean gene diversity (F_{ST} and G_{ST}) from our study and that from comparable studies based on global analysis of species. Means of categories of the most important variables for predicting response are italicized (see Tables 6 model selection and 7 predictor importance below). Footnotes indicate the most analogous category reported in the other reviews.

	This study				Hamrick & Godt (1989)		Hamrick *et al.* (1992)		Gitzendanner & Soltis (2000)		Nybom (2004)	
	Allozymes		Microsatellites		Allozymes		Allozymes		Allozymes		Microsatellites	
Variable	*n*	F_{ST}/G_{ST} (SE)	*n*	F_{ST} (SE)	*n*	G_{ST} (SE)	*n*	G_{ST} (SE)	*n*	F_{ST}/G_{ST} (SE)	*n*	F_{ST}
Range size												
Widespread	18	0.16 (0.01)	32	0.13 (0.01)	87	0.21 (0.03)*	9	0.03 (0.01)*	22	0.22 (0.03)*	13	0.25*
Regional	25	0.18 (0.02)	25	0.12 (0.01)	186	0.22 (0.02)†	127	0.07 (0.01)†			9	0.28†
Localized	31	0.14 (0.02)	24	0.14 (0.01)	82	0.24 (0.02)‡	40	0.12 (0.02)‡	22	0.21 (0.04)‡	6	0.23‡
Form												
Tree	27	*0.18 (0.02)*	49	0.13 (0.01)	131	0.08 (0.01)§	195	0.08 (0.01)§			17	0.19§
Shrub	29	*0.17 (0.02)*	24	0.14 (0.01)								
Herb	18	*0.11 (0.01)*	8	0.11 (0.02)	119	0.23 (0.02)¶	164	0.13 (0.01)¶				
Abundance												
Semi-continuous	23	0.14 (0.01)	35	*0.09 (0.01)*								
Patchy	51	0.16 (0.02)	46	*0.16 (0.01)*								
Biome												
East	19	0.16 (0.02)	33	0.11 (0.01)	322	0.25 (0.02)**	125	0.09 (0.01f				
Tropical	4	0.27 (0.02)	19	0.14 (0.02)	15	0.17 (0.02)††	3	0.12 (0.03)††				
West	51	0.15 (0.01)	29	0.14 (0.01)	322	0.25 (0.02)**	125	0.09 (0.01)**				
Disjunction												
Yes	21	*0.21 (0.03)*	24	*0.15 (0.02)*								
No	53	*0.14 (0.01)*	57	*0.12 (0.01)*								

SE, standard errors; *n*, sample size.

*'Widespread' (Hamrick & Godt, 1989; Gitzendanner & Soltis, 2000; Nybom, 2004), 'widespread' woody plants only (Hamrick *et al.*, 1992).

†'Regional' (Hamrick & Godt, 1989; Nybom, 2004), 'regional' woody plants only (Hamrick *et al.*, 1992).

‡'Narrow' (Hamrick & Godt, 1989; Nybom, 2004), 'narrow' woody plants only (Hamrick *et al.*, 1992), 'rare' (Gitzendanner & Soltis, 2000).

§'Long-lived perennial Woody' (Hamrick & Godt, 1989; Hamrick *et al.*, 1992), long-lived perennial (Nybom, 2004).

¶'Short-lived perennial Herbaceous' (Hamrick & Godt, 1989; Hamrick *et al.*, 1992), 'short-lived perennial' (Nybom, 2004).

**'Temperate' (Hamrick & Godt, 1989), 'temperate' woody plants only (Hamrick *et al.*, 1992).

††'Tropical' (Hamrick & Godt, 1989), 'tropical' woody plants only (Hamrick *et al.*, 1992).

continent. Many of the observed associations were consistent with accepted paradigms based on population genetic theory and previous meta-analyses of northern temperate and Neotropical floras, providing a robust basis for the predictions of influence of the species attributes assessed on genetic parameters. However, we also report a few notable exceptions: plant growth form appears to reflect the confounding influence of different variables, and there was a significant effect of range disjunction that has been poorly studied (Hamrick, 2004). Marker type influenced our ability to detect differences in genetic diversity and differentiation, most likely reflecting the lower number of alleles, and thus lower resolving power, of allozymes compared to microsatellites (Sunnucks, 2000). We also observed considerable redundancy in different genetic diversity metrics as has been previously reported (Barrett *et al.*, 2005).

Genetic diversity

Our expectations for genetic diversity with respect to plant range, growth form and abundance were mostly confirmed from microsatellite studies of Australian plants, but we observed weaker trends for data derived from allozymes. We found that wide ranging and more abundant species had greater genetic diversity, which is consistent with the theoretical and previously observed global trends in these groups of species (Hamrick & Godt, 1989; Hamrick *et al.*, 1992; Nybom & Bartish, 2000). Both wider ranging and more abundant species should be buffered against genetic diversity loss due to random genetic drift as a result of larger effective population sizes (i.e. the number of reproductive individuals in a population). An unexpected trend in this study was that Australian shrubs assessed using microsatellites had lower genetic diversity than either trees or herbs. This was particularly surprising as many shrub species share attributes with trees (e.g. longevity; long-distance gene flow), but this result may be partly due to the confounding effect of Distribution, because 43% of the shrubs assessed here had localized distributions compared with only 15% for trees. As shrubs are not well studied globally, additional genetic studies on shrub species would help to develop a more comprehensive picture of global patterns for this life form. Species with small, localized ranges are more

Table 6 General linear models of species attributes predicting population genetic response variables (H_E, expected heterozygosity; F_{ST}/G_{ST}, population differentiation). % DE, per cent deviance explained by the model; ΔAIC_c, indicator of difference between model Akaike information criterion corrected for small samples sizes (AIC_c) and the minimum AIC_c in the model set; ${}_wAIC$, weight that show the relative likelihood of model *j*; *k*, the number of parameters; only models with a ΔAIC_c less than the null model (~ 1) or with ΔAIC_c < 4 are shown.

Model	% DE	ΔAIC_c	${}_wAIC$	*k*
Expected heterozygosity (H_E)				
H_E ~ Marker + Abundance + Form + Biome	81.06	0.00	0.46	7
H_E ~ Marker + Abundance + Disjunction + Form + Biome	81.08	1.94	0.17	8
H_E ~ Marker + Abundance + Form + Range + Biome	81.24	2.19	0.15	9
Population differentiation (F_{ST})				
F_{ST} ~ Marker + Abundance + Disjunction + Form	16.10	0.00	0.45	6
F_{ST} ~ Marker + Abundance + Disjunction + Form + Biome	17.16	2.50	0.13	8
F_{ST} ~ Marker + Abundance + Disjunction + Form + Range	16.87	3.04	0.10	8
F_{ST} ~ Marker + Abundance + Form	13.01	3.40	0.08	5

Table 7 The relative importance of each species attributes in predicting population genetic response variables (H_E, expected heterozygosity; F_{ST}/G_{ST}, population differentiation). The index of the relative importance of predictor variable *i* (AIC_i) is the sum of Akaike weights (${}_wAIC$) over all models that include predictor *i*. This importance weight gives evidence for how strong the support is for each predictor variable, regardless of whether the predictor is in the best-fitting model or not (see Burnham & Andersen, 2002 pp. 167–169), with the most important variables italics in both cases.

Response variable	Predictor variable	AIC_i
H_E	*Abundance*	0.98
	Biome	0.99
	Disjunction	0.27
	Form	0.86
	Range	0.91
F_{ST}	*Abundance*	0.98
	Biome	0.19
	Disjunction	0.85
	Form	0.83
	Range	0.18

likely to be influenced by the effects of genetic drift reducing genetic diversity and may explain our results.

Our observation of differences in the three Australian biomes, with greatest diversity in the eastern biome than in the western or tropical biome, was also unexpected. The differences in H_E may be explained by a combination of confounding effects of other life-history attributes and historical biogeographic factors of the three regions. The studies conducted in the eastern biome had a greater proportion of trees (62%) compared to those in the west (30%), as well as a greater proportion of species with widespread distribution (east 45% vs. west 26%); both of these attributes were also correlated with greater genetic diversity. Historical biogeographic factors may also have influenced our result as the impacts of increasing aridification and climate cycles over two million years during the Pleistocene led to expansion of the arid zone and contraction of tropical and mesic environments to the edges of the continent; this effect was more pronounced in the western mesic and northern tropical regions than in the eastern mesic region (Byrne *et al.*, 2008b). In addition, the eastern mesic region has a longer latitudinal gradient with more diverse topography and greater elevation range, which would allow species to either move south, or move higher in altitude, in response to Pleistocene climatic oscillations. Both these historical biogeographic factors are likely to have reduced the intensity of bottlenecks in the eastern biome compared to the western and tropical biomes.

Population genetic differentiation

Our expectations for the effect of range disjunctions and species abundance on population differentiation were confirmed. Species with distributions that include range disjunctions where gene flow is expected to be limited showed a higher level of differentiation than species with non-disjunct distributions. The effect of range disjunction on population differentiation was consistent for both allozyme and microsatellite data, indicating that this strong effect is readily detected. While some of these species may have disjunct ranges due to recent widespread habitat fragmentation in southern Australia (Bradshaw, 2012; Guerin *et al.*, 2016), it is more likely that the high levels of divergence reflect genetic processes associated with historical ecogeographic barriers to gene flow over significant time frames (Byrne *et al.*, 2008b, 2011b). Abundance was also found to influence population differentiation as predicted, due to increased mean differentiation in patchily distributed species, although this was only observed for microsatellite studies.

We were surprised to observe deviations from our expectations for genetic differentiation (measured with allozymes), and plant growth form as the greater genetic differentiation in Australian trees compared to herbs was the opposite of the trends observed in global analyses. The low genetic differentiation observed for Australian herbs (0.11) was more similar to that observed for long-lived perennial woody plants (0.08) reported in earlier global reviews than for

herbaceous species (0.23; Hamrick & Godt, 1989). This is surprising because 93% of herbs included in our study were classified as insect-pollinated, which is a pollination syndrome that should increase the strength of population differentiation due to limited capacity for gene flow compared with pollination by large animals or wind (Rossetto *et al.*, 2007, 2009). This unexpected result may also be due to the dominance of terrestrial orchids in our dataset (28% of studies) as these species have readily dispersed dust-like seed (Jersáková & Malinová, 2007) whose widespread dispersal should reduce population differentiation compared to many other herbaceous species. Other herbaceous species in our dataset are likely to be primarily outcrossing as few Australian herbs are obligate selfers [e.g. *Drosera* (Stace *et al.*, 1997); *Ranunculus* (Pickering, 1997); *Stylidium* (Coates, 1982)]. Therefore, these Australian herbs are unlikely to show the high genetic differentiation typical of selfing species that have been observed in other floras (Hamrick & Godt, 1989). Observations of weak genetic differentiation in Australian herbs suggest that these species may have broader geographic scales of pollen and seed dispersal than has been observed elsewhere. Alternatively, our findings may reflect the contraction of these species from larger and more continuous populations in the more recent past. This may be a productive area of further research because we may be underestimating the pollen dispersal capacity of insects in Australian systems as high dispersal has been observed in some studies on trees and shrubs (e.g. Byrne *et al.*, 2008a; Millar *et al.*, 2011, 2014).

Our results also showed high levels of genetic differentiation for allozyme studies of Australian trees (0.18), which were on average double the estimates for trees in global studies (0.08; Hamrick & Godt, 1996). This result confirms previous observations comparing Australian trees to conifers and Northern Hemisphere wind-pollinated temperate/boreal angiosperms (Moran & Hopper, 1987; Moran, 1992). This may be due to the high prevalence of animal and particularly insect pollination in Australian trees compared to the dominance of wind pollination in temperate/boreal Northern Hemisphere trees. We did note one extreme outlier in the tree dataset, the highly localized *Eucalyptus caesia* G_{ST} = 0.60, that may have a strong effect on our mean value for trees. However, even when this outlier was removed, the level of differentiation was still high (mean for trees with *E. caesia* = 0.18; mean for trees without *E. caesia* = 0.16). Moran & Hopper (1987) noted the same trend when just widespread Australian trees are compared with Northern Hemisphere trees and suggest that in addition to pollination syndrome, this difference could also be due to a more patchy distribution of widespread Australian trees due to their greater edaphic specialization.

CONCLUSIONS

We show that aggregating population genetic data across many studies can provide important insights into the associations between species attributes, using an extremely broad and diverse sample of the Australian flora, and the level and structuring of population genetic diversity in these species. The plant attributes that had the greatest influence on genetic diversity across this sample of the Australian flora were range size, growth form, species abundance and biome. The best predictors of population genetic differentiation were range disjunctions and abundance. Most of these findings were consistent with global observations, based largely on Northern Hemisphere or Neotropical floras, providing further evidence for the robustness of our understanding of genetic diversity and differentiation in plant species. However, we found some notable differences with global trends, which highlights that caution is needed when extrapolating trends from global analysis to regional floras. The unexpected lower levels of genetic diversity in Australian shrubs compared to trees and herbs appear to be a result of confounding effects of distribution that would need to be considered in general application of broad predictions. We also noted an unexpected difference in the levels of genetic diversity in eastern Australian species compared to those from western and tropical biomes that appears associated with effects of species distribution in these plants, and demonstrates the strength of the influences of variables despite different environments. For genetic differentiation, we identified a notable impact of range disjunction. This relationship has rarely been evaluated in previous studies of this kind, and our analysis suggests range disjunction merits more attention as a possible driver of differentiation in global studies.

Our study has identified general associations between the attributes of Australian plant species and the level and structuring of genetic diversity, affirming the observations of previous studies of different regions. This is important because these associations provide simple and cost-effective surrogates for predicting population genetic diversity and differentiation, although not necessarily adaptive variation, where this information is not readily available. Such predictions assist in the inclusion of a genetic component into decision-making approaches and will assist in the development of rapid and cost-effective frameworks for the conservation and management of the Australian flora.

ACKNOWLEDGEMENTS

We thank the Australian plant population genetics research community. This research was supported by the joint resources of CSIRO and the Western Australian Department of Parks and Wildlife. We thank Andrew Young, Andy Shepherd and Craig James for their support of this project.

REFERENCES

Baker, H. (1955) Self-compatibility and establishment after "long-distance" dispersal. *Evolution*, **9**, 347–348.

Barbará, T., Palma-Silva, C., Paggi, G.M., Bered, F., Fay, M. & Lexer, C. (2007) Cross-species transfer of nuclear microsatellite markers: potential and limitations. *Molecular Ecology*, **16**, 3759–3767.

Barrett, M., Krauss, S. & Dixon, K. (2005) *Preliminary assessment of genetic variation and differentiation in* Darwinia masonii *– stage 1*. Report # 29 from the Genetics Laboratory, BGPA Science, Report commissioned by Mt Gibson Iron Ltd. Botanic Gardens and Parks Authority, Perth Australia.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7. Available at: http://CRAN.R-project.org/package=lme4.

Bell, G. & Gonzalez, A. (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters*, **12**, 942–948.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Binks, R.M., Millar, M.A. & Byrne, M. (2015) Contrasting patterns of clonality and fine-scale genetic structure in two rare sedges with differing geographic distributions. *Heredity*, **115**, 235–242.

Box, E. (2002) Vegetation analogs and differences in the Northern and Southern Hemispheres: a global comparison. *Plant Ecology*, **163**, 139–154.

Box, G.E.P. & Cox, D.R. (1964) An analysis of transformations. *Journal of the Royal Statistical Society. Series B (Methodological)*, **26**, 211–252.

Bradshaw, C.J.A. (2012) Little left to lose: deforestation and forest degradation in Australia since European colonization. *Journal of Plant Ecology*, **5**, 109–120.

Braithwaite, R.W. (1990) Australia's unique biota: implications for ecological processes. *Journal of Biogeography*, **17**, 347–354.

Breed, M.F., Stead, M.G., Ottewell, K.M., Gardner, M.G. & Lowe, A.J. (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, **14**, 1–10.

Broadhurst, L., Lowe, A., Coates, D., Cunningham, S., McDonald, M., Vesk, P. & Yates, C. (2008) Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications*, **1**, 587–597.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*, 2nd edn. Springer, New York, NY.

Byrne, M. (2008) Eucalypt phylogeny, diversity and evolution. *Plant genome: biodiversity and evolution. 1E: phanerogam – angiosperm* (ed. by A.K. Sharma and A. Sharma), pp. 303–346. Science Publishers, Enfield, NH.

Byrne, M., Elliott, C.P., Yates, C.J. & Coates, D.J. (2008a) Maintenance of high pollen dispersal in *Eucalyptus wandoo*, a dominant tree of the fragmented agricultural region in Western Australia. *Conservation Genetics*, **9**, 97–105.

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. & Wyrwoll, K.H. (2008b) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, **17**, 4398–4417.

Byrne, M., Stone, L. & Millar, M.A. (2011a) Assessing genetic risk in revegetation. *Journal of Applied Ecology*, **48**, 1365–1373.

Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P. & Weston, P. (2011b) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography*, **38**, 1635–1656.

Catullo, R.A., Ferrier, S. & Hoffmann, A.A. (2015) Extending spatial modelling of climate change responses beyond the realized niche: estimating, and accommodating, physiological limits and adaptive evolution. *Global Ecology and Biogeography*, **24**, 1192–1202.

Christmas, M., Breed, M. & Lowe, A.J. (2016) Constraints to and conservation implications for climate change adaptation in plants. *Conservation Genetics Resources*, **17**, 305–320.

Coates, D. (1982) Chromosome variation and species relationships in the scale-leaved triggerplants (*Stylidium* section *Squamosae*). *Australian Journal of Botany*, **30**, 121–130.

Dick, C., Hardy, O., Jones, F. & Petit, R. (2008) Spatial scales of pollen and seed-mediated gene flow in tropical rain forest trees. *Tropical Plant Biology*, **1**, 20–33.

Duminil, J., Fineschi, S., Hampe, A., Jordano, P., Salvini, D., Vendramin, G.G. & Petit, R.J. (2007) Can population genetic structure be predicted from life-history traits? *The American Naturalist*, **169**, 662–672.

Frankham, R. (2015) Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. *Molecular Ecology*, **24**, 2610–2618.

Gitzendanner, M.A. & Soltis, P.S. (2000) Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany*, **87**, 783–792.

Griffin, A., Moran, G. & Fripp, Y. (1987) Preferential outcrossing in *Eucalyptus regnans* F. Muell. *Australian Journal of Botany*, **35**, 465–475.

Grossenbacher, D., Runquist, R., Goldberg, E. & Brandvain, Y. (2015) Geographic range size is predicted by plant mating system. *Ecology Letters*, **18**, 706–713.

Guerin, G.R., Biffin, E., Baruch, Z. & Lowe, A.J. (2016) Identifying centres of plant biodiversity in South Australia. *PLoS One*, **11**, e0144779.

Hamrick, J.L. (2004) Response of forest trees to global environmental changes. *Forest Ecology and Management*, **197**, 323–335.

Hamrick, J.L. & Godt, M.J.W. (1989) Allozyme diversity in plant species. *Plant population genetics, breeding, and genetic resources* (ed. by A.H.D. Brown, M.T. Clegg, A.L. Kahler and B.S. Weir), pp. 43–63. Sinauer Associates Inc., Sunderland, MA.

Hamrick, J.L. & Godt, M.J.W. (1996) Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351**, 1291–1298.

Hamrick, J.L., Linhart, Y.B. & Mitton, J.B. (1979) Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Annual Review of Ecology and Systematics*, **10**, 173–200.

Hamrick, J.L., Godt, M.J.W. & Sherman-Broyles, S.L. (1992) Factors influencing levels of genetic diversity in woody plant species. *New Forests*, **6**, 95–124.

Hartl, D. & Clark, A. (2007) *Principles of population genetics*, 4th edn. Sinauer Associates, Sunderland, MA.

Hedrick, P.W. (1999) Perspective: highly variable loci and their interpretation in evolution and conservation. *Evolution*, **53**, 313–318.

Hopper, S. (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil*, **322**, 49–86.

Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008) Ecological consequences of genetic diversity. *Ecology Letters*, **11**, 609–623.

Husson, F., Josse, J., Le, S. & Mazet, J. (2014) *FactoMineR: multivariate exploratory data analysis and data mining with R*. package version 1.28. Available at: http://CRAN.R-project.org/package=FactoMineR

Jersáková, J. & Malinová, T. (2007) Spatial aspects of seed dispersal and seedling recruitment in orchids. *New Phytologist*, **176**, 237–241.

Kuparinen, A., Savolainen, O. & Schurr, F.M. (2010) Increased mortality can promote evolutionary adaptation of forest trees to climate change. *Forest Ecology and Management*, **259**, 1003–1008.

Leimu, R., Mutikainen, P., Koricheva, J. & Fischer, M. (2006) How general are positive relationships between plant population size, fitness and genetic variation. *Journal of Ecology*, **94**, 942–952.

Loveless, M.D. & Hamrick, J.L. (1984) Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics*, **15**, 65–95.

Mast, A., Olde, P., Makinson, R., Jones, E., Kubes, A., Miller, E. & Weston, P.H. (2015) Paraphyly changes understanding of timing and tempo of diversification in subtribe Hakeinae (Proteaceae), a giant Australian plant radiation. *American Journal of Botany*, **102**, 1634–1646.

Millar, M.A., Byrne, M. & Coates, D.J. (2010) The maintenance of disparate levels of clonality, genetic diversity and genetic differentiation in disjunct subspecies of the rare *Banksia ionthocarpa*. *Molecular Ecology*, **19**, 4217–4227.

Millar, M.A., Byrne, M. & O'Sullivan, W.O. (2011) Defining entities in the *Acacia saligna* (Fabaceae) species complex using a population genetics approach. *Australian Journal of Botany*, **59**, 137–148.

Millar, M.A., Coates, D.J. & Byrne, M. (2014) Extensive long-distance pollen dispersal and highly outcrossed mating in historically small and disjunct populations of *Acacia woodmaniorum* (Fabaceae), a rare banded iron formation endemic. *Annals of Botany*, **114**, 961–971.

Moran, G.F. (1992) Patterns of diversity in Australian trees species. *New Forests*, **6**, 49–66.

Moran, G.F. & Hopper, S.D. (1987) Conservation of the genetic resources of rare and widespread eucalypts in remnant vegetation. *Nature conservation: the role of native vegetation* (ed. by D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins), pp. 151–162. Surry Beatty & Sons, Perth, WA.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Dafonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nei, M. (1973) Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences USA*, **70**, 3321–3323.

Nei, M. (1977) F-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics*, **41**, 225–233.

Newton, A.C., Allnutt, T., Gillies, A.C.M., Lowe, A.J. & Ennos, R.A. (1999) Molecular phylogeography, intraspecific variation and the conservation of tree species. *Trends in Ecology and Evolution*, **14**, 140–145.

Nybom, H. (2004) Comparison of different nuclear DNA markers for estimating intraspecific genetic diversity in plants. *Molecular Ecology*, **13**, 1143–1155.

Nybom, H. & Bartish, I.V. (2000) Effects of life history traits and sampling strategies on genetic diversity estimates obtained with RAPD markers in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 93–114.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, **51**, 933–938.

Ottewell, K.M., Bickerton, D.C., Byrne, M. & Lowe, A.J. (2016) Bridging the gap: a genetic assessment framework for population-level threatened plant conservation prioritization and decision-making. *Diversity and Distributions*, **22**, 174–188.

Pannell, J. (2015) Evolution of the mating system in colonizing plants. *Molecular Ecology*, **24**, 2018–2037.

Pauls, S., Nowak, C., Balint, M. & Pfenninger, M. (2013) The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology*, **22**, 925–946.

Perring, M., Standish, R., Price, J., Craig, M., Erickson, T., Ruthrof, K., Whiteley, A., Valentine, L. & Hobbs, R. (2015) Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere*, **6**, 1–25.

Pickering, C.M. (1997) Breeding systems of Australian *Ranunculus* in the alpine region. *Nordic Journal of Botany*, **17**, 613–620.

Pierson, J.C., Beissinger, S.R., Bragg, J.G., Coates, D.J., Oostermeijer, J.G.B., Sunnucks, P., Schumaker, N.H., Trotter, M.V. & Young, A.G. (2015) Incorporating evolutionary processes into population viability models. *Conservation Biology*, **29**, 755–764.

Primmer, C.R., Moller, A.P. & Ellegren, H. (1996) A wide-range survey of cross-species microsatellite amplification in birds. *Molecular Ecology*, **5**, 365–378.

R Core Team (2015) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. "https://www.R-project.org/.

Rockman, M.V. (2012) The QTN program and the alleles that matter for evolution: all that's gold does not glitter. *Evolution and Development*, **66**, 1–17.

Rossetto, M., Crayn, D., Ford, A., Ridgeway, P. & Rymer, P. (2007) The comparative study of range-wide genetic structure across related, co-distributed rainforest trees reveals contrasting evolutionary histories. *Australian Journal of Botany*, **55**, 416–424.

Rossetto, M., Crayn, D., Ford, A., Mellick, R. & Sommerville, K. (2009) The influence of environment and life-history traits on the distribution of genes and individuals: a comparative study of 11 rainforest trees. *Molecular Ecology*, **18**, 1422–1438.

Rossetto, M., Yap, J.-Y.S., Kooyman, R. & Laffan, S. (2015) From ratites to rats: the size of fleshy fruits shapes species distributions and continental rainforest assembly. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151998.

Shapiro, S.S. & Wilk, M.B. (1965) An analysis of variance test for normality (complete samples). *Biometrika*, **52**, 591–611.

Specht, R.L. (1981) Major vegetation formations in Australia. *Ecological biogeography of Australia* (ed. by A. Keast), pp. 163–229. Junk, The Hague.

Spielman, D., Brook, B.W. & Frankham, R. (2004) Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences USA*, **101**, 15261–15264.

Stace, H.M., Chen, L. & James, S.H. (1997) Self-incompatibility, seed abortion and clonality in the breeding systems of several Western Australian *Drosera* species (Droseraceae). *Australian Journal of Botany*, **45**, 191–201.

Stebbins, G.L. (1957) Self fertilization and population variability in the higher plants. *The American Naturalist*, **91**, 337–354.

Suding, K., Higgs, E., Palmer, M., Callicott, J., Anderson, C., Baker, M., Gutrich, J., Hondula, K., LaFevir, M., Larson, B., Randall, A., Ruhl, J. & Schwartz, K. (2015) Committing to ecological restoration. *Science*, **348**, 638–640.

Sunnucks, P. (2000) Efficient genetic markers for population biology. *Trends in Ecology and Evolution*, **15**, 199–203.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., Lonsdorf, E.V., Allan, G.J., DiFazio, S.P., Potts, B.M., Fischer, D.G., Gehring, C.A., Lindroth, R.L., Marks, J.C., Hart, S.C., Wimp, G.M. & Wooley, S.C. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.

Wright, S. (1951) The genetic structure of populations. *Annals of Eugenics*, **15**, 313–345.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Australian plant taxa and associated references.

BIOSKETCH

The authors have an interest in genetic analysis for conservation and restoration. LB and MBy conceived the study, obtained funding and led the data interpretation and writing, MBr undertook the data analysis, and all authors identified data and contributed to writing.

Editor: Chris Burridge