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Standing genomic variation within coding and regulatory regions contributes to the adaptive capacity to climate in a foundation tree species

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Abstract

Global climate is rapidly changing, and the ability for tree species to adapt is dependent on standing genomic variation; however, the distribution and abundance of functional and adaptive variants are poorly understood in natural systems. We test key hypotheses regarding the genetics of adaptive variation in a foundation tree: genomic variation is associated with climate, and genomic variation is more likely to be associated with temperature than precipitation or aridity. To test these hypotheses, we used 9,593 independent, genomic single-nucleotide polymorphisms (SNPs) from 270 individuals sampled from *Corymbia calophylla*'s entire distribution in south-western Western Australia, spanning orthogonal temperature and precipitation gradients. Environmental association analyses returned 537 unique SNPs putatively adaptive to climate. We identified SNPs associated with climatic variation (i.e., temperature [458], precipitation [75] and aridity [78]) across the landscape. Of these, 78 SNPs were nonsynonymous (NS), while 26 SNPs were found within gene regulatory regions. The NS and regulatory candidate SNPs associated with temperature explained more deviance (27.35%) than precipitation (5.93%) and aridity (4.77%), suggesting that temperature provides stronger adaptive signals than precipitation. Genes associated with adaptive variants include functions important in stress responses to temperature and precipitation. Patterns of allelic turnover of NS and regulatory SNPs show small patterns of change through climate space with the exception of an aldehyde dehydrogenase gene variant with 80% allelic turnover with temperature. Together, these findings provide evidence for the presence of adaptive variation to climate in a foundation species and provide critical information to guide adaptive management practices.

KEYWORDS

Eucalyptus sensu lato, genotype environment association, landscape genomics, local adaptation, standing genetic variation

1 | INTRODUCTION

Patterns of local adaptation are the result of natural selection to environmental pressures (Kawecki & Ebert, 2004), and exploration of the genomic basis of local adaptation can improve our understanding of the response of naturally occurring organisms to climate change (Savolainen, Lascoux, & Merilä, 2013). Given the predicted impacts of climate change on natural ecosystems and

primary production, there is much interest in determining the relationships between genomic variation and adaptation to climate (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008). If organisms are unable to respond to new climatic conditions, they must either track their ecological niche through migration or die from increased climate pressures (Aitken et al., 2008; Merilä & Hoffmann, 2016). However, a species' adaptive potential can be used to improve management strategies that aim to mitigate future impacts of climate change.

Standing genetic variation occurs throughout the genome; it is the variants occurring within (coding) or near (regulatory) genes that are known to be important for organisms to respond to environmental pressures (Futuyma, 2013). The majority of genomic variants are thought to be neutral, where they do not directly alter phenotype and are not subjected to selection pressure (but see Ehrenreich[, 2017] for discussion of linkage and epistatic interactions), while variants within coding regions may contribute to adaptive processes through changes in amino acid composition (Zou et al., 2017). In addition, changes within noncoding *cis*-regulatory elements have been found to be a major cause of phenotypic divergence between and within species (Wittkopp & Kalay, 2012). Identifying single-nucleotide polymorphisms (SNPs) in genic and regulatory regions that are associated with climate would provide a better understanding of the relationships between genotype and environment, and a species' capacity to respond to climate change.

Precipitation and temperature have been identified as being primary drivers of local adaptation and species distributions limits (Cahill et al., 2014), both of which are expected to change in the future. Intraspecific evolution sorts genomic variants to maximize fitness in climates differing in precipitation and temperature, leading to patterns of local adaptation (Kawecki & Ebert, 2004). Although local adaptation is not ubiquitous (Havens et al., 2015; Hereford, 2009; Leimu & Fischer, 2008), there is supporting evidence from ecological transplants (Leimu & Fischer, 2008), experimental manipulations (Simon et al., 2017), genetic surveys (Rellstab et al., 2016; Sork et al., 2016) and genomic studies (Lasky et al., 2014). Recently developed environmental association analytical methods (Ahrens et al., 2018; Hoban et al., 2016; Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015) can assist in identifying patterns of local adaptation, highlighting genetic variants associated with environmental factors. It is important to note that these associations between genetic variants and climate do not explicitly indicate the presence of local adaptation because fitness cannot be directly linked to climate (Sork, 2018). Rather, these associations provide initial evidence that individuals may be adapted to local climate. The availability of complete, annotated, genome sequences can then enhance our understanding of the genetics of local adaptation with functional gene annotation linked with SNPs that may result in amino acid changes (nonsynonymous [NS] SNPs) and/or changes within regulatory regions (Kryazhimskiy & Plotkin, 2008). Furthermore, identifying the distribution and abundance of adaptive variants provides insights into their rates of change with key climatic determinants and the capacity to respond to climate change.

The foundation tree, *Corymbia calophylla* (family Myrtaceae; *Eucalytpus* sensu lato), occurs across many forest and woodland ecosystem types in south-western Western Australia within the globally recognized biodiversity hotspot (Myers, 2003). This region is particularly vulnerable to climate change with predictions for hotter and drier conditions, along with more frequent and intense extremes (Matesanz & Valladares, 2014). This was evident during the 2010/2011 drought and heat wave conditions, which resulted in large scale forest collapse in the northern part of its range (Matusick, Ruthrof, Brouwers, Dell, & Hardy, 2013). Recent studies on *C. calophylla* have shown that the temperature-of-origin was a more important determinant than precipitation and aridity for growth characteristics, hydraulic traits and physiological performance (Ahrens et al., 2019; Aspinwall et al., 2017; Blackman, Aspinwall, Tissue, & Rymer, 2017). Specifically, photosynthesis and dark respiration elicit plastic and adaptive responses to different temperature conditions among provenances (Aspinwall et al., 2017). In addition, leaf hydraulic conductance shows regional patterns of adaptation to temperature, where cool-climate provenances have greater leaf hydraulic vulnerability (Blackman et al., 2017). Investigation of growth was found to be moderately heritable, such that slow-growth strategies evolved in provenances from warm regions and fast-growth strategies evolved in cooler regions (Ahrens et al., 2019). These traits are likely genetically determined and their differences are the product of adaptation to local climate. This local adaptation has developed in the presence of widespread gene flow, with low levels of genetic structure across the entire distribution (Sampson et al., 2018). This combination of attributes (i.e., large distribution, traits under selection and high levels of gene flow), along with the availability of fully annotated genome sequences in related species (*Eucalyptus grandis* Myburg et al., 2014; *Corymbia citriodora* A. Healey, M. Shepherd, A. Baten, K. W. Barry, J. Butler, J. S. Freeman, A. Furtado, D. Grattapaglia, G. J. King, D. Lee, J. Lovell, B. M. Potts, J. Schmutz, O. B. da Silva Junior, B. Simmons, R. Vaillancourt, & R. J. Henry, unpublished data), makes *C. calophylla* an ideal species to investigate the genomics of local adaptation and quantify adaptive genetic variation associated with climate.

We aimed to develop our understanding of the underlying genomic variation associated with along climatic gradients. We tested hypotheses developed from previous experiments documenting phenotypic adaptations (Blackman et al., 2017; Aspinwall et al., 2017; Ahrens et al., 2019): (a) genomic variation is associated with climate, and (b) genomic variation is more likely to be associated with temperature than precipitation or aridity. To support or refute these hypotheses, we employed a reduced-representation genomic sequencing approach to search for adaptive variation across the climatically heterogeneous distribution of *C. calophylla*. Genomic variants associated with climate were mapped to eucalypt genomes to identify their location and putative function.

2 | METHODS

2.1 | Sample collection and climatic data

Sampling locations were chosen based on existing occurrence records to cover the entire species geographic and climatic distribution (Figure 1). Importantly, sampled populations were independent (>50 km separation) and included replicated comparisons of the climate-of-origin across the geographic distribution. A stratified design such as this assists in the partitioning of neutral and adaptive genetic variation. A total of 270 mature trees from natural forests and woodlands were analysed with 10 individuals sequenced from 27 populations across a geographic area of 76,608 km^2 (Figure 1).

Climatic variables for analysis in this study were chosen based on previous work that linked environment to physiological trait differentiation (Aspinwall et al., 2017; Blackman et al., 2017). Thus, we used maximum temperature of the warmest month (T_{MAX}), mean annual precipitation (P_{MA}) and aridity index (AI) as our climatic predictors when searching for signatures of selection. Of all the temperature and precipitation variables (e.g., bioclim 1–19), T_{MAX} and P_{MA} were found to be the most correlated to physiology in another study (Ahrens et al., 2019), and AI was included due to its importance in adaptive studies on physiology of *C. calophylla* (Aspinwall et al., 2017; Blackman et al., 2017). T_{MAX} (Bio5) and P_{MA} (Bio12) climatic layers were downloaded from WORLDCLIM v2 (Fick & Hijmans, 2017). Aridity index was downloaded from the Consortium for Spatial Information (http://www.cgiar-csi.org/) and calculated as the ratio of annual precipitation and potential evapotranspiration (i.e., water availability over atmospheric water demand). All three climatic layers were downloaded at 30 arc-seconds resolution (*c.* 1 km per pixel) and consisted of data collected between 1970 and 2000, which represent climate exposure and selective pressures of the mature, sampled trees. Climate layers were displayed using Quantum GIS (QGIS Development Team) along with the coordinates of each population with climatic data then extracted for each population. Visualization of the climate variables is given in Supporting Information (Figure S1). These three climatic variables (T_{MAX}, P_{MA} and AI) are predicted to change under future scenarios (Bates, Hope, Ryan, Smith, & Charles, 2008; Field, Barros, Mach, & Mastrandrea, 2014; Centre for Australian Climate and Weather Research CSIRO). Across the 27 sampled populations, the range of T_{MAX} was 25.6–33.1°C (mean 29.2°C), the range of P_{MA} was 561–1,187 mm (mean 860.7 mm), and the range of AI was 0.4–1.0 (mean 0.7).

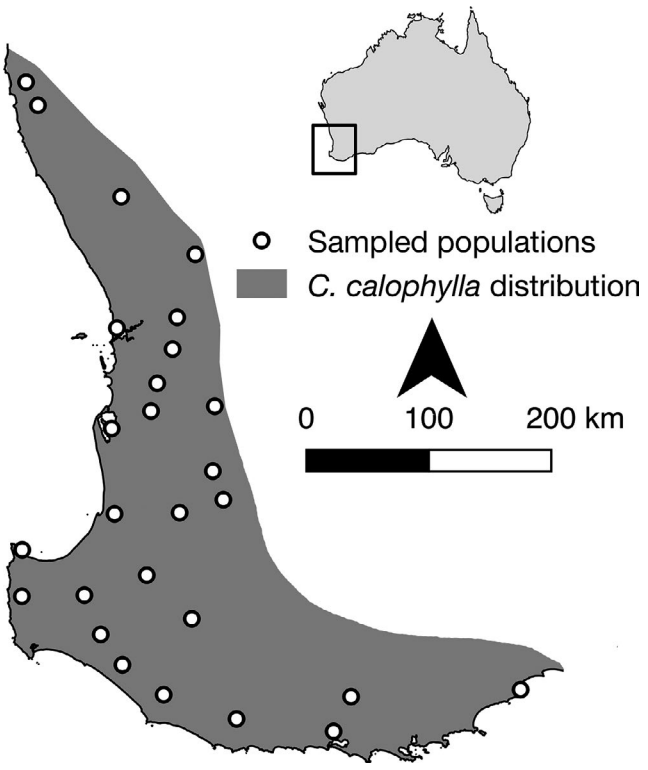

FIGURE 1 Sampling locations of *Corymbia calophylla* in south-western Australia. Distribution of *C. calophylla* is shown in grey

2.2 | SNP generation and bioinformatics

DNA extractions were performed on 20 mg of freeze dried leaf material using a modified CTAB protocol (Doyle & Doyle, 1990) with 1% sodium sulphite (Byrne, Macdonald, & Francki, 2001) and 1% w/v polyvinylpyrrolidone (MW 40,000) added to the extraction buffer. Quality and quantity of DNA extracts were estimated using gel electrophoresis and a Qubit fluorometer (Invitrogen). DNA samples (400 ng) were sequenced using DArTseq™ protocols (Diversity Arrays Technology Pty Ltd) that represent a combination of a double digest complexity reduction method and next generation sequencing platforms (Kilian et al., 2012). A detailed description of the DArTseq™ methodology can be found in Kilian et al. (2012) and Grewe et al. (2015). Briefly, reduction of the genome was performed using a combination of *Pst*I and *Hpa*II enzymes in digestion/ligation reactions principally as per Kilian et al. (2012) with adapters that include individual varying length barcodes, flowcell attachment sequence and sequencing primer, similar to Elshire et al. (2011). Raw fastq files were demultiplexed and aligned using Diversity Array Technology's proprietary bioinformatics pipeline. Poor quality sequences filtered out of the Fastq files with a Phred pass score of 30 (probability of incorrect base is 1 in 1,000). Minimum read depth for each individual was set to 6 and average read depth was 82.8 across all SNPs, ensuring call quality for all SNPs. Read lengths consisted of 75 bp and only nucleotide substitutions were considered a SNP for the SNP calling algorithm (proprietary DArTsoft14).

Further SNP filtering was performed in R (R Core Team, 2015) using custom script. SNPs were kept if they were called in at least 175 individuals (35% missing data); however, most of the SNPs (8,705 of 9,593, or 91%) met a 15% missing data threshold. A threshold of 35% missing data was chosen because on average there would still be data from a minimum of 6–7 individuals within a population to calculate population-level allele frequency sufficient for downstream environmental association analyses (EAA) analysis. However, we compared this data set with data sets developed with 20% and 10% missing data and found similar patterns (Table S1). Minor allele frequency was set to a minimum of 10 total calls (i.e., an allele frequency of 0.019) occurring in at least two populations. Only one random SNP per 75 bp read was retained.

All SNPs were mapped to the highly curated, chromosome-level *C. citriodora* var *variegata* genome (M. Shepherd, unpublished), recording chromosome number and location. Linkage disequilibrium was computed for each of the 11 chromosomes using the function *LD.Measures* in *LdcorSV* and visualized using the function *LDHeatmap* in the package of the same name in R. Visualization of LD across chromosomes also allowed for visualization of genomic sampling distribution within the 11 chromosomes. The LD r^2 value was used as the coefficient to ensure sufficient independence among SNPs, and linkage disequilibrium pruning was employed in R for an r^2 value >0.5 between two SNPs. If the r^2 value between two SNPs were >0.5, then only one of the two SNPs were randomly kept for analysis to avoid any inherent linkage bias.

2.3 | Analytics

2.3.1 | Population structure

In order to inform the EAA approaches, we explored demographic processes with our data set by estimating F_{ST} and ancestral genetic clustering methods. The HIERFSTAT package (Goudet, 2005) in R was used to estimate population-level *F*-statistics using Weir and Cockerham's method (Weir & Cockerham, 1984). The sparse nonnegative matrix factorization (SNMF) method within the R package LEA (Frichot & Francois, 2015) was run for each *k*-value between 1 and 10. Each *k*-value was run 10 times, and the 10 runs were combined for a consensus. The optimal *k*-value was chosen by comparing the cross-entropies as described in the SNMF manual (Frichot & Francois, 2014) and choosing the *k*-value(s) with the lowest cross-entropy score. The consensus of the optimum *k*-values was created in CLUMPP (Jakobsson & Rosenberg, 2007), and the graphical parameters were drawn in the program DISTRUCT (Rosenberg, 2004). We present the output for four different *k*-values to show the hierarchical relationship between several ancestral genetic clusters.

A redundancy analysis (RDA) was performed to understand the relationship between climate and genetic structure, by estimating the proportion of genetic variance in the entire data set that is explained by environmental factors. Here, we constrain the dependent variables (individuals) by the explanatory variables (climate). First, the missing data were imputed as the most common allele in the locus, because RDA requires a full data set with no missing data. The RDA analysis was performed using the *rda* function in the VEGAN package 2.5-1 in R (Oksanen, Blanchet, & Friendly, 2018). The *anova.cca* function was used to calculate overall significance of the RDA plot, and if this was found to be significant, then significance of each climate variable was calculated, and significance tests used 999 permutations.

2.3.2 | Environmental association analysis

In order to test the hypothesis that climate is associated with genomic variation, EAA were used to search for correlations between local allele frequencies and environmental variables. We used three programs to provide different comparative approaches and greater confidence in the candidate SNPs. We used BAYENV2, BAYPASS and LFMM for the following reasons: first, the methods use different ways to control for population structure; second, the methods provide different advantages for detecting types of SNPs (e.g., polygenic and small-effect alleles); and third, BAYPASS provides an improvement on BAYENV2's algorithm (details below), but we also use BAYENV2 to make direct comparisons to previous studies. Latent factor mixed models (LFMM; Frichot, Schoville, Bouchard, & Francois, 2013) use ancestral population groups to account for population structure and tests linear associations between climatic factors and allele frequencies. It is an efficient and powerful method for different demographic scenarios and sampling designs and is effective in identifying associations that are polygenic (Lotterhos & Whitlock, 2015; De Mita et al., 2013). We used LFMM v2.00 with individual genotypes (missing data were imputed as described in the LFMM manual), running 15,000 iterations for burn-in with a run of 30,000 iterations. We performed 100 runs and calculated median *z*-scores with the R script supplied by the LFMM developers. The optimal number of ancestral population groups (latent factors; K_{LFMM}) was calculated based on the SNMF and cross-entropy results described above, which follow the description in the SNMF and LFMM manual (Frichot & Francois, 2015). An FDR of 0.001 was applied to all runs due to correlation between the climate factors and population structure. Even though patterns of population structure were weak, there was still concern that current population structure might increase the call rate of false positives. BAYENV2 uses population-level allele frequencies to find associations between individual SNPs and climate, while controlling for population structure with a covariation matrix (an F_{ST} analog) (Günther & Coop, 2013). We first calculated a covariance matrix as instructed in the BAYENV2 documentation using 100,000 iterations across 9,593 SNPs. The covariation matrix was estimated between populations using allele frequencies for all SNPs to describe covariation across populations and was used in the environmental association analysis to avoid confounding population effects. Bayes factors were independently calculated for every combination between the three climatic variables and every SNP. The mean from five independent runs was calculated using the script supplied in the downloadable content. We calculated climate associations within three climatic variables using 100,000 iterations. Bayes factors were recorded for each SNP/environment combination; a Bayes factor quantifies the evidence for association and, in this case, provides a statistic for ranking SNPs by their allele frequency correlation with an environmental variable using a single run for each SNP and environmental variable of the MCMC algorithm under a null distribution (Coop, Witonsky, Rienzo, & Pritchard, 2010). Bayes factors were expressed in deciban units (dB) via the transformation $10\log_{10}(BF)$. Possible associations were considered significant if the BF was >10.0 on the dB unit scale, following the Jeffrey's rule that anything above 10 is "strong evidence," between 15 and 20 is "very strong evidence" and >20 is "decisive evidence" (Kass & Raftery, 1995). BAYPASS 2.1 was also used to identify climatic associations with all SNPs (Gautier, 2015a). The BAYPASS model is based on the BAYENV model with a reprogramming of the MCMC algorithm and also implements monitoring of the parameters

and priors of the original models, allowing for the introduction of parameters such as spatial dependency among consecutive markers (Gautier, 2015a). Similar to BAYENV2, a population covariance matrix was produced using the core model and a standard covariate model was used to identify associations between SNP and the three climate variables, producing an empirical Bayesian *p*-value (eBPis) for each SNP/climate combination. An association was deemed significant if the eBPis value is >3, as described in the instruction manual (Gautier, 2015b). For each of the three program outputs, ranks were assigned based on *p*-value (LFMM), BF (BAYENV2) and eBPis (BAYPASS) for all SNPs, providing three independent climate association ranks.

2.3.3 | Annotation

For annotation, candidate SNPs were annotated with the *E. grandis* genome (Myburg et al., 2014) using the blastn function in BLAST (https://blast.ncbi.nlm.nih.gov/) to identify potential variants accompanying coding genes. Sequences with an *E*-value of at most 1×10^{-8} and a score of at least 60.0 were considered. Chromosome location of candidate SNPs was recorded, noting the placement within and around coding genes (i.e., coding or regulatory regions). Codon and amino acid changes were recorded for the identification of NS SNPs. Regulatory regions were defined as being within 1,000 base pairs upstream of a gene to capture *cis*-regulatory elements (Riethoven, 2010; Vandepoele, Quimbaya, Casneuf, Veylder, & Peer, 2009), but all SNPs in regulatory regions were within 200 base pairs of a gene.

2.3.4 | Landscape Genomics Modelling

General dissimilarity modelling (GDM) was used to compute allelic turnover and genetic dissimilarity between sites as a function of climatic differences and geographic distances between sites (Fitzpatrick & Keller, 2015). First, a reference population pairwise F_{ST} matrix was created with all SNPs using the HIERFSTAT package in R (Goudet, 2005). Second, a population-level environmental data set was created that included population names, latitude and longitude, and the three climate variables. Then, F_{ST} matrices were created separately for each of the putatively adaptive SNPs that were identified as NS or in the regulatory region. A GDM analysis, using the GDM package v 1.3.7 in R (Manion et al., 2018), was performed on an F_{ST} matrix for each candidate SNP and on the reference SNP set to estimate allelic turnover through climatic space. GDM analysis removes variation that is associated with geographic distance and the remaining genetic variation is compared to climate, thus the *y*-axes on the spline plots are labelled partial genetic distance. Spline plots show relative importance of climate with respect to allelic turnover, and data points for the spline plots were estimated for the whole climate range (i.e., each spline plot has 200 data points). The significance of climate variables on the dependent variable (in this case a SNP) is calculated by the difference between two models, with and without the climate variable, and is termed deviance (Ferrier, Manion, Elith, & Richardson, 2007) and is analogous to percentage of variation explained. To test the hypothesis that temperature is a more important variable compared to P_{MA} and AI, we used the *t.test* function in R to compare deviance means among the three climate variables. For the most significant SNP associated with T_{MAX}, a PCA was performed on the GDM output and the eigenvectors of the PCA were indexed and predicted across the geographic range of the species. We used GGPLOT2 to display predicted allelic turnover on a map of south-western Western Australia (Wickham, 2009).

3 | RESULTS

3.1 | SNP variation

DArTseq technologies returned 36,385 SNPs that were refined down to 9,593 independent SNPs following the filtering steps described in the methods. The number of SNPs per chromosome ranged from 401 to 1,037 with a mean of 709 SNPs/chromosome. The r^2 for linkage disequilibrium among chromosome pairwise comparisons ranged from 0.005 and 0.006, and comparisons among individuals ranged from 0.23 to 0.37 with a mean of 0.29. The linkage disequilibrium heatmaps showed that the SNPs are represented across the genome with the largest gaps within chromosomes ranging from 371,434 to 1.95M bp (Figure S2), with the largest gap among all chromosomes in chromosome 5.

3.2 | Population structure

Low levels of genetic differentiation were estimated across the species distribution (F_{ST} = 0.055 ± 0.001 95% CI). The system was predominantly outcrossing, with a mean inbreeding coefficient of 0.22 (range 0.18–0.25; Table S2). Genetic clustering of populations revealed extensive patterns of admixture, particularly evident in the slow change between genetic clusters for all *k*-values (SNMF; Figure S3). The cross-entropy scores intimated that the optimal number of clusters (*k*-value) was 6 (Figure S4). The SNMF output showed five genetic clusters that can be described geographically with two gene pools evident in the northern populations, two in the central populations and one in the southern populations with clinal admixture among populations, and the sixth genetic cluster was evident in two individuals in one population (Figure S3).

The RDA analysis revealed that a significant amount of genetic variation is associated with the three climate variables (65.4%, $F = 3.42$, $p = 0.001$) (Figure 2). Each of the two axes explained a significant amount of variation (Axis 1: $F = 6.58$, $p = 0.001$; Axis 2: $F = 2.06$, $p = 0.001$), and the three climate variables were significant (T_{MAX}: $F = 6.50$, $p = 0.001$; P_{MA}: $F = 1.78$, $p = 0.001$; AI: $F = 1.97$, $p = 0.001$). This output reflected the geography of sampled individuals, with the northern populations located in the top right corner of the plot and the southern populations located in the left side of the plot (Figure 2).

3.3 | Environmental association analysis

In total, 537 unique SNPs were found to be significantly associated with at least one climate across all three EAA approaches (Table S3). There were differences in the number of SNP associations identified among the three EAA approaches (Figure 3). There were fewer SNPs shared among

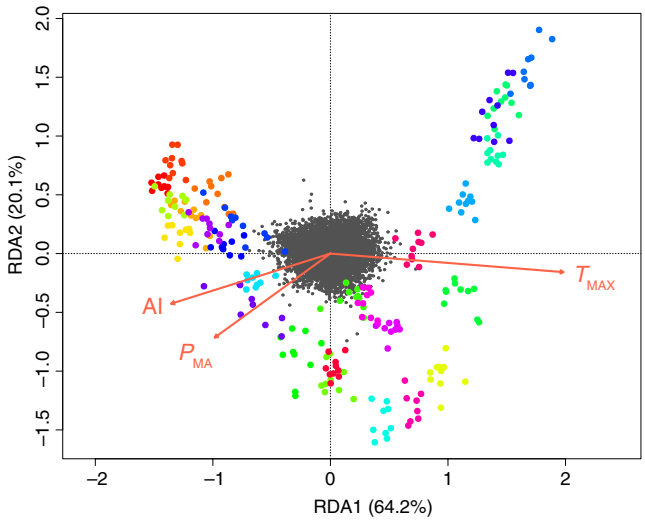

FIGURE 2 Redundancy analysis showing the relationship between the independent climate parameters with population structure. Individuals are coloured points and colours represent populations. Small black points are SNPs. The percentage of explained variance for each axis is provided. T_{MAX} = maximum temperature of the warmest month; P_{MA} = mean annual precipitation; AI = aridity index

LFMM and BAYENV2, and LFMM and BAYPASS than between BAYENV2 and BAYPASS. Statistical linkage disequilibrium was consistently low among candidate SNPs within climate association groups for P_{MA} (r^2 = 0.007 ± 0.0002 *SE*), AI (r^2 = 0.007 ± 0.0002) and T_{MAX} (r^2 = 0.01 ± 0.00007).

3.4 | Annotation

The annotations for all candidate SNPs are provided in the Supporting Information (Table S3, tabs 1–3), along with program rank, change in population allele frequency, chromosome number, gene, codons and translated amino acids. All 11 chromosomes were represented within the significant associations for each of the three climatic variables, with no clear clustering patterns when mapped to the *C. citriodora* genome (Figure 4). In addition, 122 significant associations were on unspecified scaffolds and are not shown in Figure 4.

Many of the candidate SNPs were linked with functionally annotated genes. Of the 458 SNPs associated with T_{MAX}, 173 SNPs mapped to within or near genes, including 18 within regulatory regions and 155 in coding regions, of those, 53 were NS (Table S3). For example, SNP j8105 was NS and located on an aldehyde dehydrogenase (ALDH) gene (Table 1), SNP j2510 was a NS SNP found on a CBL gene (Table 1), and SNP j4967 was found in the regulatory region and was located 25 bp from a gene in the ABC transporter gene family (Table S3). For P_{MA}, 31 of the 75 SNPs mapped to within or near genes in the reference genome. Four P_{MA} SNPs were found within regulatory regions and 27 were found within coding regions, and of those, 11 were NS. For annotations, the SNP j5880, for example, was found in the regulatory region adjacent to the ninja-family protein AFP3 gene and SNP j3344 is a NS SNP located on a chromatin remodelling gene (Table 1). For AI, 38 of the 78 SNPs mapped to gene regions. Four AI SNPs were found within regulatory regions and 34 were found within coding regions, and of those, 14 were NS (Table S3). For annotations of SNPs associated with AI, for example, SNP j6444 was NS and located in the leucine-rich repeat receptor-like serine/threonine-protein kinase gene (Table 1), SNP j6054, a synonymous SNP, was located on a dynamin-related protein 4C (Table S3), and j1424, a NS SNP, was located on a gene linked to a carbohydrate-binding module family (Table 1).

3.5 | Landscape modelling

The SNPs identified as either NS (78) or within regulatory regions (26) were used in the GDM analysis to quantify allelic turnover

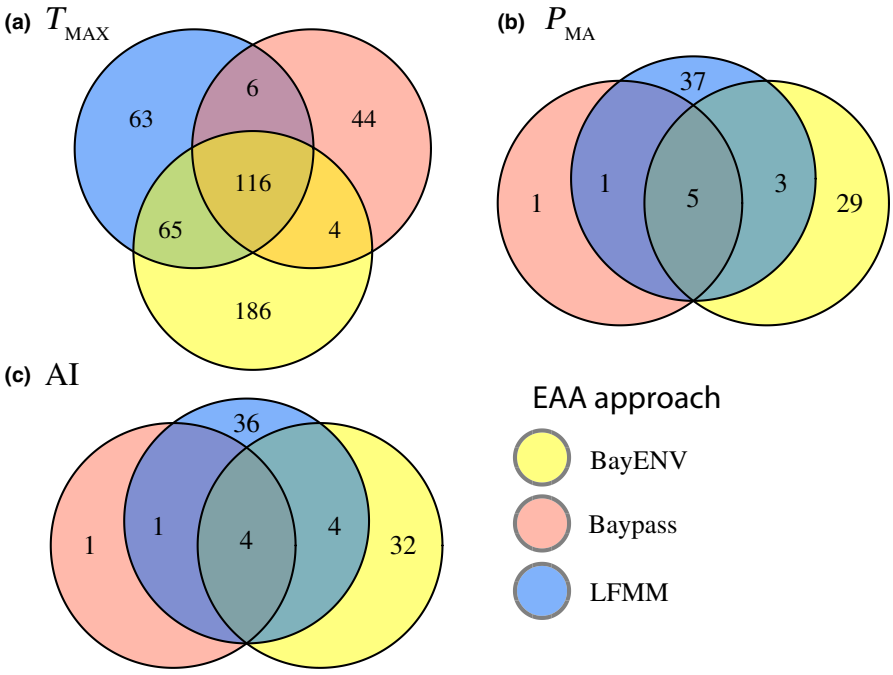

FIGURE 3 Venn diagrams showing the intersections between approaches of environmental association analyses. Candidate SNPs associated with maximum temperature of the warmest month (a; T_{MAX}), mean annual precipitation (b; P_{MA}) and aridity index (c; AI) [Colour figure can be viewed at wileyonlinelibrary.com]

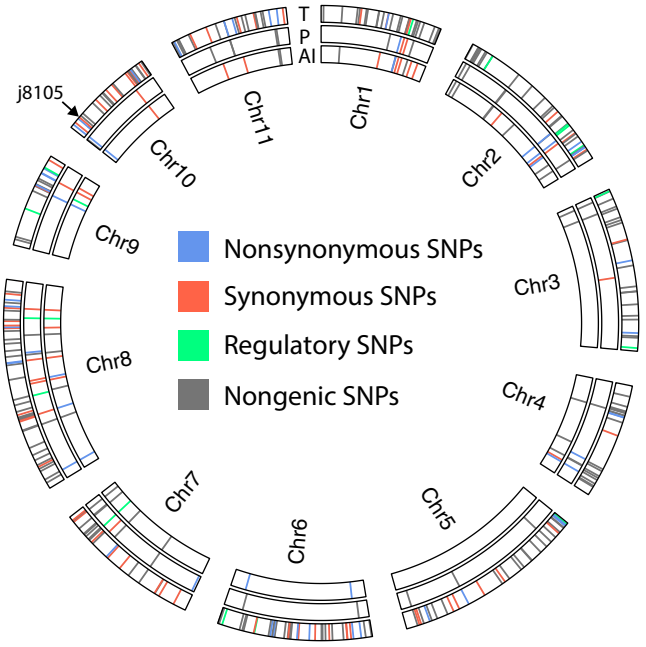

FIGURE 4 Distribution of candidate SNPs throughout the genome. SNP j8105 explains the most deviance in general dissimilarity model analysis. The outer ring shows the SNPs associated with maximum temperature of the warmest month (*T*), the second-ring shows the SNPs associated with mean annual precipitation (*P*), and the third ring shows the SNPs associated with aridity index (AI). Colour indicates whether the SNP is synonymous, nonsynonymous, regulatory or nongenic

through climatic space (Figure 5). The majority of SNPs associated with the three climatic variables showed small-to-moderate response (i.e., deviance explained) to climate in terms of allelic turnover distributed along the climatic gradients. On average, the SNPs associated with T_{MAX} explained more deviance (27.35%) compared with P_{MA} (5.93%) and AI (4.77%), and the deviance for T_{MAX} was significantly greater than the other two variables ($p < 0.01$ for both tests). One SNP (j8105) in particular explained more deviance (53%) than all other NS and regulatory SNPs (Figure 5a). The allelic turnover for this SNP changed gradually throughout the range. Mapped in geographic space, the allelic turnover of j8105 occurred in the middle of the distribution in a north-south direction (Figure 6).

4 | DISCUSSION

4.1 | Adaptation to climate

Our study identified patterns between genotype and climate similar to those identified in other studies on eucalypts, where temperature was found to identify a greater number of adaptive variants (Dillon et al., 2014; Jordan, Dillon, & SK, Prober SM, 2017; Steane et al., 2017, 2014). These associations indicate that climate is shaping patterns of genetic variation, possibly creating locally adapted populations, supporting our first hypothesis. Specifically, these studies found significant associations with temperature variables and concluded that temperature is potentially an important driver of adaptation. Collectively, these studies highlight implications for future evolution and ecosystem management as widespread eucalypts are foundation species in forest and woodland ecosystems. Low differentiation is common among widespread *Eucalyptus* species due to high levels of gene flow and connectivity (Byrne, 2008; Dillon et al., 2015; Jordan, Dillon, Prober, & Hoffmann, 2016; Mora, Arriagada, Ballesta, & Ruiz, 2017; Steane et al., 2014; 2017). Similarly, analysis here shows low levels of population structure in *C. calophylla*, as illustrated by the high admixture among putative genetic clusters and low estimate of population differentiation that was similar to previous estimates using nuclear microsatellite markers ($F_{ST} = 0.033$; Sampson et al., 2018). The low level of population structure facilitates analytical approaches to detect the genetic signatures of local adaptation.

The rapid change in the south-western Australian Mediterranean-type climate may create a mismatch between genotype and climate. Patterns of plasticity and adaptation in *C. calophylla* significantly associated with climate have been revealed experimentally for hydraulic, photosynthetic and dark respiratory traits, providing physiological tolerance to temperature and water availability (Aspinwall et al., 2017; Blackman et al., 2017). In this study, multiple candidate SNPs within coding and regulatory regions were identified, and therefore, we surmise that mutations in both regions are important to support the adaptive process to climate. While SNPs within coding regions can result in phenotypic differences, SNPs in regulatory regions, particularly in *cis*-regulatory elements, may also result in phenotypic divergence (Wittkopp & Kalay, 2012) that may be more efficient in driving phenotypic evolution for two reasons. First, expression patterns of genes (controlled through the regulatory network) are a process that can be adjusted and "fine-tuned" to meet context-dependent functional demands (a continuous variable), whereas protein structure is more static (discrete states with few forms). Second, SNPs within regulatory regions are mostly codominant, in contrast to mostly recessive alleles in coding regions. Changes to phenotype are immediate when mutations are codominant; otherwise, in coding regions, drift would be the primary force to increase allele frequencies for the change to become phenotypically evident (Wray, 2007).

Current patterns of adaptation to climate are likely driven by many alleles of small-effect for complex traits, particularly in forest trees (Savolainen et al., 2013). Identification of many genes that putatively control responses to climatic stress is indicative of a quantitative genetic system where numerous SNPs additively affect the response to climate (Falconer & Mackay, 1996; Lynch & Walsh, 1998; Mackay, Stone, & Ayroles, 2009). While we cannot differentiate between large- and small-effect alleles, we assume that most of, if not all, the SNPs identified as significant associations are alleles of small-effect based on past studies and reviews (Savolainen et al., 2013). Indeed, climate explains a small portion of allelic turnover for all but one genomic variant detected, and allelic turnover among adaptive variants occurs at different climate points, indicating that climate

TABLE 1 Gene annotation showing the top five results for nonsynonymous SNPs within coding regions and SNPs within regulatory regions within each of the three environmental variables (T_{MAX} = maximum temperature of the warmest month; P_{MA} = mean annual temperature; AI = aridity index)

Climate	Region	SNP	BAYENV	BAYPASS	LFMM	Fold-change	chr	BLAST *e*-val	Blast score	Gene annotation from the *Eucalyptus grandis* genome	Ref-codon	AA-ref	SNP codon	AA-SNP
T_{MAX}	Coding	j8105	1	1	1	1.00	10	6.11E-19	93.3	Aldehyde dehydrogenase family 3 member F1	TAT	Tyrosine	TTT	Phenylalanine
	Coding	j2510	170	112	52	0.93	11	4.70E-14	77	CBL-interacting serine/threonine-protein kinase 21-like	TCA	Serine	TAC	Tyrosine
	Coding	j4251	33	8	22	0.75	11	1.44E-20	98.7	LOB domain-containing protein 1	GAG	Glutamic Acid	AAG	Lysine
	Coding	j8842	155	377	68	0.72	4	7.44E-18	89.7	UPF0481 protein At3g47200	CAG	Glutamine	CGG	Arginine
	Coding	j9366	106	45	70	0.75	11	6.11E-19	93.3	UDP-glycosyltransferase 74G1	GAG	Glutamic Acid	GGG	Glycine
	Regulatory	j9442	3	2	2	0.94	u	1.10E-15	82.4	Kinesin-like protein KIN-4C				
	Regulatory	j8693	157	100	137	0.78	1	3.17E-16	84.2	Protein trichome birefringence-like 36				
	Regulatory	j9587	142	277	67	0.70	2	1.18E-21	102	Laccase-17				
	Regulatory	j8931	269	234	304	0.78	3	4.70E-14	77	Uncharacterized				
	Regulatory	j4967	209	164	86	0.65	6	1.18E-21	102	ABC transporter G family member 29				
P_{MA}	Coding	j55	21	1,246	724	0.56	8	3.20E-09	60.8	Wall-associated receptor kinase-like 3	CCG	Proline	TTG	Leucine
	Coding	j3302	19	253	445	0.45	9	1.55E-19	95.1	Ribosome biogenesis protein WDR12 homolog	GAT	Aspartic Acid	TAT	Tyrosine
	Coding	j3344	15	193	1,360	0.45	2	4.17E-14	77	protein CHROMATIN REMODELING 19	CCC	Alanine	ACC	Threonine
	Coding	j7806	7	23	341	0.25	10	5.79E-25	113	Diphosphomevalonate decarboxylase MVD2	CTT	Leucine	ATT	Isoleucine
	Coding	j5814	33	547	2,893	0.22	7	2.02E-24	111	Probable leucine-rich repeat receptor-like protein kinase At5g49770	CTG	Leucine	CGG	Arginine
	Regulatory	j5880	26	57	92	0.78	7	9.18E-10	62.6	Ninja-family protein AFP3				
	Regulatory	j1734	36	26	12	0.75	u	1.12E-08	59	Protein TIC 20-IV, chloroplastic, transcript variant X3, mRNA				

(Continues)

TABLE 1 (Continued)

Climate	Region	SNP	BAYENV	BAYPASS	LFMM	Fold-change	chr	BLAST *e*-val	Blast score	Gene annotation from the *Eucalyptus grandis* genome	Ref-codon	AA-ref	SNP codon	AA-SNP
	Regulatory	j8099	23	1,,301	1,425	0.30	8	4.45E-20	96.9	Root phototropism protein 3	TAG	stop codon	GAG	Glutamic Acid
	Regulatory	j9092	28	3,051	4,287	0.20	8	7.53E-11	66.2	Probable serine/threonine-protein kinase				
AI	Coding	j6444	614	10	11	0.73	8	2.77E-23	107	Probable LRR receptor-like serine/threonine-protein kinase	CAA	Glutamine	CGA	Arginine
	Coding	j4455	167	7	12	0.85	8	1.00E-08	60	Serine/threonine-protein kinase STE20	AAC	Asparagine	AAA	Lysine
	Coding	j7743	259	12	4	0.64	8	4.00E-21	100	Putative E3 ubiquitin-protein ligase XBAT34	ATG	Methionine	GTG	Valine
	Coding	j1740	245	175	25	0.75	2	1.00E-08	59	Uncharacterized	GCT	Alanine	GGT	Glycine
	Coding	j7806	9	30	572	0.25	10	6.52E-25	113	Diphosphomevalonate decarboxylase MVD2	CTT	Leucine	ATT	Isoleucine
	Regulatory	j6846	26	326	1940	0.20	9	5.72E-13	73.4	Phosphate transporter PHO1 homolog 9				
	Regulatory	j8099	8	1,080	1777	0.30	8	5.02E-20	96.9	Root phototropism protein 3	TAG	stop codon	GAG	Glutamic Acid
	Regulatory	j4217	20	5,825	3,433	0.53	u	8.49E-11	66.2	Protein MICRORCHIDIA 7				
	Regulatory	j5880	19	58	132	0.78	7	1.03E-09	62.6	Ninja-family protein AFP3				

Note: Relative ranks are given based on levels of significance for each environmental association analysis approach. Fold-change is the allele frequency turnover among populations. Chromosome number is given (chr) from *Corymbia citriodora* mapping, along with the NCBI blast e-val score and blast score for annotation results from the *E. grandis* genome, with the reference and SNP codon and their amino acids (AA). u—unspecified scaffold from *C. citriodora* mapping.

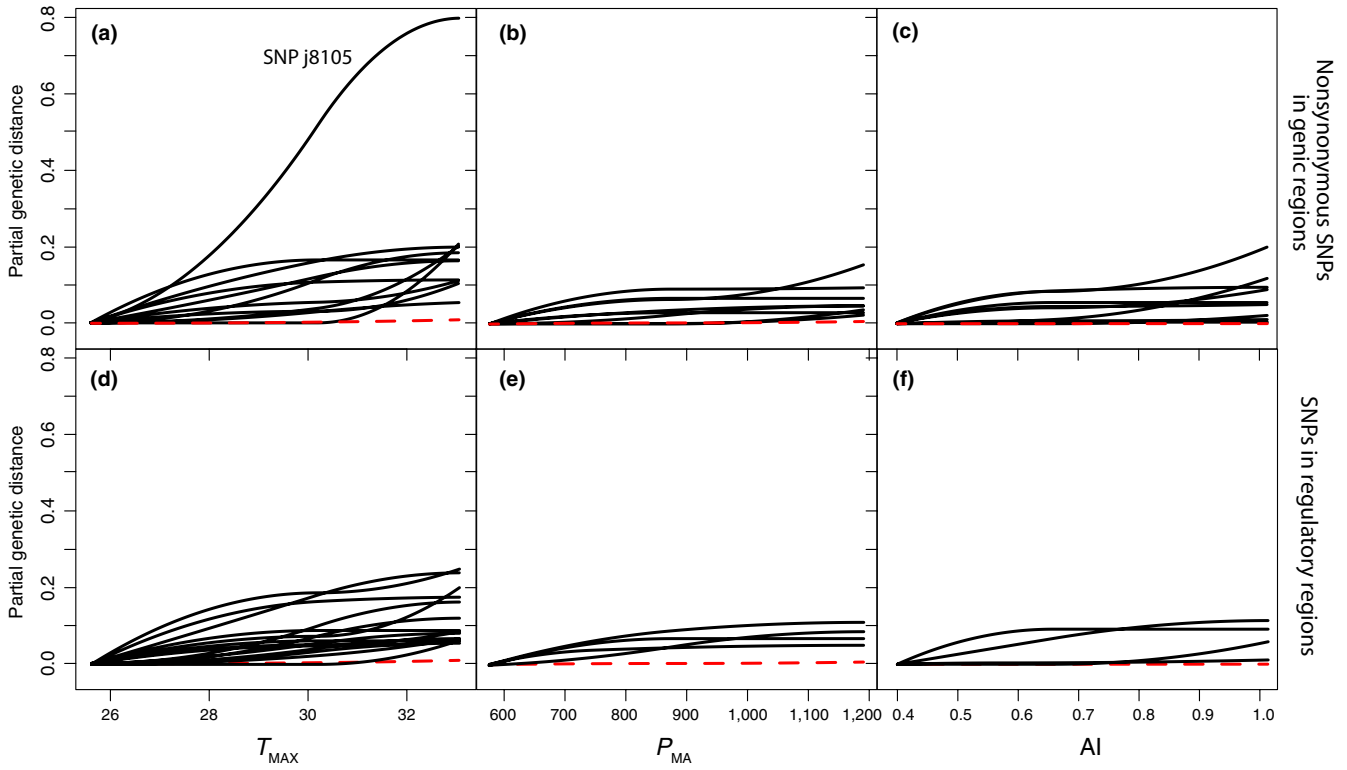

FIGURE 5 Allelic turnover for nonsynonymous SNPs within genic regions (a–c) and SNPs within regulatory regions (d–f) in climatic space. Variation of genetic distance associated with geographic distance is removed leaving genetic distance variation explained by climatic distance for maximum temperature of the warmest month (T_{MAX}; a & d), mean annual precipitation (P_{MA}; b & e) and aridity index (AI; c & f). Each black line represents one significant SNP. Dashed line indicates the allelic turnover for the whole data set (9,593 SNPs) [Colour figure can be viewed at wileyonlinelibrary.com]

affects each SNP differently. This finding could be indicative of additive genetic variation involving many genes, which is consistent with adaptive patterns of multilocus traits (Shaw & Etterson, 2012), but further experiments would have to be performed to confirm the polygenic signature. On the other hand, it is possible that climate explains a small portion of the variation for all but one significantly associated SNP because other environmental factors could be influencing these SNP patterns, particularly if the genes associated with the SNP of interest contribute to other pathways and are pleiotropic.

All EAA approaches identified more putatively adaptive SNPs associated with T_{MAX} than with P_{MA} and AI, and the SNPs associated with T_{MAX} explained significantly more variation. Therefore, our second hypothesis that temperature is more important than both P_{MA} and AI was supported. This pattern could, however, have been found if that the population structure follows the change in temperature across the landscape, increasing the chance of detection of false positives, although this covariation may also decrease the detection of true positives (Lotterhos & Whitlock, 2015; de Villemereuil, Frichot, Bazin, François, & Gaggiotti, 2014). Given limited genetic structure and high levels of gene flow throughout the distribution of *C. calophylla*, this was not likely to be a major factor in the analysis. Furthermore, the EAA approaches accounted for population structure in different ways, and our findings reflect the consensus providing a conservative list of candidate SNPs. Alternatively, the candidate SNPs may be under selection from another correlated bioclimatic factor that was not included in our analyses. The targeted, hypothesis-driven approach taken in this study cannot discount other factors; however, it does quantify the relative importance of maximum summer temperatures over annual rainfall and aridity in the process of local adaptation to climate. Temperature appears to be the climatic factor that is most important for genetic adaptation, potentially because it is spatially and temporally predictable compared to variable rainfall patterns (SOE, 2016). This is supported by the high deviance explained by the GDM analysis and also supported by other research in *C. calophylla* where temperature explains more variation than precipitation in physiological traits (Blackman et al., 2017). Indeed, many studies reveal significant associations between tree physiology and temperature-of-origin (Aspinwall et al., 2017; Blackman et al., 2017; Meier & Leuschner, 2008; van Ommen Kloeke, Douma, Ordoñez, Reich, & Bodegom, 2012; Swenson & Enquist, 2007), as well as global patterns evaluated for 15 traits (Moles et al., 2014).

Linkage disequilibrium among genomic SNPs was low for *C. calophylla*, indicating that all SNPs were independent of one another. Linkage disequilibrium in *E. grandis* has been shown to decay on average between 4 and 6 kb and is variable throughout the genome (Silva-Junior & Grattapaglia, 2015), and another study on *Eucalyptus camaldulensis* found that LD decays much quicker at 200 bp (Hendre, Kamalakannan, & Varghese, 2012). Using the high and low decay range of linkage

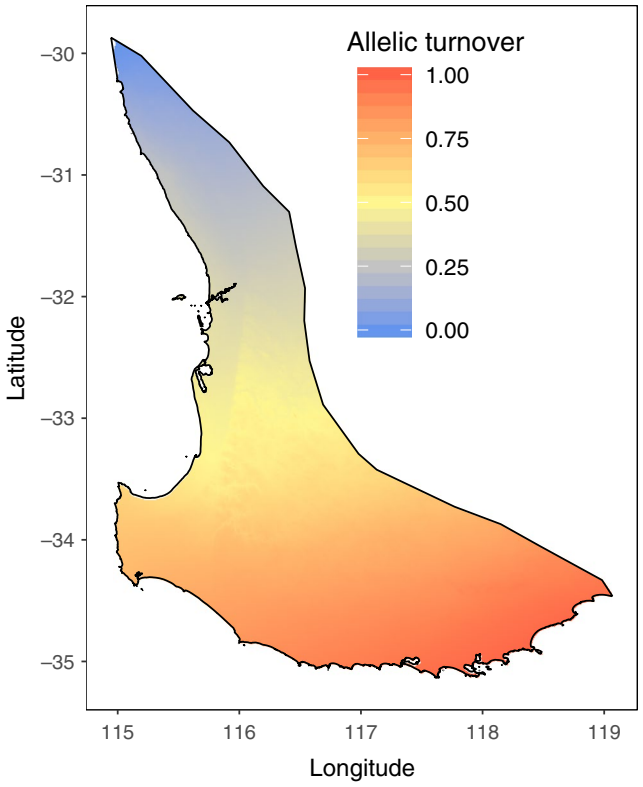

FIGURE 6 Allelic turnover in geographic space for SNP j8105 associated with maximum temperature of the warmest month (T_{MAX}). The most variation was explained for this SNP (53%) compared to all other SNPs identified in the study (see Figure 5). It is a nonsynonymous SNP and is associated with gene function related to heat stress

disequilibrium in *Eucalyptus* species (recognizing that LD varies within a genome i.e., 6,000 and 200 bp) and the genome size of *C. citriodora* (360 Mb), we estimate that there are between 60,000 and 2.4 million linkage groups present in the *C. calophylla* genome, and the present data set (9,593 SNPs) sampled between 15.9% and 0.4% of the genome. This genome sampling illustrates that our findings are likely a small portion of the genome potentially under selection, yet, we were able to find associations between numerous SNPs and climatic variables. This also implies that the SNPs found to be associated with climate may reflect polygenic patterns of adaptation because there are likely many more genes that are involved in climate adaptation that were not sampled.

4.2 | Gene function

Our analyses found significant SNP-climate associations including NS and synonymous SNPs in genic regions and SNPs within regulatory regions. While we recognize that synonymous SNPs, and SNPs outside of gene space, could be functionally important, here we focus on NS and regulatory SNPs as they provide the best opportunity to describe the gene function and the climate variable driving these patterns of adaptive variation.

The gene functions associated with T_{MAX} were compelling because their functions were associated with temperature. For example, the ALDH gene (associated with j8105) has been strongly linked to temperature adaptation and regulation of aldehyde homeostasis under stressful conditions (Perozich, Nicholas, Wang, Lindahl, & Hempel, 1999) and has been found to be induced by heat stress (Zhao, Missihoun, & Bartels, 2017). SNP j8105 was NS, indicating that the change in amino acid (from tyrosine to phenylalanine) could have a downstream phenotypic effect. Likewise, the ABC transporter gene families (associated with the SNP j4967) are known to mediate stress tolerance of seed germination (Hwang et al., 2016) and show a diverse response to high temperatures in rice (Zhang et al., 2012). In the presence of this SNP (j4967) in the regulatory region, it might contribute to adaptation if it is within a regulatory element or it may be linked to other genetic changes within the nearby gene. Lastly, the CBL gene (associated with the NS SNP j2510) has been shown to induce stress signal under low temperatures in *Chrysanthemum nankingense* and aids in low temperature tolerance (Ren et al., 2014).

Gene functions associated with P_{MA} were also compelling due to their association with drought stress. For example, the ninja-family protein AFP3 gene (associated with the NS SNP j5880) has been shown to be a negative regulator of abscisic acid (ABA) response, and the chromatin remodelling gene (associated with the NS SNP j3344) has been linked to regulation of ABA and stress tolerance (Sridha & Wu, 2006). ABA is known to play a major role to drought response in plants (Fujita et al., 2013) by controlling stomatal closure (Assmann & Jegla, 2016), and the hormones ABA and ethylene are known to control growth when under drought stress (Humplík, Bergougnoux, & Volkenburgh, 2017; Valluru, Davies, Reynolds, & Dodd, 2016). There are many functions, aside from drought stress response, associated with the ABA phytohormone (Humplík et al., 2017), indicating that the genes regulating ABA are likely pleiotropic.

The gene functions associated with AI were more ambiguous in terms of function and how it relates to climate. For example, LRR serine/threonine-protein kinase (associated with NS SNP j6444) genes are known to interact with a diverse group of proteins leading to variations in specificity of signal response, and appear to play a central role in signalling during pathogen recognition, the subsequent activation of plant defence mechanisms and developmental control (Afzal, Wood, & Lightfoot, 2008). Pathogens are known to occur in greater frequency when water availability is higher (Johnson, Alldredge, & Vakoch, 1996; Johnson, Carnegie, & Henson, 2009; Woods, Coates, & Hamann, 2005), and pathogen recognition could play an important role for organism in a mesic climate. Likewise, the polygalacturonase gene (associated with SNP j8937) has been shown to be involved with cell elongation and flower development in *Arabidopsis* (Xiao, Somerville, & Anderson, 2014) and is known to protect crops against pathogens (Kalunke et al., 2015). The synonymous SNP j6054 was linked to dynamin-related protein 4C, and the dynamin-related protein family is known to be involved with peroxisomal and mitochondrial division (Mano, Nakamori, Kondo, Hayashi, & Nishimura, 2004). While this SNP (j6054) is synonymous, it is in LD with a NS SNP (separated by 3 bp on the same sequence fragment) that was randomly dropped from data frame in the LD bioinformatic step.

There are many physiological processes involved in adaptation to temperature and precipitation (Allen et al., 2010), and these are most likely complex traits determined by numerous genetic variants of small-effect (Gomulkiewicz, Holt, Barfield, & Nuismer, 2010; Lande, 1983). Therefore, it is recognized that the genes identified here are most likely a part of the broader process of adaptation to climate. However, by identifying a fraction of functional genes putatively controlling the response to climate we can use these patterns as a proxy for understanding and monitoring the adaptive process and improve future management strategies.

These SNP-climate associations with T_{MAX} and P_{MA} are highly informative although confirmation of gene function must be performed through experimental molecular approaches (e.g., CRISPR/Cas system; Le Cong et al., 2013; Liu, Hu, Palla, Tuskan, & Yang, 2016). On the other hand, SNPs associated with AI are less compelling because the genes are not explicitly linked to climatic variables, and two of the genes described here have been shown to be responsive to pathogens. While these candidate SNPs may represent a valuable proxy for abiotic selective pressures, they should be interpreted with caution and further experimental evidence is needed, particularly for the SNPs identified in regulatory regions because their relationship to *cis*-regulatory elements could not be confirmed.

5 | CONCLUSION

Our study investigating climate-associated genetic variation as evidence of local adaptation in a foundational forest tree species has found numerous genomic variants distributed across the genome within coding and regulatory regions with gene function associated with response to climate. The evolutionary response to climate change by trees, such as *C. calophylla*, will be determined by standing genetic variation and gene flow along climatic gradients. Our findings indicate that *C. calophylla* populations show patterns of climate-associated genetic variation that may provide evidence of local adaptation to their current conditions. The presence of high recombination rates, variation within genes and regulatory regions, and amino acid changes demonstrate that *C. calophylla* may be well equipped, as a species, to adapt to future climates. Connectivity between populations may allow for the adaptive variants to migrate within and among populations naturally. However, generation times for trees are often long and overlapping, and gene migration occurs regionally, with overlapping gene pools, so genetic adaptation may not occur quickly enough to avoid the negative impacts associated with rapid climate change. Therefore, adaptive management practices such as assisted gene migration (Aitken & Whitlock, 2013) and climate-adjusted provenancing (Prober et al., 2015) may facilitate enhanced ecosystem resilience and function under climate change. Such practices are permitted under the forest management plan for the region (Conservation & Parks Commission, 2014) and can be achieved through empirically driven planting designs for forest management and rehabilitation.

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AUTHOR CONTRIBUTION

P.R. and M.B. developed the idea. All authors designed the experiment. C.A. analysed and interpreted the data. C.A. wrote the first draft of the manuscript. All authors read, edited and approved the final manuscript.

DATA ACCESSIBILITY

Genomic data sets generated and analysed (LFMM, BAYPASS,BAYENV2 and GDM) in this study are available in the DRYAD archives under accession https://doi.org/10.5061/dryad.03g3s3q.

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REFERENCES

Afzal, A. J., Wood, A. J., & Lightfoot, D. A. (2008). Plant receptor-like serine threonine kinases: Roles in signaling and plant defense. *Molecular Plant-Microbe Interactions*, *21*, 507–517. https://doi.org/10.1094/MPMI-21-5-0507

Ahrens, C. W., Mazanec, R. A., Paap, T., Ruthrof, K. X., Challis, A., Hardy, G., … Rymer, P. D. (2019). Adaptive variation for growth and resistance to a novel pathogen along climatic gradients in a foundation tree. *Evolutionary Applications*. https://doi.org/10.1111/eva.12796

Ahrens, C. W., Rymer, P. D., Stow, A., Bragg, J. G., Dillon, S. K., Umbers, K. D. L., & Dudaniec, R. Y. (2018). The search for loci under selection: Trends, biases and progress. *Molecular Ecology*, *27*, 1342–1356. https://doi.org/10.1111/mec.14549

Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747

Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*, *1*, 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks

for forests. *Forest Ecology and Management*, *259*, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Aspinwall, M. J., Vårhammar, A., Blackman, C. J., Tjoelker, M. G., Ahrens, C., Byrne, M., … Rymer, P. D. (2017). Adaptation and acclimation both influence photosynthetic and respiratory temperature responses in *Corymbia calophylla*. *Tree Physiology*, *37*, 1095–1112. https://doi.org/10.1093/treephys/tpx047

Assmann, S. M., & Jegla, T. (2016). Guard cell sensory systems: Recent insights on stomatal responses to light, abscisic acid, and CO_2. *Current Opinion in Plant Biology*, *33*, 157–167. https://doi.org/10.1016/j.pbi.2016.07.003

Bates, B. C., Hope, P., Ryan, B., Smith, I., & Charles, S. (2008). Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climatic Change*, *89*, 339–354. https://doi.org/10.1007/s10584-007-9390-9

Blackman, C. J., Aspinwall, M. J., Tissue, D. T., & Rymer, P. D. (2017). Genetic adaptation and phenotypic plasticity contribute to greater leaf hydraulic tolerance in response to drought in warmer climates. *Tree Physiology*, *37*, 583–592. https://doi.org/10.1093/treephys/tpx005

Byrne, M. (2008). Phylogeny, diversity and evolution of eucalypts. In A. K. Sharma, & A. Sharma (Eds.), *Plant genome: Biodiversity and evolution* (Vol. 1, Part E, pp. 303–346). Plymouth, UK: Science Publishers.

Byrne, M., Macdonald, B., & Francki, M. (2001). Incorporation of sodium sulfite into extraction protocol minimizes degradation of Acacia DNA. *BioTechniques*, *30*, 742–744, 748.

Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., … Wiens, J. J. (2014). Causes of warm-edge range limits: Systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, *41*, 429–442. https://doi.org/10.1111/jbi.12231

Cong, L., Ran, F. A., Cox, D., Lin, S., Barretto, R., Habib, N., … Zhang, F. (2013). Multiplex genome engineering using CRISPR/Cas systems. *Science*, *339*, 819–823. https://doi.org/10.1126/science.1231143

Conservation and Parks Commission. (2014). Forest management Plan 2014–2023. Retrieved from https://www.dpaw.wa.gov.au/images/documents/conservation-management/forests/FMP/20130282_WEB_FOREST_MGT_PLAN_WEB.pdf

Coop, G., Witonsky, D., Di Rienzo, A., & Pritchard, J. K. (2010). Using environmental correlations to identify loci underlying local adaptation. *Genetics*, *185*, 1411–1423. https://doi.org/10.1534/genetics.110.114819

De Mita, S., Thuillet, A.-C., Gay, L., Ahmadi, N., Manel, S., Ronfort, J., & Vigouroux, Y. (2013). Detecting selection along environmental gradients: Analysis of eight methods and their effectiveness for outbreeding and selfing populations. *Molecular Ecology*, *22*, 1383–1399. https://doi.org/10.1111/mec.12182

de Villemereuil, P., Frichot, É., Bazin, É., François, O., & Gaggiotti, O. E. (2014). Genome scan methods against more complex models: When and how much should we trust them? *Molecular Ecology*, *23*, 2006–2019.

Dillon, S., McEvoy, R., Baldwin, D. S., Rees, G. N., Parsons, Y., & Southerton, S. (2014). Characterisation of adaptive genetic diversity in environmentally contrasted populations of *Eucalyptus camaldulensis* Dehnh. (River Red Gum). *PLoS ONE*, *9*, e103515. https://doi.org/10.1371/journal.pone.0103515

Dillon, S., McEvoy, R., Baldwin, D. S., Southerton, S., Campbell, C., Parsons, Y., & Rees, G. N. (2015). Genetic diversity of *Eucalyptus camaldulensis* Dehnh. following population decline in response to drought and altered hydrological regime. *Austral Ecology*, *40*, 558–572.

Doyle, J., & Doyle, J. (1990). Isolation of plant DNA from fresh tissue. *Focus*, *12*, 13–15.

Ehrenreich, I. M. (2017). Epistasis: Searching for interacting genetic variants using crosses. *Genetics*, *206*, 531–535. https://doi.org/10.1534/genetics.117.203059

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE*, *6*, e19379. https://doi.org/10.1371/journal.pone.0019379

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics*, 3rd ed. Harlow, UK: Longmans Green.

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*, 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Field, C. B., Barros, V. R., Mach, K., & Mastrandrea, M. (2014). *Climate change 2014: Impacts, adaptation, and vulnerability*. Cambridge, UK; New York, NY: Cambridge University Press.

Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, *18*, 1–16. https://doi.org/10.1111/ele.12376

Frichot, E., & Francois, O. (2014). A short manual for sNMF: A program to estimate ancestry coefficients. Retrieved from http://membres-timc.imag.fr/Olivier.Francois/snmf/files/note.pdf

Frichot, E., & Francois, O. (2015). LEA: An R package for landscape and ecological association studies. *Methods in Ecology and Evolution*, *6*, 925–929.

Frichot, E., Schoville, S. D., Bouchard, G., & Francois, O. (2013). Testing for associations between loci and environmental gradients using latent factor mixed models. *Molecular Biology and Evolution*, *30*, 1687–1699. https://doi.org/10.1093/molbev/mst063

Fujita, Y., Nakashima, K., Yoshida, T., Fujita, M., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2013). Role of abscisic acid signaling in drought tolerance and preharvest sprouting under climate change. In N. Tuteja & S. S. Gill (Eds.), *Climate change and plant abiotic stress tolerance* (pp. 521–554). Weinheim, Germany: Wiley-VCH Verlag GmbH & Co. KGaA.

Futuyma, D. J. (2013). *Evolution*. Sunderland, MA: Sinauer Associates.

Gautier, M. (2015a). Genome-wide scan for adaptive divergence and association with population-specific covariates. *Genetics*, *201*, 1555–1579.

Gautier, M. (2015b). baypass version 2.1 User manual. Retrieved from http://www1.montpellier.inra.fr/CBGP/software/baypass/files/BayPass_manual_2.1.pdf

Gomulkiewicz, R., Holt, R. D., Barfield, M., & Nuismer, S. L. (2010). Genetics, adaptation, and invasion in harsh environments. *Evolutionary Applications*, *3*, 97–108.

Goudet, J. (2005). Hierfstat, a package for R to compute and test variance components and Fstatistics. *Molecular Ecology Notes*, *5*, 184–186.

Grewe, P. M., Feutry, P., Hill, P. L., Gunasekera, R. M., Schaefer, K. M., Itano, D. G., … Davies, C. R. (2015). Evidence of discrete yellowfin tuna (*Thunnus albacares*) populations demands rethink of management for this globally important resource. *Scientific Reports*, *5*, 16916. https://doi.org/10.1038/srep16916

Günther, T., & Coop, G. (2013). Robust identification of local adaptation from allele frequencies. *Genetics*, *195*, 205–220. https://doi.org/10.1534/genetics.113.152462

Havens, K., Vitt, P., Still, S., Kramer, A. T., Fant, J. B., & Schatz, K. (2015). Seed sourcing for restoration in an era of climate change. *Natural Areas Journal*, *35*, 122–133. https://doi.org/10.3375/043.035.0116

Hendre, P. S., Kamalakannan, R., & Varghese, M. (2012). High-throughput and parallel SNP discovery in selected candidate genes in *Eucalyptus camaldulensis* using Illumina NGS platform. *Plant Biotechnology Journal*, *10*, 646–656.

Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist*, *173*, 579–588. https://doi.org/10.1086/597611

Hoban, S., Kelley, J. L., Lotterhos, K. E., Antolin, M. F., Bradburd, G., Lowry, D. B., … Whitlock, M. C. (2016). Finding the genomic basis of local adaptation: Pitfalls, practical solutions, and future directions. *American Naturalist*, *188*, 379–397. https://doi.org/10.1086/688018

Humplík, J. F., Bergougnoux, V., & Van Volkenburgh, E. (2017). To stimulate or inhibit? that is the question for the function of abscisic acid. *Trends in Plant Science*, *22*, 830–841. https://doi.org/10.1016/j.tplants.2017.07.009

Hwang, J.-U., Song, W.-Y., Hong, D., Ko, D., Yamaoka, Y., Jang, S., … Lee, Y. (2016). Plant ABC transporters enable many unique aspects of a terrestrial plant's lifestyle. *Molecular Plant*, *9*, 338–355. https://doi.org/10.1016/j.molp.2016.02.003

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*, 1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Johnson, D. A., Alldredge, J. R., & Vakoch, D. L. (1996). Potato late blight forecasting models for the semiarid environment of south-central Washington. *Phytopathology*, *86*, 480–484. https://doi.org/10.1094/Phyto-86-480

Johnson, I. G., Carnegie, A. J., & Henson, M. (2009). Growth, form and *Quambalaria* shoot bight tolerance of spotted gum in north-eastern New South Wales, Australia. *Silvae Genetica*, *58*, 180–191.

Jordan, R., Dillon, H. A. A., & SK, Prober SM,, (2017). Evidence of genomic adaptation to climate in *Eucalyptus microcarpa*: Implications for adaptive potential to projected climate change. *Molecular Ecology*, *26*, 6002–6020.

Jordan, R., Dillon, S. K., Prober, S. M., & Hoffmann, A. A. (2016). Landscape genomics reveals altered genome wide diversity within revegetated stands of *Eucalyptus microcarpa* (Grey Box). *New Phytologist*, *212*, 992–1006.

Kalunke, R. M., Tundo, S., Benedetti, M., Cervone, F., De Lorenzo, G., & D'Ovidio, R. (2015). An update on polygalacturonase-inhibiting protein (PGIP), a leucine-rich repeat protein that protects crop plants against pathogens. *Frontiers in Plant Science*, *6*, 43. https://doi.org/10.3389/fpls.2015.00146

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association*, *90*, 773–795. https://doi.org/10.1080/01621459.1995.10476572

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*, 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Kilian, A., Wenzl, P., Huttner, E., Carling, J., Xia, L., Blois, H., … Uszynski, G. (2012). Diversity arrays technology: A generic genome profiling technology on open platforms. In F. Pompanon & A. Bonin (Eds.), *Data production and analysis in population genomics: Methods and protocols* (pp. 67–89). Totowa, NJ: Humana Press.

Kryazhimskiy, S., & Plotkin, J. B. (2008). The population genetics of dN/dS. *PLoS Genetics*, *4*, e1000304. https://doi.org/10.1371/journal.pgen.1000304

Lande, R. (1983). The response to selection on major and minor mutations affecting a metrical trait. *Heredity*, *50*, 47–65. https://doi.org/10.1038/hdy.1983.6

Lasky, J. R., Des Marais, D. L., Lowry, D. B., Povolotskaya, I., McKay, J. K., Richards, J. H., … Juenger, T. E. (2014). Natural variation in abiotic stress responsive gene expression and local adaptation to climate in *Arabidopsis thaliana*. *Molecular Biology and Evolution*, *31*, 2283–2296. https://doi.org/10.1093/molbev/msu170

Leimu, R., & Fischer, M. (2008). A meta-analysis of local adaptation in plants. *PLoS ONE*, *3*, e4010. https://doi.org/10.1371/journal.pone.0004010

Liu, D., Hu, R., Palla, K. J., Tuskan, G. A., & Yang, X. (2016). Advances and perspectives on the use of CRISPR/Cas9 systems in plant genomics research. *Current Opinion in Plant Biology*, *30*, 70–77. https://doi.org/10.1016/j.pbi.2016.01.007

Lotterhos, K. E., & Whitlock, M. C. (2015). The relative power of genome scans to detect local adaptation depends on sampling design and statistical method. *Molecular Ecology*, *24*, 1031–1046. https://doi.org/10.1111/mec.13100

Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits* (Vol. *1*, pp. 535–557). Sunderland, MA: Sinauer.

Mackay, T. F., Stone, E. A., & Ayroles, J. F. (2009). The genetics of quantitative traits: Challenges and prospects. *Nature Reviews Genetics*, *10*, 565.

Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., Mokany, K., & Fitzpatrick, M. C. (2018). *gdm: Generalized dissimilarity modeling. R package version 1.3.7*. Retrieved from https://cran.rproject.org/web/packages/gdm/index.html

Mano, S., Nakamori, C., Kondo, M., Hayashi, M., & Nishimura, M. (2004). An Arabidopsis dynamin-related protein, DRP3A, controls both peroxisomal and mitochondrial division. *The Plant Journal*, *38*, 487–498.

Matesanz, S., & Valladares, F. (2014). Ecological and evolutionary responses of Mediterranean plants to global change. *Environmental and Experimental Botany*, *103*, 53–67. https://doi.org/10.1016/j.envexpbot.2013.09.004

Matusick, G., Ruthrof, K., Brouwers, N. C., Dell, B., & Hardy, G. S. J. (2013). Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *European Journal of Forest Research*, *132*, 497–510. https://doi.org/10.1007/s10342-013-0690-5

Meier, I. C., & Leuschner, C. (2008). Leaf size and leaf area index in *Fagus sylvatica* forests: Competing effects of precipitation, temperature, and nitrogen availability. *Ecosystems*, *11*, 655–669. https://doi.org/10.1007/s10021-008-9135-2

Merilä, J., & Hoffmann, A. A. (2016). *Evolutionary impacts of climate change*. Oxford, UK: Oxford University Press.

Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L. … Bonser, S. P. (2014). Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, *25*, 1167–1180.

Mora, F., Arriagada, O., Ballesta, P., & Ruiz, E. (2017). Genetic diversity and population structure of a drought-tolerant species of Eucalyptus, using microsatellite markers. *Journal of Plant Biochemistry and Biotechnology*, *26*, 274–281. https://doi.org/10.1007/s13562-016-0389-z

Myburg, A. A., Grattapaglia, D., Tuskan, G. A., Hellsten, U., Hayes, R. D., Grimwood, J., … Schmutz, J. (2014). The genome of *Eucalyptus grandis*. *Nature*, *510*, 356–362. https://doi.org/10.1038/nature13308

Myers, N. (2003). Biodiversity hotspots revisited. *BioScience*, *53*, 916–917.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2018). *vegan: Community Ecology Package. R package version 2.5-1*. Retrieved from https://cran.rproject.org/web/packages/vegan/index.html

Perozich, J., Nicholas, H., Wang, B.-C., Lindahl, R., & Hempel, J. (1999). Relationships within the aldehyde dehydrogenase extended family. *Protein Science*, *8*, 137–146. https://doi.org/10.1110/ps.8.1.137

Prober, S. M., Byrne, M., McLean, E. H., Steane, D. A., Potts, B. M., Vaillancourt, R. E., & Stock, W. D. (2015). Climate-adjusted provenancing: A strategy for climate-resilient ecological restoration. *Frontiers in Ecology and Evolution*, *3*, 65. https://doi.org/10.3389/fevo.2015.00065

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

Rellstab, C., Gugerli, F., Eckert, A. J., Hancock, A. M., & Holderegger, R. (2015). A practical guide to environmental association analysis in landscape genomics. *Molecular Ecology*, *24*, 4348–4370. https://doi.org/10.1111/mec.13322

Rellstab, C., Zoller, S., Walthert, L., Lesur, I., Pluess, A. R., Graf, R., … Gugerli, F. (2016). Signatures of local adaptation in candidate genes of oaks (*Quercus* spp.) with respect to present and future climatic conditions. *Molecular Ecology*, *25*, 5907–5924.

Ren, L., Sun, J., Chen, S., Gao, J., Dong, B., Liu, Y., … Jiang, J. (2014). A transcriptomic analysis of *Chrysanthemum nankingense* provides insights into the basis of low temperature tolerance. *BMC Genomics*, *15*, 844. https://doi.org/10.1186/1471-2164-15-844

Riethoven, J.-J.-M. (2010). Regulatory regions in DNA: Promoters, enhancers, silencers, and insulators. In I. Ladunga (Ed.), *Computational biology of transcription factor binding* (pp. 33–42). Totowa, NJ: Humana Press.

Rosenberg, N. A. (2004). distruct: A program for the graphical display of population structure. *Molecular Ecology Notes*, *4*, 137–138. https://doi.org/10.1046/j.1471-8286.2003.00566.x

Sampson, J., Tapper, S. L., Coates, D., Hankinson, M., Mcarthur, S., & Byrne, M. (2018). Persistence with episodic range expansion from the early Pleistocene: The distribution of genetic variation in a forest tree *Corymbia calophylla* (Myrtaceae). *Biological Journal of the Linnean Society*, *123*, 545–560.

Savolainen, O., Lascoux, M., & Merilä, J. (2013). Ecological genomics of local adaptation. *Nature Reviews Genetics*, *14*, 807–820. https://doi.org/10.1038/nrg3522

Shaw, R. G., & Etterson, J. R. (2012). Rapid climate change and the rate of adaptation: Insight from experimental quantitative genetics. *New Phytologist*, *195*, 752–765. https://doi.org/10.1111/j.1469-8137.2012.04230.x

Silva-Junior, O. B., & Grattapaglia, D. (2015). Genome-wide patterns of recombination, linkage disequilibrium and nucleotide diversity from pooled resequencing and single nucleotide polymorphism genotyping unlock the evolutionary history of *Eucalyptus grandis*. *New Phytologist*, *208*, 830–845.

Simon, T. N., Bassar, R. D., Binderup, A. J., Flecker, A. S., Freeman, M. C., Gilliam, J. F., … Pringle, C. M. (2017). Local adaptation in Trinidadian guppies alters stream ecosystem structure at landscape scales despite high environmental variability. *Copeia*, *105*, 504–513. https://doi.org/10.1643/CE-16-517

SOE. (2016). State of the environment report. Australia Federal Government. Retrieved from https://soe.environment.gov.au/theme/atmosphere/key-findings

Sork, V. L. (2018). Genomic studies of local adaptation in natural plant populations. *Journal of Heredity*, *109*, 3–15. https://doi.org/10.1093/jhered/esx091

Sork, V. L., Squire, K., Gugger, P. F., Steele, S. E., Levy, E. D., & Eckert, A. J. (2016). Landscape genomic analysis of candidate genes for climate adaptation in a California endemic oak, *Quercus lobata*. *American Journal of Botany*, *103*, 33–46.

Sridha, S., & Wu, K. (2006). Identification of AtHD2C as a novel regulator of abscisic acid responses in Arabidopsis. *The Plant Journal*, *46*, 124–133.

Steane, D. A., McLean, E. H., Potts, B. M., Prober, S. M., Stock, W. D., Stylianou, V. M., … Byrne, M. (2017). Evidence for adaptation and acclimation in a widespread eucalypt of semi-arid Australia. *Biological Journal of the Linnean Society*, *121*, 484–500. https://doi.org/10.1093/biolinnean/blw051

Steane, D. A., Potts, B. M., McLean, E., Prober, S. M., Stock, W. D., Vaillancourt, R. E., & Byrne, M. (2014). Genome-wide scans detect adaptation to aridity in a widespread forest tree species. *Molecular Ecology*, *23*, 2500–2513. https://doi.org/10.1111/mec.12751

Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*, 451–459. https://doi.org/10.3732/ajb.94.3.451

Valluru, R., Davies, W. J., Reynolds, M. P., & Dodd, I. C. (2016). Foliar abscisic acid-to-ethylene accumulation and response regulate shoot growth sensitivity to mild drought in wheat. *Frontiers in Plant Science*, *7*, 4119. https://doi.org/10.3389/fpls.2016.00461

van Ommen Kloeke, A. E. E., Douma, J. C., Ordoñez, J. C., Reich, P. B., & van Bodegom, P. M. (2012). Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions. *Global Ecology and Biogeography*, *21*, 224–235. https://doi.org/10.1111/j.1466-8238.2011.00667.x

Vandepoele, K., Quimbaya, M., Casneuf, T., De Veylder, L., & Van de Peer, Y. (2009). Unraveling transcriptional control in Arabidopsis using cis-regulatory elements and coexpression networks. *Plant Physiology*, *150*, 535–546. https://doi.org/10.1104/pp.109.136028

Weir, B. S., & Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution*, *38*, 1358–1370.

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag.

Wittkopp, P. J., & Kalay, G. (2012). Cis-regulatory elements: Molecular mechanisms and evolutionary processes underlying divergence. *Nature Reviews Genetics*, *13*, 59–69. https://doi.org/10.1038/nrg3095

Woods, A., Coates, K. D., & Hamann, A. (2005). Is an unprecedented *Dothistroma* needle blight epidemic related to climate change? *BioScience*, *55*, 761–769.

Wray, G. A. (2007). The evolutionary significance of *cis*-regulatory mutations. *Nature Reviews Genetics*, *8*, 206. https://doi.org/10.1038/nrg2063

Xiao, C., Somerville, C., & Anderson, C. T. (2014). Polygalacturonase involved in expansion1 functions in cell elongation and flower development in *Arabidopsis*. *The Plant Cell*, *26*, 1018–1035.

Zhang, X., Li, J., Liu, A., Zou, J., Zhou, X., Xiang, J., … Chen, X. (2012). Expression profile in rice panicle: Insights into heat response mechanism at reproductive stage. *PLoS ONE*, *7*, e49652. https://doi.org/10.1371/journal.pone.0049652

Zhao, J., Missihoun, T. D., & Bartels, D. (2017). The role of Arabidopsis aldehyde dehydrogenase genes in response to high temperature and stress combinations. *Journal of Experimental Botany*, *68*, 4295–4308. https://doi.org/10.1093/jxb/erx194

Zou, Y.-P., Hou, X.-H., Wu, Q., Chen, J.-F., Li, Z.-W., Han, T.-S., … Guo, Y.-L. (2017). Adaptation of *Arabidopsis thaliana* to the Yangtze River basin. *Genome Biology*, *18*, 239. https://doi.org/10.1186/s13059-017-1378-9

SUPPORTING INFORMATION

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

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