

CLIMATE ADAPTATION AND ECOLOGICAL RESTORATION IN EUCALYPTS

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ABSTRACT: Eucalypts are the cornerstone of ecological restoration efforts across the highly modified agricultural landscapes of southern Australia. ‘Local provenancing’ is the established strategy for sourcing germplasm for ecological restoration plantings, yet this approach gives little consideration to the persistence of these plantings under future climates. This paper provides a synopsis of recent and ongoing research that the authors are undertaking on climate adaptation in eucalypts, combining new genomic approaches with ecophysiological evidence from provenance trials. These studies explore how adaptive diversity is distributed within and among populations, whether populations are buffered against change through capacity for phenotypic plasticity, and how this informs provenancing strategies. Results to date suggest that eucalypts have some capacity to respond to future environmental instability through adaptive phenotypic plasticity or selection of putatively adaptive alleles. Despite this, growing evidence suggests that eucalypts will still be vulnerable to change. Provenancing strategies that exploit adaptations found in non-local provenances could thus confer greater climate-resilience in ecological restoration plantings, although they will also need to account for potential interactions between climate adaptations and other factors (e.g. cryptic evolutionary variation, non-climate-related adaptations, herbivory and elevated CO₂).

Keywords: acclimation, adaptive capacity, *Eucalyptus*, genome-wide scans, plasticity

Eucalypts (comprising the genera *Eucalyptus*, *Corymbia* and *Angophora*) underpin ecological restoration efforts across the intensively-used agricultural landscapes of southern Australia. It is estimated that about 47 million ha of eucalypt woodlands have been cleared across this region (Booth et al. 2015), resulting in land degradation and biodiversity decline (Prober & Smith 2009; Lindenmayer et al. 2010). Eucalypts are replanted to restore eroded, salinised or otherwise degraded landscapes, for biodiversity conservation and carbon sequestration, and for alternative farm-based incomes (Smith et al. 2013). As one of the most ubiquitous ecosystem dominants in mesic Australia, eucalypts also underpin plantation forestry across Australia (and in the many countries into which they have been introduced — Booth 2013; Booth et al. 2015).

Recognition that plant populations are often genetically differentiated along environmental gradients has contributed to the widespread adoption of a ‘local

provenancing’ approach to sourcing germplasm for ecological restoration in these landscapes (Broadhurst et al. 2008). This approach is based on the assumption that local populations are best adapted to local conditions, and that introduction of non-local germplasm could lead to problems such as outbreeding depression or genetic swamping of local populations (Byrne et al. 2011; Weeks et al. 2011; Larcombe et al. 2016). However, global climate change is likely to have significant implications for the long-term success of local provenancing approaches. In Australia, mean temperatures have increased by nearly one degree since 1910, and cool-season rainfall in the south-east and south-west has declined since the mid-1990s (BoM 2014). With such changes expected to accelerate in the future (<http://www.climatechangeinaustralia.gov.au/en/>, IPCC 2013), climate-based local adaptations are likely to become decoupled from their locations. For long-lived trees such as eucalypts, developing and implementing

provenancing strategies to enhance the climate resilience of restoration investments is thus increasingly urgent (Prober et al. 2015).

This paper reports recent and ongoing studies that the authors are undertaking on climate adaptation in eucalypts, with particular emphasis on provenancing strategies for ecological restoration. Our work builds on earlier studies examining variation among populations of eucalypt species in relation to climate (e.g. Ladiges 1974, 1975; Harwood 1980; Potts 1985; Gibson et al. 1995; Li et al. 2000; Warren et al. 2005). We ask whether we can use the adaptive genetic variation that is already present in eucalypts to facilitate the longer-term climate-resilience of restoration or commercial plantings, and hence maintain the ecosystem services they provide. Understanding adaptive capacity can also inform how natural populations of eucalypts might adjust plastically or adapt genetically to climate change, and whether adaptation could be facilitated by assisted gene flow (Aitken & Whitlock

2013). Central to these questions is how adaptive diversity is distributed within and among populations, and the extent to which populations are buffered against change by individuals being able to adjust their physiology or morphology through phenotypic plasticity (Nicotra et al. 2010). In particular, if fixed differences in adaptive genetic variation exist between populations, targeted provenancing approaches could be crucial for success.

METHODOLOGICAL APPROACHES

We are using a combination of two main approaches to understand climate adaptation potential in eucalypts — provenance trials (in natural and controlled environments) and genomic surveys. Provenance trials (also called common gardens) are a traditional approach, involving different provenances (i.e. populations of a species that come from particular locations) planted together in the same environment (Matyas 1996; Figure 1).

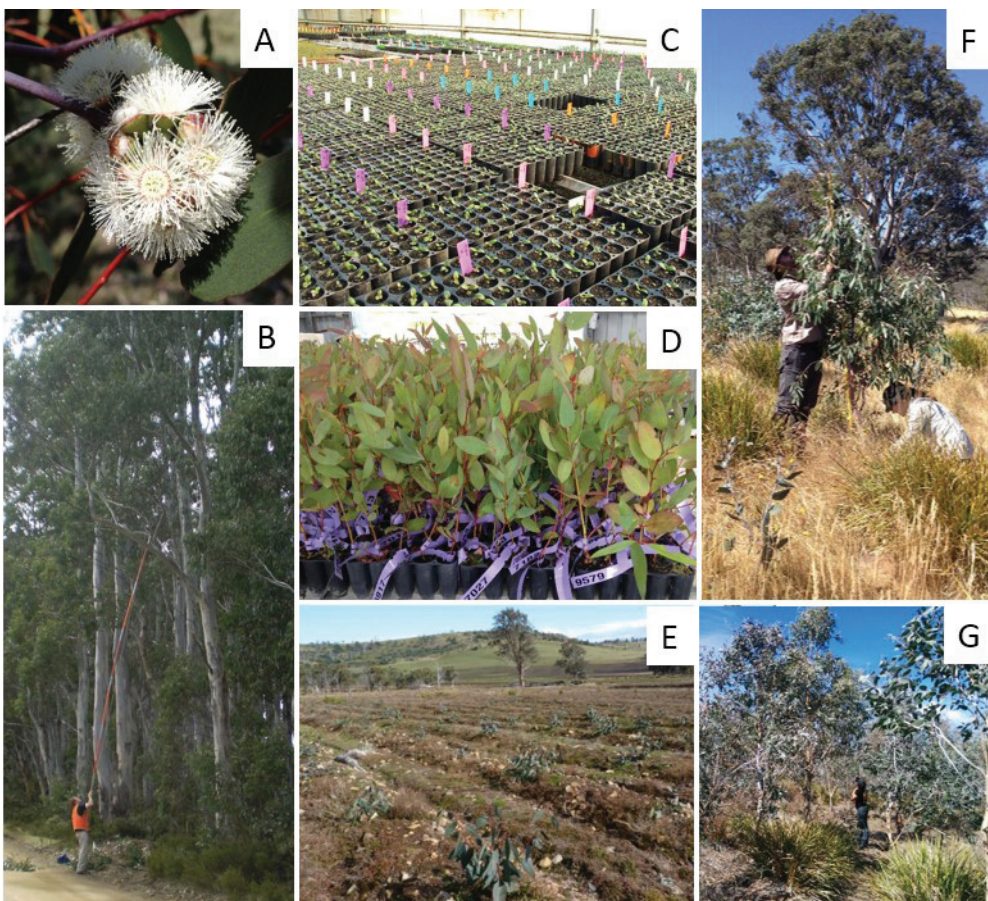


Figure 1: Steps in undertaking provenance trials, illustrated for *Eucalyptus pauciflora* in Tasmania. (a) Flowers of *E. pauciflora*: a widespread species being studied in field and glasshouse genetics trials in Tasmania (photo: T. Bailey); (b) Seed was collected from open pollinated wild trees from provenances across the geographical distribution of *E. pauciflora* in Tasmania (photo: J. Worth); (c) Seedlots from each individual tree (family) were grown in separate seedling trays and randomised within a commercial nursery (photo: T. Bailey); (d) Individual seedlings from each family were labelled and sorted into experimental designs ready for growing on in glasshouse studies or field trials (photo: T. Bailey); (e) Planted common garden field trial of individually pedigreed *E. pauciflora* at 10 months of age (photo: P. Tilyard); (f) Tree height and stem diameter were measured in *E. pauciflora* provenance trial at 3 years 3 months of age (photo: T. Bailey); (g) Reproduction was measured in *E. tenuiramis* and *E. pauciflora* provenance trials at 5 years of age (photo: P. Tilyard).

For most eucalypt studies, genetic material (i.e. germplasm) is sourced from multiple open-pollinated trees (i.e. families) usually collected at least two canopy heights apart to avoid sampling siblings. Seed is then either bulked at the provenance level or maintained at the individual family level, the latter being more powerful in quantitative genetic analysis (Eldridge et al. 1993). Within a common garden trial, the germplasm is randomised (with respect to families and provenances) into replicated experimental designs (e.g. randomised complete block design or randomised incomplete block design) to allow the statistical detection of genetic-based differences among families or provenances. This interpretation is supported by the fact that maternal environment effects have been shown to diminish rapidly with age in eucalypts (López et al. 2003).

Provenance trials are used to identify genetic differences in climate-related functional traits (e.g. leaf thickness or water use efficiency) and performance (e.g. growth rate and survival) among provenances, from which we can infer likely influences of a changing climate (Matyas 1994). The identification of plastic responses requires trials in multiple environments with the same genetic treatments; differences in phenotypic plasticity or performance among genetic treatments can then be detected as genotype-by-environment (GxE) interactions. Reciprocal provenance trials provide a particularly powerful way to detect GxE interactions. These involve a comparison of at least two trials along different parts of an environmental gradient from which provenances have been sampled (i.e. at two environmentally different ‘home-sites’).

While provenance trials are a benchmark approach to understanding adaptation, with long-lived organisms such as eucalypts they are expensive, time-consuming and, in field environments, vulnerable to failure. New genomic techniques, including candidate gene analysis, genome-wide screening and whole-genome sequencing, offer exciting ways to investigate the genetic basis of climate adaptation (Angeloni et al. 2012; Savolainen et al. 2013; Hoffmann et al. 2015). We have begun applying these techniques to survey eucalypts and characterise putatively adaptive genetic variation that is correlated with climate variables. Where available, combining data from provenance trials and genomic analysis allows more powerful interpretation of each. Various modelling approaches can also be employed to make more explicit projections of effective provenancing strategies (e.g. Steane et al. 2014).

Our genomic studies have predominantly employed genome-wide scans using molecular markers such as DArTSeq (Sansaloni et al. 2011; Petroli et al. 2012). These use ‘genomic representation’ approaches that utilise restriction enzymes to produce DNA fragments, which are

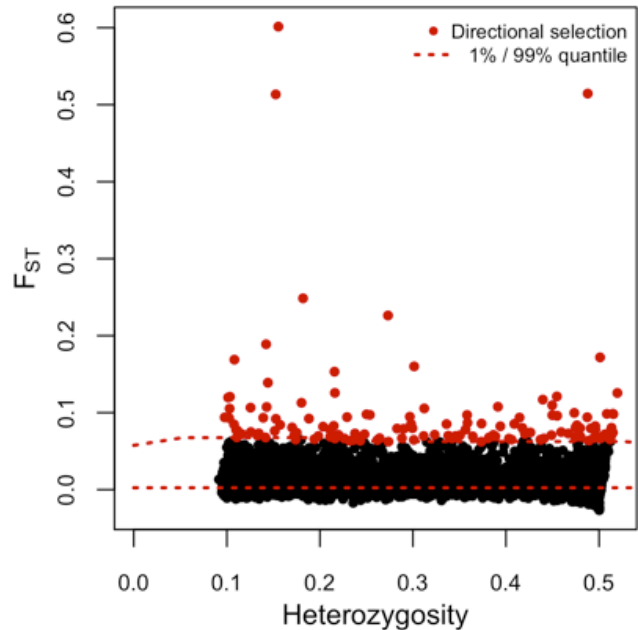


Figure 2: Example output of Arlequin F_{ST} outlier test (Excoffier et al. 2009) using *Eucalyptus microcarpa* DArTseq data (R. Jordan, S. Dillon, A. Hoffmann, S. Prober unpub. data). Loci are tested against a simulated neutral model of differentiation (F_{ST}) adjusted for allele frequency (heterozygosity). Those loci more differentiated than expected, falling outside the 99% quantile, are deemed ‘outliers’ under directional selection (red dots).

subsequently sequenced using next-generation platforms to produce thousands of markers from across the genome. Methods for identifying putatively adaptive alleles from genome-wide scans (or whole genotypes) are still being refined, but currently a common approach uses ‘ F_{ST} outlier analysis’ (e.g. Excoffier et al. 2009; Figure 2). This involves detecting markers that have greater differentiation among populations than would be expected under neutral evolution (i.e. drift). Association analyses can then relate these putatively adaptive alleles to ecological predictor variables to identify potential drivers of local adaptation. The recent release of the *E. grandis* Hill ex Maiden genome (Myburg et al. 2014) allows putatively adaptive alleles to be mapped to genomic locations, enabling the identification of genes, gene regions, or gene networks that may be associated with a marker, and thus potentially with climate adaptation.

A SNAPSHOT OF CLIMATE ADAPTATION STUDIES IN EUCALYPTS

Recent and emerging climate adaptation studies in eucalypts include more than 10 species and species-complexes studied by the authors, including genomic studies for five species (Table 1). Within each species, sampled provenances span mean annual rainfall ranges from 110 mm (*E. loxophleba* subsp. *lissophloia* L.A.S. Johnson & K.D. Hill — D.A. Steane, E.H. McLean, B.M.

Potts, S.M. Prober, W.D. Stock, V.M. Stylianou, R.E. Vaillancourt, M. Byrne unpub. data) to 2350 mm (*E. ovata* Labill., P.A. Harrison, B. Potts, R. Vaillancourt unpub. data) and mean annual temperature ranges from 0.7°C (*E. tricarpa* L.A.S. Johnson & K.D. Hill — McLean et al. 2014; Steane et al. 2014) to 14.1°C (*E. camaldulensis* Dehnh. — S. Dillon & others unpub. data). The focus to date has been on widespread, insect-pollinated eucalypts, and there is considerable scope to expand to eucalypts of different distributional and functional types.

Overall, evidence is emerging for both phenotypic and genotypic responses to climatic variation, with some traits showing high phenotypic plasticity, and other traits and genomic markers showing signatures of putatively adaptive differentiation among populations along climate gradients.

Phenotypic plasticity

A suite of traits appears relatively plastic in eucalypts, with plasticity often occurring in directions expected to promote adaptation to climate (i.e. ‘adaptive plasticity’, Nicotra et al. 2010). These include plasticity in physiological traits such as maximum photosynthetic rate, transpiration rate and measures of water use efficiency (*E. loxophleba* subsp. *lissophloia* — Stylianou 2011; *E. tricarpa* — McLean et al. 2014), and for *E. globulus* Labill., increasing wood density and extractives content and decreasing cellulose and lignin content on dry sites (Freeman et al. 2013). Provenance trials of *E. gunnii* Hook f. established along an altitudinal gradient in Tasmania have also shown that most traits

associated with extension growth (e.g. internode length, leaf size, plant height) exhibit strong plasticity. Parallel trends at the genetic level suggest this plasticity is adaptive (Kremer et al. 2014).

A number of traits appear variable in climate-related plasticity (e.g. leaf traits such as specific leaf area and leaf size — Li et al. 2000; Warren et al. 2006; Stylianou 2011; McLean et al. 2014). This variation could depend on the magnitude of climatic variation between provenance trials and sites of origin of provenances in each study; in some cases, variation in phenotypic plasticity appears to be genetically-based and associated with climate of origin (see below).

So far, evidence for adaptive benefits of phenotypic plasticity revealed in these studies has mostly been correlative, relying on relationships between plasticity and functional traits that are considered indicative of adaptation to climate. More direct demonstration of the benefits of observed plasticity to climate adaptation (e.g. using selection gradient analysis — van Kleunen & Fischer 2001; Nicotra et al. 2010, 2015) is needed to confirm correlative evidence.

Climate-related genetic variation in functional traits

A range of studies is also revealing a suite of potentially adaptive traits in eucalypts that appear to be strongly related to climate. Evidence that divergent selection has shaped population divergence in functional traits (or fitness surrogates) arises when (i) population differentiation is higher than expected based on drift ($Q_{st} > F_{st}$) and (ii) there

Table 1: Details for eucalypt species currently or recently studied by the authors to examine trait or genomic variation in relation to climate. DArTseq (Diversity Arrays Technology Pty. Ltd.) used to perform genome scans; SE South-eastern Australia.

Species	Location	# Provenances sampled	Common gardens	Genomic analysis of adaptive capacity	Mean annual rainfall range sampled (mm)	Mean annual temperature range sampled (°C)
<i>E. camaldulensis</i>	Aust	81	4	Candidate genes	190–2090	13.2–27.3
<i>E. globulus</i>	Tas	13	9	-	730–1790	10.5–14.1
<i>E. gunnii-archeri</i>	Tas	6	4	-	810–1290	6.0–8.9
<i>E. loxophleba</i> subsp. <i>lissophloia</i>	WA	9	1	DArTseq	250–360	16.7–19.6
<i>E. microcarpa</i>	SE	25	1	DArTseq	370–680	13.5–17.8
<i>E. ovata</i>	Tas	51	3	-	450–2800	8.2–13.4
<i>E. pauciflora</i>	SE	37	5	-	450–2000	6.0–13.9
<i>E. salubris</i>	WA	9	-	DArTseq	220–370	15.6–18.4
<i>E. risdonii-tenuiramis</i>	Tas	40	3	-	590–1030	8.7–12.5
<i>E. tenuiramis</i>	Tas	10	2	-	530–870	8.7–12.3
<i>E. tricarpa</i>	Vic	9	2	DArTseq	440–1200	13.7–14.4

is a significant association with a climatic or environmental gradient. In *E. globulus*, such signals of adaptation and correlations with climate have been detected in field trials for numerous wood properties (Stackpole et al. 2011) and foliar chemistry (O'Reilly-Wapstra et al. 2013; Gosney et al. 2016), as well as disease (Hamilton et al. 2013) and drought susceptibility (Dutkowski & Potts 2012). There is also evidence that the ontogenetic timing of transition to adult foliage and the onset of flowering are adaptive, although the broad-scale association with climate may be non-linear (Jordan et al. 2000; Foster et al. 2007).

In *E. pauciflora* Sieber ex Spreng., glasshouse trials of 37 Tasmanian provenances (Gauli et al. 2015) found that the mean maximum temperature of the site of origin was the most significant climate variable associated with provenance divergence. Adaptation to increasing maximum temperature appears to involve decreased investment in defence (i.e. oil glands), increased investment in recovery mechanisms (e.g. lignotubers; Figure 3), and delayed ontogenetic maturation. Similar responses to increasing maximum temperature were observed for a similar set of traits in a glasshouse study of 51 *E. ovata* provenances sampled across Tasmania (P.A. Harrison, B. Potts, R. Vaillancourt unpub. data). These parallel responses to increasing maximum temperature in *E. pauciflora* and *E. ovata* provide evidence for adaptive syndromes along climate gradients; however, in a study of *E. tricarpha*, production of defence compounds showed a different relationship with climate (Andrew et al. 2010).

A number of studies have highlighted the genetic basis of plasticity itself (Nicotra et al. 2010), with genetic variation in trait plasticity potentially influencing responses

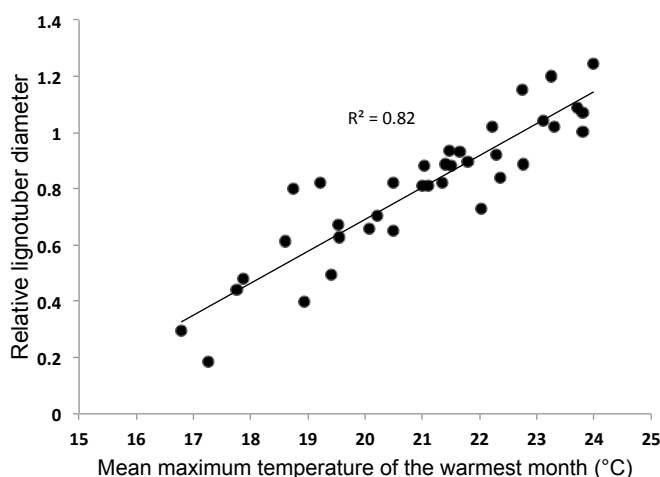


Figure 3: Regression of mean relative lignotuber diameter (measured in a glasshouse trial) against maximum temperature of the warmest period (weekly values) for *Eucalyptus pauciflora* provenances at their sites of origin in Tasmania. Modified from Gauli et al. (2015).

to climate change. In particular, provenances of *E. tricarpha* from dry (but not wet) environments grew thicker leaves (with lower specific leaf area) in a dry field trial and thinner leaves in a wetter one, a feature likely to be of benefit in dry environments with variable rainfall (Figure 4; McLean et al. 2014). On the other hand, provenances from wet environments were better able to adjust their leaf size than those from dry environments (Figure 4), possibly reflecting a greater importance of being able to produce large leaves when shaded in denser forests. (McLean et al. 2014). This genetic variation in plasticity concurs with an earlier study

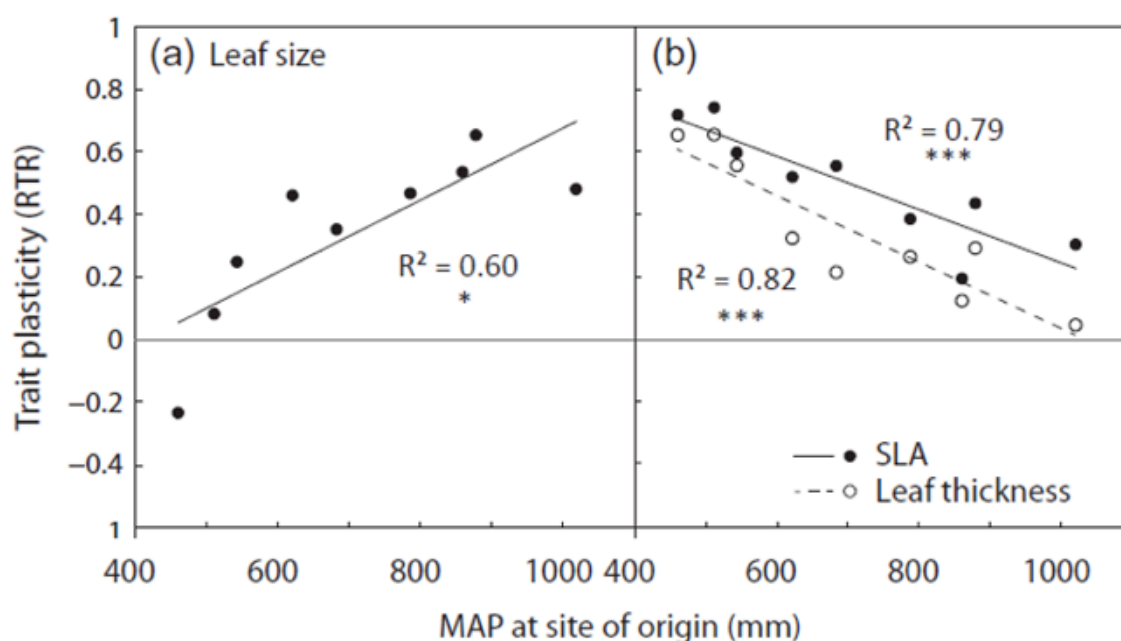


Figure 4: Climate-related variation in plasticity for (a) leaf size and (b) specific leaf area (SLA) and leaf thickness in *Eucalyptus tricarpha*. RTR, relative trait range; MAP, mean annual precipitation; modified from McLean et al. (2014).

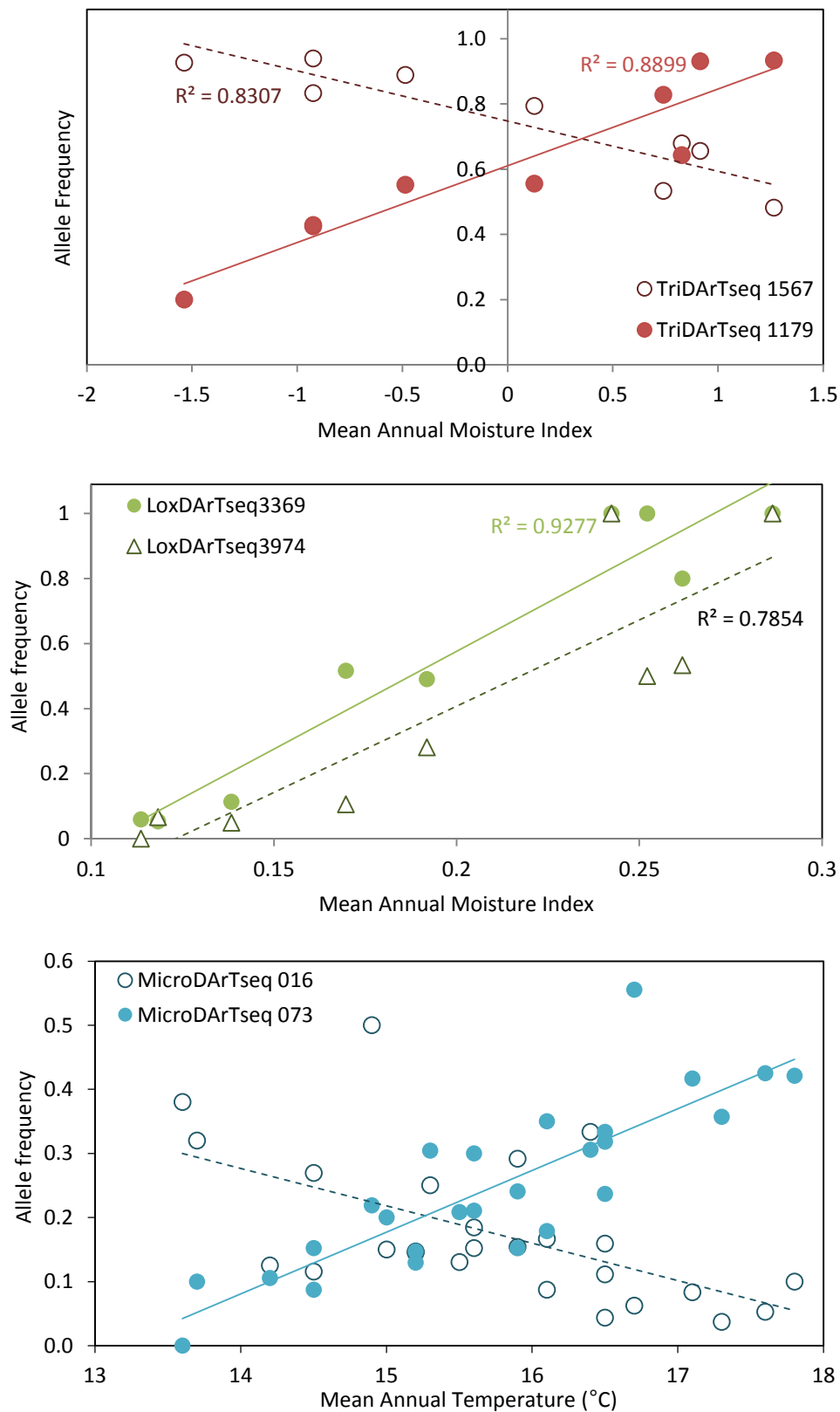


Figure 5: Examples of correlations between putatively adaptive DArTseq markers and climate variables in forest and woodland eucalypts: change in frequency of two alleles across an aridity gradient in (a) *Eucalyptus tricarpa* (redrawn from Steane et al. 2014), and (b) *E. loxophleba* subsp. *lissophloia* (D.A. Steane, E.H. McLean, B.M. Potts, S.M. Prober, W.D. Stock, V.M. Stylianou, R.E. Vaillancourt, M. Byrne unpub. data). (c) Change in allele frequency across a temperature gradient in a range-wide study of *E. microcarpa* (R. Jordan, S. Dillon, A. Hoffman, S. Prober unpub. data).

by Li et al. (2000) that found water-use efficiency and ratios of leaf area to root mass and stem area were plastic in the provenances of *E. microtheca* F. Muell. originating from drier locations, but were much less plastic in provenances from wetter locations.

Climate-related genetic variation in putatively adaptive alleles

Relationships between putatively adaptive genomic markers and climate are emerging for a range of eucalypt species, including *E. tricarpa* (Steane et al. 2014), *E. microcarpa* (Maiden) Maiden (R. Jordan, S. Dillon, A. Hoffman, S. Prober unpub. data), and *E. loxophleba* subsp. *lissophloia* (D.A. Steane, E.H. McLean, B.M. Potts, S.M. Prober, W.D. Stock, V.M. Stylianou, R.E. Vaillancourt, M. Byrne unpub. data; Table 1; Figure 5). For example, a study of 26 provenances of the widespread woodland tree *E. microcarpa* suggests relationships among 89 putatively adaptive alleles and climate (predominantly temperature) variables (R. Jordan, S. Dillon, A. Hoffman, S. Prober unpub. data; Figure 5). In a low rainfall region of Western Australia, outlier analysis identified strong relationships between genomic markers and aridity in *E. loxophleba* subsp. *lissophloia*, even across relatively short rainfall (110 mm) and temperature (2.9°C) gradients (Figure 5; D.A. Steane, E.H. McLean, B.M. Potts, S.M. Prober, W.D. Stock, V.M. Stylianou, R.E. Vaillancourt, M. Byrne unpub. data). These results are consistent with an earlier study that found correlations between a gene-based microsatellite marker in *E. gomphocephala* DC. and increasing summer heat stress and aridity; and between a flowering gene and precipitation and/or photoperiod (Bradbury et al. 2013).

Importantly, the genomic data also reveal that many (although not all) putatively adaptive alleles remain present across the sampled range of a species (Figure 5). This suggests potential for selection to increase the frequency of adaptive alleles within local populations as the climate changes, especially during recruitment events when seedling density is high. Whether natural selection could occur sufficiently rapidly or would benefit from intervention is not yet known.

Although the emerging relationships between genomic data and climate are striking, they remain as simple correlations, and further research is needed to strengthen these findings and establish causal patterns. Towards this, the *E. tricarpa* studies mentioned above (Steane et al. 2014; McLean et al. 2014) have related putatively adaptive alleles with functional traits (Figure 6), and a population level association study is being undertaken for putatively adaptive alleles in *E. microcarpa* (R. Jordan, S. Dillon, A. Hoffman, S. Prober unpub. data).

Another way to consolidate findings once a larger suite of species has been surveyed will be to seek common patterns across species. Such an analysis for three eucalypt species for which we have comparable datasets suggests adaptation is a genome-wide phenomenon involving a range of mutations in a diversity of genes and gene families (D.A. Steane, B.M. Potts, E.H. McLean, L. Collins, B.R. Holland, S.M. Prober, W.D. Stock, R.E. Vaillancourt, M. Byrne unpub. data). This analysis identified only three instances where outlier markers from two species were co-located on the *E. grandis* genome. While each co-location is unlikely to have occurred by chance alone, the relatively low number indicates we still have much to learn about the genomic basis of adaptation to climate in eucalypts (D.A. Steane, B.M. Potts, E.H. McLean, L. Collins, B.R. Holland, S.M. Prober, W.D. Stock, R.E. Vaillancourt, M. Byrne unpub. data). It is possible that, although the same traits may appear to be involved in climate adaptation in different species, the genes underlying this variation differ among species. Further, common adaptive responses to climate could result from the way genes interact within networks rather than from replicated changes in specific genes.

Plant performance

Despite evidence for phenotypic plasticity in some functional traits, the presence of adaptive genetic variation among provenances of eucalypt species predicts an ultimate home advantage in plant performance under current climates, consistent with many (but not all) provenance trials around the world (Broadhurst et al. 2008). This was confirmed for *E. tricarpa*, where a home advantage in growth rate was observed in both dry and wet trials after 12 years, despite evidence for plasticity in leaf traits (McLean et al. 2014). In Tasmania, early results indicate more rapid development of a home-site advantage for the Tasmanian endemic *E. tenuiramis* Miq., than for Tasmanian provenances of the more widespread *E. pauciflora* (Bailey et al. 2013; T. Bailey, P. Harrison, A. Gauli, B. Potts unpub. data; Figure 7); it will be of interest to establish whether this corresponds with greater adaptive genetic differentiation among populations of *E. tenuiramis* than *E. pauciflora*.

As global climate change decouples climate-related local adaptations from provenance locations, home-site advantages may become less common. Long-term provenance field trials of *E. gunnii-archeri* in central Tasmania may be already detecting this signal, with a switch from local to non-local superiority. For example, at the lowest elevation trial, survival diminished in the local *E. gunnii* provenance compared with a provenance originating from an even lower (warmer) elevation, but this trend did

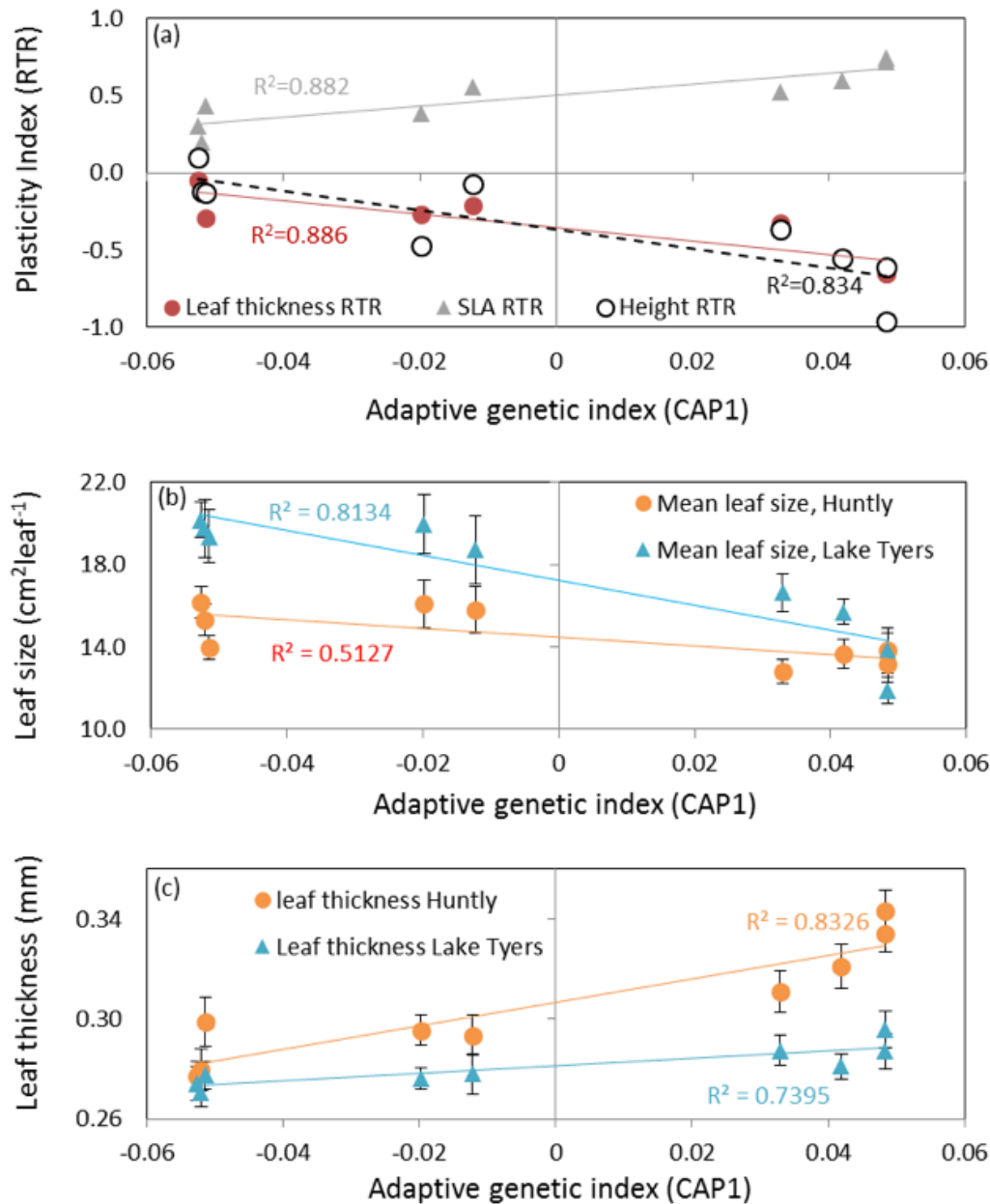


Figure 6: Examples of correlations between genomic variation and (a) plasticity estimates for three traits (SLA, specific leaf area; RTR, relative trait ratio), (b,c) functional traits, of *Eucalyptus tricarpa* (redrawn from Steane et al. 2014). Genomic variation is expressed as position on an axis resulting from ordination of genomic data (CAP1), used as an 'adaptive genetic index'. Huntly and Lake Tyers are provenance trials towards the dry and wet end of the gradient respectively. See Steane et al. (2014) for more detail.

not become evident until 25 years after planting (Potts 1985; Figure 8). Maximum temperatures in the region of the field trial have increased by 0.21°C per decade over the last 50 years and late summer/autumn rainfall has decreased by 25% (Sanger et al. 2011), which may have contributed to the observed change in provenance performance. This shift coincides with extensive dieback in the local *E. gunnii* in this region and a shift in its regeneration niche to deeper soils (Calder & Kirkpatrick 2008; Sanger et al. 2011).

INTERACTIONS AND WILDCARDS

While some general patterns are emerging regarding adaptation to climate in eucalypts, we are also encountering important exceptions and interactions that will need to be accounted for in future ecological restoration efforts. First, cryptic evolutionary patterns could complicate attempts to capture adaptive variation in plantings. We observed this in the widespread species *E. salubris* F. Muell. of south-western Australia, where genomic surveys revealed two

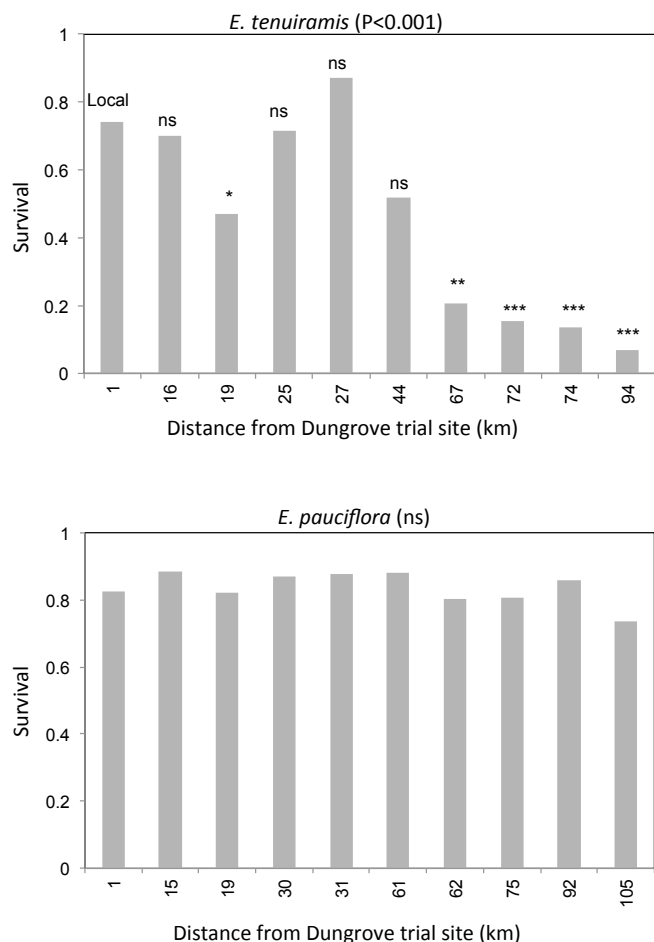


Figure 7: The proportion of plants surviving 3.3 years after planting 10 provenances each of *Eucalyptus tenuiramis* and *E. pauciflora* at the Dungrove trial site in Tasmania (described in Bailey et al. 2013; T. Bailey, P. Harrison, A. Gauli, B. Potts unpub. data). Provenances with significantly different survival to the local Dungrove provenance are marked with asterisks; ns = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

distinct evolutionary lineages. This overriding evolutionary signature made it difficult to detect climate signals in functional traits and genomic markers relating to aridity (Steane et al. 2015).

Second, exploitation of broad-scale variation in adaptive capacity may be confounded by local variation in water availability, temperature or other factors driving local adaptation. For example, a recent study (S. Dillon, E. Fraval, R. Mellick, D. Bush, S. Southerton unpub. data) found strong differentiation in candidate adaptive genes of *E. camaldulensis* over short hydrological gradients from the riparian zone to drier floodplains, consistent across 12 different locations. This points to potential for adaptation to extreme niches over short spatial scales, even in the face of high gene flow. At the landscape level, many of the identified loci were related to broader climate variation. Curiously, in some cases alleles that were

most common in (wetter) riparian sites were also more common in hotter, drier regions, suggesting complex and scale-dependent drivers of adaptation. Similar local scale variation related to topography or soils has been found in earlier ecophysiological studies, e.g. for several traits (frost resistance, susceptibility to infection by leaf spotting fungi and browsing by native mammals) in field trials of *E. obliqua* L'Hér. in Tasmanian forests (Wilkinson 2008), for drought resistance in *E. viminalis* Labill. (Ladiges 1975, 1976) and for frost resistance in glasshouse trials of *E. pauciflora* from the Australian Alps (Harwood 1980).

Third, climate change is occurring in a context of increasing atmospheric CO_2 concentrations, which is not accounted for in most field provenance trials, but is beginning to be addressed through controlled environment studies. For example, emerging results from a study of 43 *E. camaldulensis* provenances (S. Dillon, A. Quentin, A. Papanicolaou, B. Furbank, L. Pinkard unpub. data) indicate genotype x environment interactions in response to CO_2 for several photosynthetic traits and expression of related genes. These interactions relate to environment at the site of origin, suggesting that variation in plasticity among provenances reflects local adaptation (adaptive plasticity). By contrast, leaf morphological traits do not appear to vary in response to CO_2 , although they vary among provenances. Current studies in *E. camaldulensis*, *E. grandis*, *E. globulus* and *E. nitens* H. Deane & Maiden (S. Dillon, R. Mellick, F. Busch, C. Blackman, L. Pinkard, M. Ivkovich, M. Brookhouse, M. Battaglia, D. Tissue, A. O'Grady, D. Bush, P. Rymer, R. Smith, S. Southerton, G. Farquhar unpub. data) are also exploring interactions between CO_2 enrichment and climatic factors (heat and water stress) to help predict plant performance under future conditions.

Finally, evidence is emerging to indicate that interactions with other ecological processes, such as herbivory, disease, soil nutrient enrichment or degradation (but see O'Brien & Krauss 2010), will also influence responses of eucalypts to climate change. This is particularly relevant when interactions involve introduced species. For example, in Tasmanian provenance trials, damage by introduced deer was significantly greater for the faster growing, low altitude *E. pauciflora* provenances, which might otherwise be more suited to a warming climate (Gauli 2014; Bailey et al. 2014). Similarly, introduced diseases such as myrtle rust (*Puccinia psidii* Winter), which affects species of the plant family *Myrtaceae* and arrived in Australia in 2010, may differentially affect species and provenances independently of their climate adaptation (Potts et al. 2016).

These (and likely other) factors suggest that uninformed 'non-local' provenancing strategies have potential to be maladaptive in some scenarios. More systematic

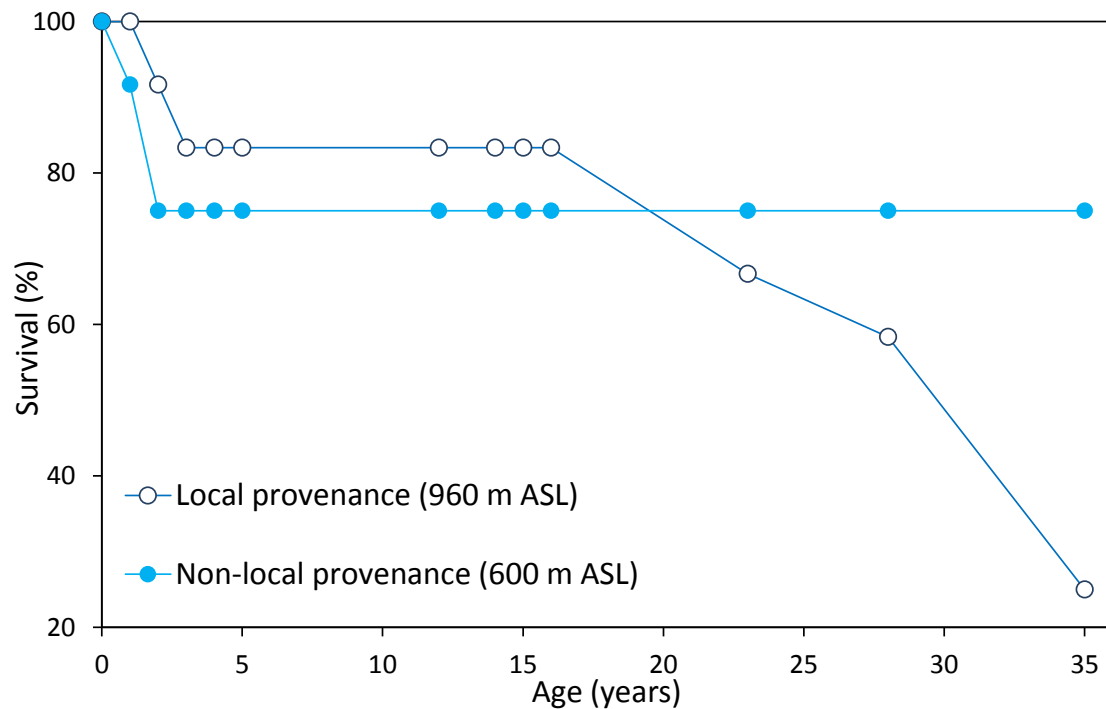


Figure 8: A 35-year provenance trial indicates declining survival of the local *Eucalyptus gunnii* provenance compared with a provenance from lower elevation, after 20 years of similar performance of the two provenances (B. Potts unpub. data). The trial was established at Pensford (960 m) on the Central Plateau of Tasmania in April 1979, with 12 seedlings from each of 6 provenances from the *E. gunnii*-*archeri* complex (Potts 1985). The two provenances shown had the best survival after age 20 years (B. Potts unpub. data). An upstream dam was built above the trial at age 30 years, but this occurred after the decline of the local provenance had commenced.

characterisation and quantification of exceptions and interactions are needed to help guide future provenancing strategies for ecological restoration. Indeed, emerging strategies argue that it may be prudent to include a mix of local and non-local provenances to guard against uncertainty (e.g. Breed et al. 2013; Prober et al. 2015).

CONCLUSIONS AND IMPLICATIONS

As long-lived, sedentary organisms, eucalypts must both withstand variation in seasonal climate over their lifespans, and adapt to local conditions for long-term persistence (Aitken et al. 2008; Donnelly et al. 2011). Consistent with this, we have observed evidence for both phenotypic plasticity and genetic adaptation to climate across a number of eucalypt species. Genomic surveys suggest that genetic adaptation to climate is likely to be a genome-wide phenomenon, involving a range of mutations in a diversity of genes and gene families across all chromosomes (Turner et al. 2008; Pujolar et al. 2014; Nicotra et al. 2015; D.A. Steane, B.M. Potts, E.H. McLean, L. Collins, B.R. Holland, S.M. Prober, W.D. Stock, R.E. Vaillancourt, M. Byrne unpub. data).

Relationships among functional traits, adaptive markers and climate indicate that, as might be expected, aspects of temperature and rainfall regimes are likely

climatic drivers of adaptation (McLean et al. 2014; Steane et al. 2014; Bragg et al. 2015; D.A. Steane, E.H. McLean, B.M. Potts, S.M. Prober, W.D. Stock, V.M. Stylianou, R.E. Vaillancourt, M. Byrne unpub. data). As it becomes feasible to analyse larger and more strategic datasets that minimise autocorrelations among climate variables, it will be possible to gain more specific insights into the drivers and mechanisms underpinning climate adaptation (e.g. maximum temperature thresholds). Supported by modelling approaches (e.g. Fitzpatrick & Keller 2015), this will improve our ability to predict impacts of climate change.

In summary, emerging evidence for adaptive phenotypic plasticity in a range of functional traits, and for range-wide presence of adaptive alleles, suggests that adjustments by individuals and selection within populations can facilitate climate adaptation in eucalypts. On the other hand, evidence for genetic adaptation to climate suggests eucalypts will still be vulnerable to climate change, especially in competitive environments (Allen et al. 2010; Donnelly et al. 2011). We thus conclude that targeted selection of seed sources to account for projected climate change has potential to confer greater climate resilience in ecological restoration. New provenancing strategies, such as admixture or climate-adjusted provenancing (e.g.

Breed et al. 2013; Prober et al. 2015), have been proposed towards this goal and are beginning to be implemented as tools for restoration practitioners (e.g. P.A. Harrison, R.E. Vaillancourt, R.M.B. Harris, B.M. Potts unpub. data). However, these strategies require field evaluation and comparison with potential for adaptive evolution of populations through natural selection of individuals with locally-present adaptive alleles.

It is also evident that adaptations to climate will interact with other factors, including cryptic evolutionary variation, local (non-climate-related) adaptations, herbivores, disease, ecological degradation and responses to elevated CO₂. A systematic approach to characterising these interactions could contribute to better guidelines to inform or adjust application of non-local provenancing strategies.

FUTURE DIRECTIONS

Our studies to date have focused on widespread, insect-pollinated eucalypts. Analysis of a broader range of species is needed to characterise the distribution of climate adaptation capacity across eucalypts and other plant species, towards a predictive framework based on distributional patterns (e.g. widespread, disjunct or narrow endemics), functional types (e.g. bird versus insect pollinated) and evolutionary groupings (Aitken & Whitlock 2013; Hoffmann et al. 2015; Prober et al. 2015). Parallel studies of interacting factors are needed so that genetic risk can be better incorporated into such frameworks. Refinement and application of genomic approaches is expected to expedite these developments and increase our understanding of the genomic basis of adaptation. Modelling tools using climate and genomic data can, in turn, improve implementation of new provenancing approaches through spatial projections.

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