Biological Conservation 203 (2016) 226–232

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Local maladaptation in a foundation tree species: Implications for restoration

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ARTICLE INFO

Article history:
Received 8 May 2016
Received in revised form 13 July 2016
Accepted 28 August 2016
Available online xxxx

Keywords:
Adaptive management
Embedded experiments
Local adaptation
Provenance trial
Revegetation
Seed sourcing

ABSTRACT

Replanting native vegetation is a broadly accepted method for restoring degraded landscapes. Traditionally, seed used for restoration has been locally sourced to avoid introducing maladapted plants and to minimize the risk of outbreeding depression. However local adaptation is not universal and is disrupted by, for example, climate change and habitat fragmentation. We established a common garden experiment of ca. 1500 seedlings sourced from one local and two non-local provenances of *Eucalyptus leucoxylon* to test whether local provenancing was appropriate. The three provenances spanned an aridity gradient, with the local provenance sourced from the most mesic area. We explored the effect of provenance on four fitness proxies after 15 months, including survival, above-ground height, susceptibility to insect herbivory, and pathogen related stress. The local provenance had the highest mortality and grew least. The local provenance also suffered most from invertebrate herbivory and pathogen related stress. These results provide evidence that no advantage would be gained during the establishment of *Eucalyptus leucoxylon* at this site by using only the local provenance from within the range we sampled. Our results suggest that incorporating more diverse seed mixes from across the aridity gradient during the restoration of *Eucalyptus leucoxylon* open woodlands would provide quantifiable benefits to restoration (e.g. 6–10% greater survival, 20–25% greater plant height, 16–45% more pathogen resistance during establishment). We demonstrated these restoration gains by embedding a common garden experiments into a restoration project, and we recommend this approach be more widely adopted because it provides an effective way to facilitate adaptive management options for restoration stakeholders based on empirical evidence.

1. Introduction

Human activities have been attributed to the degradation of billions of hectares of land (Gibbs and Salmon, 2015; Nkonya et al., 2016). Ecological restoration is recognized as the principal strategy to actively reverse this degradation (Aronson and Alexander, 2013), and revegetation through active planting is one of the most common restoration tools employed to achieve this goal. A number of restoration commitments of unprecedented scale have recently been made to address land degradation (Broadhurst et al., 2016). For example, the Bonn Challenge commits to restore 150 million ha by 2020 and the 2014 New York Declaration on Forests restoration goal extends this to 350 million ha by 2030. However, it remains unclear whether projects implementing such ambitious targets will succeed in their objectives unless existing levels of uncertainty in current practice are addressed (Suding et al., 2015).

Seed is the fundamental component of restoration plantings, and choosing the origin of the seed is an early commitment in the restoration process that has important consequences (Hufford and Mazer, 2003; McKay et al., 2005; Broadhurst et al., 2008). Historically, the preferential use of local seed – local provenancing – has been encouraged to optimise restoration outcomes (Hufford and Mazer, 2003; McKay et al., 2005). A local provenancing strategy is assumed to maximise success by preserving local adaptation, but what constitutes a ‘local provenance’ is not easily defined, so provenancing often defaults to arbitrary spatial boundaries (McKay et al., 2005; Jones, 2013). In addition, assuming a local advantage does not acknowledge the impact of important drivers of ecosystem change on local adaptation (e.g. climate change, habitat fragmentation), which may ultimately limit future restoration success (Godefroid et al., 2011; Breed et al., 2013).

Local adaptation is common in plants, but not ubiquitous (Leimu and Fischer, 2008; Hereford, 2009). It has been shown to be driven by both biotic (e.g. herbivory and pathogen resistance Crémieux et al., 2008) and abiotic factors (e.g.climate Turesson, 1922; Clausen et al., 1941; Hereford, 2009). However, Leimu and Fischer (2008) reported in their meta-analysis that the magnitude of local adaptation is independent of geographical transfer distance (i.e. the transfer of seed between 0.003 km and 3500 km had no effect on the strength of adaptation). Furthermore, climate change and habitat fragmentation can both reduce

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http://dx.doi.org/10.1016/j.biocon.2016.08.036
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the likelihood and strength of local adaptation. Fragmentation tends to increase inbreeding and reduce adaptive capacity, and climate change is shifting adaptive landscapes (i.e. the relationship between a given site and the optimal phenotype at that site) (Jump and Peñuelas, 2005; Lowe et al., 2005; Breed et al., 2015). As such, it has been argued that strictly adhering to local provenancing could limit the evolutionary potential of restoration plantings (Sgrò et al., 2011; Breed et al., 2013; Havens et al., 2015).

The effects of intentionally mixing local and non-local provenances on plant fitness was recognized by Darwin (1876), and has been exploited in plant breeding for centuries (Schnable and Springer, 2013). Mixing genotypes also comes with risks as it can lead to the introduction of maladapted individuals and outbreeding depression (Lesica and Allendorf, 1999), where interpopulation crosses experience a decline in progeny fitness (Hufford and Mazer, 2003; Vander Mijnsbrugge et al., 2010). These concerns have merit, chiefly when provenances with different ploidy levels are used (Weeks et al., 2011), where transfer is being considered over very long distances, or dramatic environmental gradients exist (Byrne et al., 2011; Breed et al., 2013). However, the concern of outbreeding depression has generally been overemphasised in the conservation genetics literature since the likelihood of outbreeding depression is low for crosses of non-threatened, predominantly outcrossing species that are used in restoration (Frankham et al., 2011).

Traditional and novel seed collection recommendations were reviewed in Breed et al. (2013), who argued for provenancing approaches that mitigated the impacts of climate change and habitat fragmentation on provenance fitness. Two themes came out of this review. First, it was suggested that local provenances should be supplemented with provenances from further afield to augment adaptive potential of plantings (e.g. composite and admixture provenancing). Secondly, it was suggested that particular provenances should be selected to match future environmental conditions based on climate modelling (e.g. predictive provenancing). Further strategies have suggested to explicitly incorporate climate resilience, as in Prober et al. (2015), who encouraged a directional selection to seed collection in line with climate predictions (i.e. climate adjusted predictive provenancing), and regionally developed cultivars selected for specific traits have also been recommended (e.g. vigour, drought tolerance and disease resistance Baer et al., 2014). With mounting evidence from translocation studies showing that some populations lack distinct local adaptation (Hancock et al., 2012; Breed et al., 2016a; Lu et al., 2016), and the numerous quantitative reviews also questioning the ubiquity of local adaptation (Leimu and Fischer, 2008; Hereford, 2009), provenance studies of core restoration species are needed to help guide the selection of appropriate provenancing strategies (Breed et al., 2013; Prober et al., 2016).

In this study we investigated how provenance influenced first season survival, growth, herbivory and pathogen resistance for a foundation tree species commonly used in restoration of southern Australian habitat, *Eucalyptus leucoxylon ssp leucoxylon* (hereafter *E. leucoxylon*). We used three provenances orientated along an east–west aridity gradient in the southern Mt. Lofty Ranges in South Australia. The local provenance was western and most mesic, and the distant provenance was eastern and most xeric (Fig. 1). The three provenances were grown in a common garden experiment to explore the following questions: (1) what effect does *E. leucoxylon* provenance have on survival, growth, herbivory or pathogen resistance? If variation is observed, (2) is this variation in line with local adaptation? From the evidence we present, we derive regional management recommendations for optimising seed sourcing strategies for *E. leucoxylon*. The findings of this study has implications for other species in the region and for conservation and restoration more generally.

2. Materials and methods

2.1. Study species and site

Eucalyptus leucoxylon is a tree that grows 8 to 30 m (Nicolle, 2013), occurs in southern Australian open woodland communities on fertile soils with a loamy horizon over clay (Armstrong et al., 2003), particularly where annual rainfall is >400 mm (Boomsma and Lewis, 1980). It is largely pollinated by birds, and to a lesser extent by insects and small mammals, and is predominantly outcrossing (Ellis and Sedgley, 1993; Ottewell et al., 2009). *E. leucoxylon* is protandrous and the close proximity of sequentially hermaphroditic inflorescences allows selfing to occur from adjacent flowers on the same plant (Ellis and Sedgley, 1993; House, 1997).

We established a common garden experiment within a 238 ha restoration site owned and managed by the South Australian Water Corporation (SA Water), near the township of Clarendon (−35.0882°S, 138.6236°E). The site was cleared >100 years ago and was managed under a grazing lease agreement until 2010. Restoration began in 2011 by SA Water and is ongoing. The local climate is Mediterranean, with hot dry summers and moderately wet winters (mean maximum summer temperature = 21.9 °C; mean maximum winter

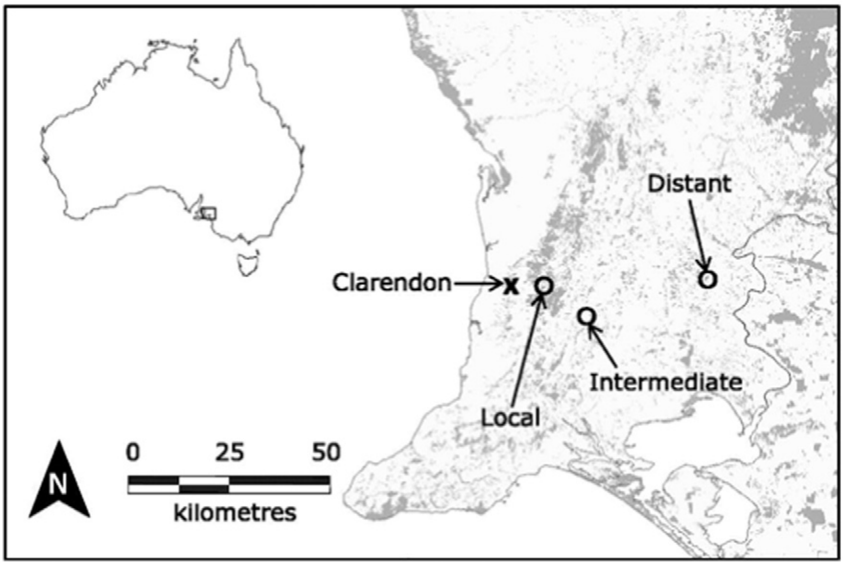

Fig. 1. Provenance localities (open circles), location of restoration site (x) and extent of remnant vegetation (grey shading).

temperature = 11.2 °C; mean annual rainfall = 790 mm. http://www.bom.gov.au/climate/data/, additional environmental data Table A1).

2.2. Seed collection and germination

We sourced seed from maternal trees of three provenances across a west-east aridity gradient to capture variation in precipitation and temperature that might contribute to establishment and performance differences across the provenances. The provenances were selected from intact native stands of >100 individuals. The stand densities of these provenances were 140 ± 21.3 SE plants ha^{-1}. Open-pollinated seed was collected from the canopies of at least 10 mature donor trees at each provenance. The provenance localities were Mt. Bold (35.1043°S, 138.6901°E; ca. 5 km from the restoration site; hereafter local provenance); Macclesfield (35.1612°S, 138.8517°E; ca. 20 km from the restoration site; hereafter intermediate provenance); and Monarto (35.1178°S, 139.1295°E; ca. 45 km from the restoration site; hereafter distant provenance) (Fig. 1).

The restoration site has a similar climate to the local provenance, with aridity, temperature and rainfall trending towards drier and hotter conditions in an easterly direction, towards the distant provenance. The restoration site has an aridity index of 1.01 (aridity index = mean annual precipitation / potential evapotranspiration), which is near the mean aridity index for the species (mean aridity index = 0.8 ± 0.01 SE). The selected provenances span a large proportion of the total range of aridity that *E. leucoxylon* occurs (e.g. 43% of the total aridity index present in the records for the species; local = 1.01; intermediate = 0.85; distant = 0.39, Atlas of Living Australia; http://spatial.ala.org.au/; Fig. A1).

Germination and rearing of seedlings was conducted in full-sun at a commercial nursery in South Australia (35.1264°S, 139.2359°E). A subset (n = 1434) of all the *E. leucoxylon* plants raised for this restoration project (n = 12,320) was randomly selected in the nursery and pots were marked for use in the common garden experiment (final sample sizes for analysis described below).

2.3. Common garden experiment

A fully randomised design was used where provenance was randomly assigned to a planting location within the restoration site (35.0882°S, 138.6235°E), and planting took place in June–July 2012. Plants were individually geo-referenced during planting using a Trimble Juno 3D GIS mobile field data collector (i.e. 1434 plants; $n_{local} = 477$; $n_{intermediate} = 513$; $n_{distant} = 444$). Each seedling was planted into ground which was mechanically prepared using a plough. A 200 × 200 × 400 mm UV stabilised corflute tree guard (Geofabrics) surrounded each seedling to protect against vertebrate herbivores (e.g. rabbits and kangaroos). We sprayed glyphosate herbicide in a 1 m radius of the planting site, with one follow-up spray 12 months post-planting. Each seedling was planted with a slow-release fertiliser tablet (Typhoon™ for Natives), and none were watered during or after planting. A mix of canopy species was planted over the entire restoration project at a density of ca. 150 stems ha^{-1}.

2.4. Fitness proxies

We scored four fitness proxies in November–December 2013 (ca. 15 months after planting; 19 months after germination) as follows. First, we scored plant survival. Plants were scored as either 'alive' if green foliage and/or a green stems were present or scored as 'dead' if no green foliage was present or no plant was found within the plant guard of a marked stake.

Plant fitness should in part be proportional to wood and stem production, which can be expressed as a function of height (Falster and Westoby, 2003). We scored aboveground height for each plant with a graduated telescopic surveyor's stave (Alumi Staff Pty. Ltd). Height was recorded as the vertical distance between the ground and the most distal photosynthetic tissue of each plant.

We scored each plant for the presence/absence of invertebrate herbivory (hereafter herbivory) and pathogen related stress (hereafter stress) to provide a proxy of biotic interactions of the plants (e.g. herbivory and stress resistance Linhart and Grant, 1996). The presence of herbivory was scored as present when ca. >5% of the entire foliage showed signs of herbivory. Stress was scored as present if leaf browning and fall were evident or leaf blight or rust was observed.

We excluded 35 ($n_{local} = 8$; $n_{intermediate} = 14$; $n_{distant} = 13$) of the 1434 plants that were planted but could not be relocated during our survey. A total of 1399 plants ($n_{local} = 469$; $n_{intermediate} = 499$; $n_{distant} = 431$) remained and were used for determining survival. Of these 1399 plants, 179 were dead ($n_{local} = 84$; $n_{intermediate} = 59$; $n_{distant} = 36$) and were excluded from provenance performance analyses. Hence, provenance effects on height, herbivory and stress was conducted on the remaining 1220 plants ($n_{local} = 385$; $n_{intermediate} = 440$; $n_{distant} = 395$).

2.5. Data analysis

We explored provenance effects on the four fitness proxies with generalised linear models in R v 3.2.3 (R Core Team, 2015). Provenance was treated as a fixed factor. The four fitness proxy response variables were treated as follows: survival, herbivory and stress were binary variables and a binomial link function was used; plant height was a continuous variable and data identity was used. Model residuals were visually assessed for normality and we used Box-Cox transformations of the data to meet normality of residuals assumptions where appropriate (Box and Cox, 1964).

Since plant height is likely to be associated with herbivory and stress among provenances, we explored the provenance effects on plant height controlling for variation of these two factors. We did this by including herbivory and stress as predictor variables together with provenance in the model exploring the variation in height, and including the herbivory × provenance and stress × provenance 2-way interactions.

To help demonstrate the influence of provenance on the fitness proxies, we calculated the relative home-site advantage for each fitness proxy by dividing the difference between local and non-local provenance fitness proxy values by the local fitness proxy value (e.g. for the relative home site height advantage of the intermediate provenance, we calculated [local height − intermediate height] / local height).

3. Results

We observed a striking difference in survival across provenances, with significantly higher survival of distant and intermediate

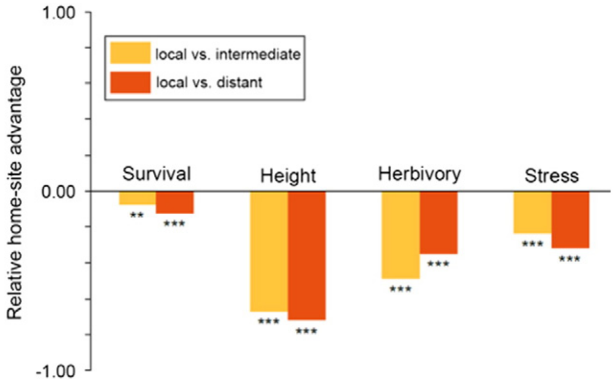

Fig. 2. Relative home-site advantage of the provenances for each of four fitness proxies. Results above the horizontal line would indicate a local advantage, and results below the line indicate local is not best. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

provenances than the local provenance (generalised linear model: link function = binomial; provenance z = −4.124; $P < 0.001$; local = 82.1%; intermediate = 88.3%, distant = 91.6%; Figs. 2, 3). Distant and intermediate provenances also grew significantly taller than the local provenance (general linear model: provenance z = −8.442; $P < 0.001$; local = 64.71 cm ± 1.25 SE; intermediate = 79.85 cm ± 1.34 SE; distant = 85.66 cm ± 1.44 SE; Fig. 4).

Distant and intermediate provenances had significantly less herbivory than the local provenances (generalised linear model: link function = binomial; provenance z = 4.894; $P < 0.001$; local = 46.6%; intermediate = 23.4%; distant = 30.0%; Figs. 2, 3), and exhibited significantly less stress than the local provenances (generalised linear model: link function = binomial; provenance z = 6.057, $P < 0.001$; local = 62%; intermediate = 20.4%; distant = 17.7%; Figs. 2, 3).

Herbivory and stress both had significant negative effects on plant height (general linear model: herbivory z = −6.451; $P < 0.001$; herbivory present = 69.36 cm ± 0.69 SE; herbivory absent = 80.19 cm ± 1.07 SE; stress z = −8.074; $P < 0.001$; stressed = 47.70 cm ± 1.65 SE; not stressed = 80.46 cm ± 0.81 SE). When we included both herbivory and stress in a model with provenance and explored their effects on height, each effect was significant as were the provenance × herbivory and provenance × stress 2-way interactions (generalised linear model: provenance: t = 73.750, $P < 0.001$; stress: t = 153.840, $P < 0.001$; effect: t = 24.742, $P < 0.001$; provenance × herbivory: F = 8.04, $P < 0.001$; provenance × stress: F = 5.57, $P < 0.01$, provenance: F = 73.50, $P < 0.001$; Figs. 5, 6).

4. Discussion

We embedded a common garden experiment into a large-scale restoration project to assess the impact of using local vs. more distant provenances on four fitness proxies for *E. leucoxylon*, a foundation tree species routinely used for restoration throughout southern Australia. Two non-local provenances from more arid environments were superior to the more mesic local provenance, indicating there would be limited benefits during establishment if a local seed source was solely used. Our findings suggest that benefits would be gained to restoration at this site with only modest adjustments to a local provenancing approach. For example, our results indicate that if the local seed sources were supplemented with the two provenances we explored, then between 6–10% greater survival, 20–25% greater plant height, and 16–45% more pathogen resistance could be obtained.

4.1. Local maladaptation

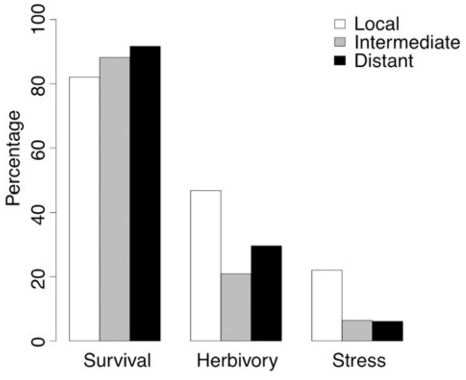

Fig. 3. Survival, herbivory and stress for the three *Eucalyptus leucoxylon* provenances.

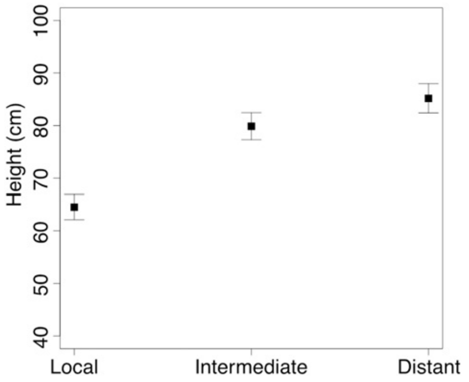

Fig. 4. Mean height of the three *Eucalyptus leucoxylon* provenances ± 95% confidence intervals.

Maladaptation is defined in a variety of ways, and we use the following definition here – lower fitness and performance of the local provenance compared with non-local provenances (Crespi, 2000). The less vigorous growth, lower survival and reduced resistance to insect herbivory and stress of the local provenance compared to the two alternate provenances indicates this local provenance is displaying maladaptation. Maladaptation can arise due to one or a combination of genetic factors (Crespi, 2000), for example a changed mating system (e.g. increased inbreeding) in the local provenance (Young et al., 1996; Breed et al., 2012a; Breed et al., 2015; Lowe et al., 2015), a legacy of founder effects in the local provenance (Travisano et al., 1995; Leimu and Fischer, 2008). Maladaptation can also be driven by environmental changes, where conditions change faster than the local provenance can adapt (Crespi, 2000; Christmas et al., 2015).

The mating system of eucalypts is often tightly linked with habitat fragmentation, where disrupted pollinator dynamics as a result of lower stand density can result in elevated selfing and reduced pollen diversity (Breed et al., 2015). Previous work has shown that these factors can impact on eucalypt fitness (Costa e Silva et al., 2010; Breed et al., 2012b; Breed et al., 2014). These fitness effects are expected to be particularly strong for predominantly outcrossing species, such as many eucalypts (Horsley and Johnson, 2007; Breed et al., 2015), which carry high genetic loads (Klekowski, 1988). Despite the populations in this study inhabiting a highly modified landscape, our sampling design specifically aimed to minimize fragmentation impacts by sourcing seed from mature, large and intact remnant stands with similar population densities. Further, the mating system of *E. leucoxylon* has been observed to be resilient to severe changes in density (Ottewell et al., 2009). Therefore, a provenance-dependent mating system effect, as a result of fragmentation impact, is unlikely to be the main cause of the maladaptation we observe.

Strong founder effects can result in severe genetic drift (Davies et al., 2010; Davies et al., 2015), which leads to a higher probability of fixation of deleterious alleles, resulting in maladaptation (Lenormand, 2002). Despite the fact that we do not have demographic history data for this species, we know that the regional refugium is likely to be in the Mt. Lofty Ranges (i.e. the local provenance), rather than the flatter, more

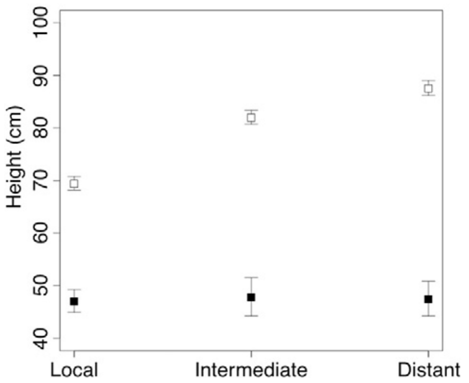

Fig. 5. Mean height of the three *Eucalyptus leucoxylon* provenances showing stressed (closed box) and not stressed (open box) plants. Error bars show 95% confidence intervals.

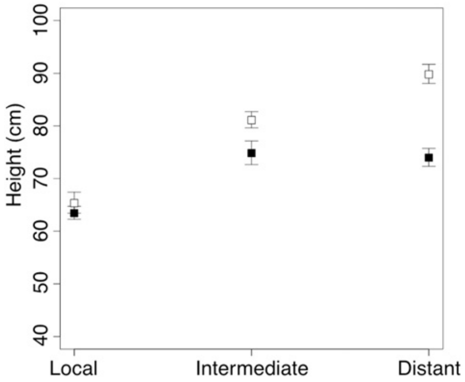

Fig. 6. Mean height of the three *Eucalyptus leucoxylon* provenances with herbivory (closed box) and without herbivory (open box). Error bars show 95% confidence intervals.

arid surrounding areas (i.e. the intermediate and distant provenances) (Byrne et al., 2008; Guerin et al., 2016). Thus, it is also unlikely that founder effects explain the maladaptation we observed in our study.

Environmental conditions might be changing faster than the local provenance can adapt, which may have driven the maladaptation we observed (Christmas et al., 2015). Aridity is likely to be a strong agent of selection in many eucalypt species (Steane et al., 2014; Booth et al., 2015; Dillon et al., 2015; Breed et al., 2016a), and it may be that we are detecting a signature of climate change impacts on the local provenance. Climate models suggest that southern Australia (including the study region) is undergoing significant increases in aridity (CSIRO and BoM, 2014). *E. leucoxylon* forms large populations with high inter-population gene flow (Ottewell et al., 2009; Nicolle, 2013), suggesting that effective population size and genetic diversity should be high (Petit and Hampe, 2006; Ottewell et al., 2010). Consequently, selection should have ample genetic variation to act upon, thus allowing selection to act efficiently (Lenormand, 2002) and not constraining adaptation in this system (Christmas et al., 2015). However, the long-lived nature of *E. leucoxylon* indicates that the selection that took place on the adult generation (the provenances used in our study) was under a pre-climate change environment, possibly resulting in an adaptation lag to the rapid climate change occurring today (Kremer et al., 2012). To further explore the extent of climate adaptation lag in *E. leucoxylon*, it is imperative to extend monitoring of this trial into the future, with a particular focus on differential recruitment between provenances. As aridity increases with climate change, a greater adaptation lag should manifest by maladaptation further increasing in years to come.

We also observed that the local provenance was more susceptible to herbivores and pathogens than the two non-local provenances in the common garden environment of this study. These results support the findings that pathogen severity in planted eucalypts is strongly affected by provenance (Stone et al., 1998), and strong negative correlations between leaf diseases and growth rate are the norm (e.g. in *Eucalyptus globulus*Carnegie et al., 1994). The differential herbivore impacts between provenances we observed was similarly observed in *Eucalyptus tereticornis* (Hancock and Hughes, 2014), where local provenances were more susceptible to phytophagous insects than non-local provenances. Follow-up studies are needed to fully explore whether the herbivore and pathogen responses identified in the local provenance were directly due to shifting herbivores and pathogens, or indirectly as a result of the poorer performance of the local provenance increasing its susceptibility to local herbivores and pathogens.

Overall, our study provides evidence of local maladaptation in *E. leucoxylon* from the southern Mt. Lofty Ranges in South Australia. To increase our understanding of the generality and spatial extent of maladaptation in this species, we need to perform more extensive trials, expanding on the number of trial sites and the number of provenances tested. Such trials could include peripheral provenances (e.g. testing performance of leading and trailing edge), which are likely to respond differently to selection and have different levels of adaptive potential (Kremer et al., 2014), or provenances that occupy past climate refugia as these could hold cryptic sources of genetic diversity (Temunovic et al., 2013). Furthermore, as highlighted recently in Prober et al. (2016), managing the potential interactions of local maladaptation with cryptic population structures, and non-climate related adaptations (e.g. community ecology issues such as pollinators), need to be managed at a site level. It would also be useful to test whether the intermediate and distant provenances were locally adapted, and a reciprocal transplant trial would resolve this query (Kawecki and Ebert, 2004).

4.2. Implications for management

We provide clear evidence that no advantage would be gained during the establishment of *E. leucoxylon* at this site by solely using the local provenance rather than including two additional provenances from more arid environments. The local and most mesic provenance performed considerably worse than two alternative and more arid provenances for each of four fitness proxies. Thus, we recommend that for *E. leucoxylon*, at least in this area, non-local and more arid provenances should be incorporated into additional restoration trials. We show that alternative and superior provenances could span up to 45 km into more arid locations. In this case, for example, even a conservative addition of more distant provenances into the seed mix, described in Broadhurst et al. (2008) as composite provenancing, would substantially reduce negative effects of exclusively using local provenancing. Thus, the results of this study provide a management option that is not reliant on local provenance (Breed et al., 2013), and is consistent with the directionality of provenance choice recommended by Prober et al. (2015). It is important that our trial is monitored into the future to study undetected responses of the non-local provenances, such as monitoring flowering time and the genotypes of recruits. It would also be important to establish additional trials that explore the responses of additional provenances from across a broader range of environments.

The ability of large restoration projects to achieve their goals will rely on the scalability of current practices to meet global demand (Merritt and Dixon, 2011), the certainty of seed supply (Broadhurst et al., 2016), and the capacity of restoration plantings to be dynamic and adjust to global change (Perring et al., 2015; Breed et al., 2016b). We were fortunate to be able to incorporate our experiment directly into a restoration project, and information garnered from this trial can be directly incorporated into the adaptive management framework of the stakeholders. Embedding experiments into restoration projects, such as we have done here, promises to improve the efficacy of restoration practices, and lead to innovation with real end-user impact (Suding et al., 2015). Undertaking these activities in partnership with the end-users will empower stakeholders and help develop strategies to scale-up restoration efforts to face the challenges set down by current global targets.

Data accessibility

Common garden data available from Aekos Digital repository for survival (Gellie et al., 2016a) DOI: 10.4227/05/57ECADFA02465, and growth (Gellie et al., 2016b) DOI: 10.4227/05/57ECB10786A57.

Acknowledgements

We would like to thank Matthew Christmas for fieldwork assistance, Phil Druce from Blackwood Seeds Pty. Ltd. for the collection and curation of seed resources. The authors also wish to thank the Australian Research Council for funding support (DE150100542 awarded to M.F.B., LP110200805 awarded to A.J.L., and DP150103414 awarded to A.J.L. and M.F.B.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.earlhumdev.2016.08.012.

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