The eco-evolutionary risks of not changing seed provenancing practices in changing environments

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June 2, 2023

Abstract

Rapidly changing environments combined with increasing global restoration initiatives require improved seed sourcing strategies for native revegetation. Sourcing seed from local populations (local provenancing) has been the long-standing default for native revegetation for numerous eco-evolutionary reasons including local adaptation and species co-evolution. However, the evidence-base has shifted, revealing risks for both non-local and local provenancing in changing environments. As alternative strategies gain interest, we argue for effective decision-making that weighs the risks of changing and not changing seed sourcing strategies in a changing environment that transcends a default position and the polarising local vs. non-local debate.

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Statement of authorship: All authors conceived this viewpoint and contributed to the writing and editing of the manuscript.

Running title: Risks of not changing provenancing practices

Article type: Viewpoint

'Abstract' (first paragraph) word count: 96

Main text (incl. 'abstract') word count: 1963

Number of references: 44

Number of figures: 0

Number of tables: 1

Data accessibility statement: No data associated with this study

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CONTEXT

Rapidly changing environments combined with increasing global restoration initiatives require improved seed sourcing strategies for native revegetation. Sourcing seed from local populations (local provenancing) has been the long-standing default for native revegetation for numerous eco-evolutionary reasons including local adaptation and species co-evolution. However, the evidence-base has shifted, revealing risks for both non-local and local provenancing in changing environments. As alternative strategies gain interest, we argue for effective decision-making that weighs the risks of changing *and not changing* seed sourcing strategies in a changing environment that transcends a default position and the polarising local vs. non-local debate.

Revegetation aims to restore ecosystems by reintroducing biodiverse plant communities that support key services and functions that humans rely upon (e.g., water filtration, carbon sequestration). How to best source seed to achieve resilient, long-term, self-sustaining plant populations has received substantial attention (Jones 2013; Prober*et al.* 2015; Bucharova 2017). Local provenancing targets adaptations that have evolved to maintain a fitness advantage to the local environment (Leimu & Fischer 2008; Hereford 2009), enhancing the establishment and long-term success of the revegetation plantings. Local provenancing also maintains important co-evolved biotic interactions such as plant-fungi and plant-pollinator relationships (Grady *et al.* 2017; Bucharova *et al.* 2021) whilst avoiding negative genetic effects of introducing non-local genotypes, such as outbreeding depression and swamping of local genotypes (Byrne *et al.* 2011; Bucharova *et al.* 2021). For these reasons, and others, local provenancing has been the long-standing default strategy for ecosystem restoration.

However, environmental change and associated impacts on plant fitness have raised concerns for the long-term viability of the default use of local provenancing. Changes to local environmental conditions (e.g., direct and indirect effects anthropogenic change, such as climate change and land-use) may decouple adaptation and fitness, resulting in greater risk of local seed being maladapted (Etterson & Shaw 2001; Anderson 2016). For example, seed sourced from small, fragmented local remnants can result in genetically depauperate, inbred progeny (Breed *et al.* 2015; Aguilar *et al.* 2019) that are less fit and more vulnerable to climate change (Nickolas *et al.* 2019). Thus, the perception that local provenancing is a 'safe' option may be misleading in a rapidly changing world (Frankham *et al.* 2011; Ralls *et al.* 2018).

Proposed alternative provenancing strategies that mix seed from local and non-local provenances aim to address these environmental change-induced issues by increasing genetic diversity or introducing putatively pre-adapted genotypes that enhance resilience and long-term adaptability to environmental change. Though there is a shift in perceptions toward these alternative strategies (e.g Australia, Hancock*et al.* 2023), concerns remain about the risk of using non-local provenances, with some sectors continuing to recommend only local provenancing (Hancock & Encinas-Viso 2021). Such hesitance possibly reflects a paucity of evidence on outcomes of using non-local provenances (Twardek *et al.* 2023). While risks associated with introducing non-local provenances in a revegetation context are valid, equally valid are the risks of using local provenances under current and future conditions.

Here, we argue that the risks of changing *and not changing* the local provenancing default in a changing environment needs to be weighed when determining the most appropriate provenancing strategy. We focus on the eco-evolutionary risks associated with provenance choice, including the short- and long-term fitness of plantings and their resilience and future adaptability, rather than whether provenances are local or non-local *per se* . We aim to help move the discussion away from a polarised local vs. non-local debate, and towards a risk-based, context-dependent rethinking of how to source seed for revegetation.

WHEN LOCAL MAY NOT BE BEST

The risks associated with maintaining the default local provenancing strategy may be greater from an eco-evolutionary perspective than using alternative strategies that include both local and non-local provenances (summarised in Table 1). While this is not an exhaustive list, we present four case studies, with the aim of highlighting the transition from a state of known risks for non-local provenances to a state of known risks for both non-local and local provenances.

Climate change shifting local advantage

As climates change, there is a risk of local adaptations becoming decoupled from environmental selective pressures, resulting in the maladaptation of local genotypes. Evidence of such decoupling was demonstrated in *Eucalyptus gunnii* , a subalpine foundation tree species endemic to Tasmania, Australia. Consistent with local adaptation, local provenances initially showed higher fitness in reciprocal common garden trials (Potts 1985). However, following two-decades of declining precipitation and increasing temperatures (Sanger *et al.* 2011), local provenance fitness declined (<30% survival), with the lower elevation, non-local provenance showing higher fitness than the local provenance (>70% survival; Prober *et al.* 2016). Similar impacts of changing environments have been observed in other forest species (Jump *et al.* 2009) and natural systems more broadly (Parmesan 2006; Scheffers *et al.* 2016).

While future change may decouple local adaptations from home environments, climate change to date may already be outpacing adaptation – an outcome known as adaptation lag. Evidence for adaptation lag was shown in *Quercus lobata* (valley oak), where two, early-age provenance trials showed greater relative growth of provenances when planted into cooler climates than their current homesite climate (˜10% greater growth; Browne *et al.* 2019). Using a genomics-informed selection model, Browne et al. (2019) predicted gains of up to 25% in relative growth of individuals pre-adapted to current environments of the test site (Browne *et al.* 2019). Optimal growth associated with historic rather than current climate is consistent with adaptation lag. While growth is a plastic trait and species may persist in suboptimal environments, similar evidence of adaptation lag has been shown in several tree species (Carter 1996; Aitken *et al.* 2008; Fréjaville *et al.* 2020).

Demographic and evolutionary history

Demographic history plays an important role in structuring the genetic and adaptive variation within and among populations (Hewitt 2000). The historical expansion from refugia or genetic bottlenecks can, for example, often leave evolutionary fingerprints that have fitness effects on modern-day populations. Such demographic processes have been argued to explain the differential survival and fecundity of two natural populations of *Arabidopsis thaliana* (Thale cress) from opposing latitudinal ends of its native European range (Sweden and Italy). While local provenances showed higher fitness on average in reciprocal transplant trials (Ågren & Schemske 2012), inter-provenance crosses between the two populations tended to have higher fecundity than the local provenance when planted in Sweden (Ågren *et al.* 2013). Furthermore, several Italian alleles provided a fitness advantage over the Swedish alleles when plants were grown in Sweden (Ågren *et al.* 2013). Demographic history, in particular postglacial expansion in northern Europe reducing genetic variation most likely led to increased fixation of these maladaptive alleles.

Novel environments from land use change

In some situation, environmental change, such as mining, agriculture, and deforestation, has resulted in novel environments. This presents a risk that the local provenances may no longer be fit for these novel, local conditions. Evidence of this is shown in two metallophyte legumes,*Mimosa acutistipula* var. *ferrea* and *Dioclea apurensis* , which are promising candidates for the restoration of degraded areas of mineral rich soils in the Amazon, Brazil. Adaptive genomic variation showed that local provenances would perform best in moderately disturbed sites (e.g., sites altered by fire) (Carvalho*et al.* 2020). However, no provenance in the sampled area matched predictions for highly disturbed sites with substantially altered conditions (i.e., ex-mining sites; (Carvalho *et al.* 2020). With no suitable local provenance, regional mixing across multiple adaptive units was recommended to capture genetic variation and enhance adaptability, thereby de-risking revegetation plantings. Together with previous findings of rapid, microgeographic adaptation post-mining (e.g. Antonovics and Bradshaw 1970; Antonovics 2006), these results highlight that provenance choice may vary dependant on site history, with environmental changes having the potential to significantly influence provenance fitness in novel environments.

Together, these examples highlight that current and future environmental changes may have reduced local provenance fitness, and thus increased the risk associated with using local provenances in particular revegetation contexts. Further, they highlight the need to consider current and future environmental change, climate and anthropogenic, as well as effects of evolutionary history (e.g. demographic history) when selecting provenances, to ensure both the short- and long-term fitness and productivity of revegetation plantings. One approach could be mixing local seed with seed from non-local provenances already occupying current or future climates, which may de-risk the long-term resilience of revegetation plantings.

MOVING AWAY FROM A DEFAULT

Reframing provenancing strategies on eco-evolutionary risks highlights that all strategies come with risks, even local provenancing. We recommend moving the discussion beyond the local vs. non-local debate and towards context-dependant choices that enhance resilience and future adaptability. Growing evidence suggests that no single strategy will be appropriate for all contexts. Rather, the most appropriate strategy in any situation will be influenced by a range of context-dependant factors.

To create resilient plantings, provenancing must consider the dynamic conditions imposed by environmental change (Aitken & Bemmels 2016). Genetic variation is a key factor in long-term evolutionary resilience and adaptability (Sgrò *et al.* 2011; Kardos *et al.* 2021). Provenancing strategies that mix local and non-local provenances aim to boost resilience by increasing genetic diversity, including adaptive variation. Considering eco-evolutionary genetics can therefore help guide whether local, non-local or a combination of both may be most appropriate to enhance genetic variation and thus adaptability in any given situation (Hoffmann *et al.* 2020). While we focussed on the eco-evolutionary risks associated with provenance choice, other factors may influence provenance choice, including ecological (e.g., biotic interactions; (Bucharova *et al.* 2021), logistical (e.g., availability of seed; (Broadhurst *et al.* 2016) and socio-cultural (e.g., significance of local genetic identity of plants; Maurice*et al.* 2013). However, these factors need to be weighed against the eco-evolutionary risks associated with not changing provenancing strategy, especially in changing environments.

Moving forward, it will be important to address barriers and knowledge gaps that currently inhibit context-dependant provenancing decisions. These include better understanding of the long-term performance, and risks associated with, both local and non-local provenances for different species in different restoration contexts and deriving practical guidance on provenancing choice (Breed *et al.* 2018). Greater direct evidence on the long-term performance of not only different provenances (e.g., local and non-local provenances) but also different provenancing strategies will also assist decision-making (Bailey *et al.* 2021). Determining whether generalized recommendations can be derived based on plant life history, functional traits and/or genomic information across species will also help guide recommendations for species without empirical data.

Several initiatives are working to address these knowledge gaps. For example, there are already several practitioner guides that incorporate climate uncertainty, evolutionary genetics, and landscape fragmentation into seed sourcing decisions with the aim of increasing genetic diversity and adaptability (Harrison *et al.* 2017; Rossetto*et al.* 2019). Establishing long-term provenance trials (as per example 1 above), especially those that are embedded within mixed species revegetation plantings (e.g. Bailey *et al.* 2021), will help generate long-term fitness data on provenances in a relevant revegetation context and thus help enable adaptive seed sourcing decisions into the future.

CONCLUDING REMARKS

With a focus on eco-evolutionary factors, our viewpoint is that no provenancing strategy is risk free. The risk of changing from the default local provenancing strategy needs to be weighed against the risk of not changing. We do not suggest local provenancing is no longer appropriate, nor that provenancing strategies must change from local. There are clear situations where local will be most appropriate and where factors not discussed in depth here (e.g., logistics and cultural) may influence provenance choice more than eco-evolutionary factors. Rather, the choice of provenancing strategy should consider all risks when determining the most appropriate provenancing strategy for a given species and context. As such, the intention of our paper is to move the discussion of provenancing away from a default strategy and whether local provenances are more-or-less appropriate than non-local provenances, and towards conscious and context-dependent provenancing decisions.

ACKNOWLEDGEMENTS

We thank Linda Broadhurst, Ary Hoffmann and Suzanne Prober for comments on an earlier draft of this manuscript. This work was supported by the Australian Research Council (grant numbers LP190100051, LP190100484, DP180100668, DP210101932 to M.F.B; and P.A.H was supported by IC150100004). All authors declare that, to the best of their knowledge, they have no conflicts of interest.

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Table 1: Examples of where only local provenancing may not be best and pose a risk to the long-term success of restoration plantings.

FIGURE REPRINT PERMISSIONS REQUIRED

ISSUE	Long term performance	Adaptation lag	Demographic history	Altered environments
	Short term fitness not indicative of long term or life-time fitness, especially for long-lived organisms	Adaptation not keeping pace with climate change, resulting in local being adapted to historic not current conditions.	Demographic history, such as recent expansion and bottlenecks, may reduce local adaptation.	Significant environmental changes, especially anthropogenic change, resulting in novel local conditions
Species	Cider gum (*Eucalyptus gunnii-archeri*)	Valley oak (*Quercus lobata*)	Thale cress *(Arabidopsis thaliana)*	Metallophyte legumes (*Mimosa acutistipula* var *ferrea* and *Dioclea apurensis*)
Location	Tasmania, Australia [1]	California, USA [2]	Sweden and Italy [3]	Amazon, Brazil [4]

Overview	35 year old provenance trial. Survival, growth and frost damage used to assess provenance performance.	Combined common garden trials and genomic analysis; assessing relative growth and associated genomic loci	Multi-year reciprocal transplant trials and genomic analysis assessing performance of both wild and F1 recombinant inbred lines.	Genomic analysis; predicting performance based on genotype-climate and genotype-phenotype associations.
Key finding	Performance of local declined over time, with non-local outperforming local after 25 years.	Predicted greater growth using non-local seed sources accounting for adaptation lag.	Swedish population was most fit in Sweden in only 3 of 5 years; Swedish alleles in Sweden were often maladaptive.	Local genotypes predicted not to match highly disturbed (ex-mining) sites.
Take home	**Local not best in long-term, despite initial short-term outcomes**	**Local already not best due to adaptation lag behind recent climate changes**	**Local not most fit due to demographic history impacts on local populations**	**Local no longer suitable where site conditions have significantly changed**

[1]Prober et al. 2016; [2] Browne et al. 2019;[3] Ågren *et al.* 2013; Ågren & Schemske 2012;[4] Carvalho et al. 2020