

Which provenance and where? Seed sourcing strategies for revegetation in a changing environment

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Abstract Revegetation is one practical application of science that should ideally aim to combine ecology with evolution to maximise biodiversity and ecosystem outcomes. The strict use of locally sourced seed in revegetation programs is widespread and is based on the expectation that populations are locally adapted. This practice does not fully integrate two global drivers of ecosystem change and biodiversity loss: habitat fragmentation and climate change. Here, we suggest amendments to existing strategies combined with a review of alternative seed-sourcing strategies that propose to mitigate against these drivers. We present a provenancing selection guide based on confidence surrounding climate change

distribution modelling and data on population genetic and/or environmental differences between populations. Revegetation practices will benefit from greater integration of current scientific developments and establishment of more long-term experiments is key to improving the long-term success. The rapid growth in carbon and biodiversity markets creates a favourable economic climate to achieve these outcomes.

Keywords Climate change · Habitat fragmentation · Inbreeding · Local adaptation · Outbreeding depression · Plant genetic resources · Revegetation

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Introduction

Revegetation is the reinstatement of native vegetation to landscapes that have experienced considerable clearing through, for example, agricultural or urban development. The rapid growth in carbon and biodiversity credit markets has created great demand for revegetation (Galatowitsch 2009; e.g. AU \$946 million Australian Government Biodiversity Fund), and consequently the economic climate is favourable to replace large areas of lost native vegetation through revegetation. This provides an opportunity to greatly benefit biodiversity conservation and reinstate disrupted ecosystem services globally (Vesk and Mac Nally 2006). Revegetation is not equivalent to ecological restoration (SER 2004), but successful restoration often depends on revegetation where restoration goals require reinstatement of plant populations.

To date, the outcomes of revegetation projects have had mixed success (Wuethrich 2007; Chazdon 2008; Godefroid et al. 2011), leading to greater attention from evolutionary and conservation biologists investigating optimal seed-

sourcing strategies in the face of increasing pressures from climate change and anthropogenic disturbance (Broadhurst et al. 2008; Crowe and Parker 2008; Byrne et al. 2011; Hoffmann and Sgrò 2011; O'Neill and Nigh 2011; Sgrò et al. 2011; Weeks et al. 2011). Additionally, since revegetation generally involves planting long-lived perennials (i.e. trees, shrubs; Broadhurst et al. 2008) biologists have tended to focus on these taxa.

The most widespread seed-sourcing practice is local provenancing (see 'Selecting a suitable seed-sourcing strategy' below for details). This practice has wide support among managers (Hamilton 2001; Broadhurst et al. 2008). A local provenancing approach holds that if local seed is used for revegetation, most seed will be locally adapted and therefore maladaptation and outbreeding depression will be minimised, increasing establishment success rates (Montalvo et al. 1997; Hufford and Mazer 2003; McKay et al. 2005; O'Brien et al. 2007; Kramer and Havens 2009; Mijnsbrugge et al. 2010; O'Brien and Krauss 2010). Definitions of 'local' vary from prescribed collecting within a set geographic distance to revegetation sites, to matching particular ecological criteria between source and site. However, several studies have raised concerns over the suitability of local populations as seed-sources given the recent changes in revegetation sites due to environmental disturbance (Lesica and Allendorf 1999; Wilkinson 2001; Kramer and Havens 2009; Johnson et al. 2010; Mijnsbrugge et al. 2010; O'Brien and Krauss 2010). Additionally, concerns relating to overharvesting and the potentially poor genetic health of local populations (i.e. inbred or bottlenecked) in modified landscapes have also been raised (Mortlock 2000; McKay et al. 2005; O'Brien et al. 2007; Broadhurst et al. 2008; Kramer and Havens 2009; Bischoff et al. 2010; O'Brien and Krauss 2010). These criticisms have led to the development of a range of alternative seed-sourcing strategies that aim to more fully capture evolutionary processes to deal with changing environmental conditions and that take into account key genetic issues associated with disturbed landscapes.

Recent seed-sourcing developments

Taking an evolutionary viewpoint, Broadhurst et al. (2008) discussed evidence supporting current guidelines and the future of revegetation with and without changes to these guidelines. They questioned local provenancing, arguing for an alternative strategy, termed 'composite provenancing'. Composite provenancing attempts to keep the benefits and reduce the risks associated with combining a local sourcing approach with material from more distant sources in a way that attempts to mimic natural gene flow dynamics.

Three studies have advocated a data intensive strategy to selecting provenances based on seed 'transfer functions' or 'universal response functions', by matching provenance growth trial data with predicted future climates using a climate modelling approach (Crowe and Parker 2008; Wang et al. 2010; Sgrò et al. 2011). For this strategy, provenances are selected based on their expected improved performance over local sources under particular projected climates—a strategy called 'predictive provenancing'.

Byrne et al. (2011) and Weeks et al. (2011) discussed aspects of genetic risks (e.g. outbreeding depression, invasive genotypes) and potential benefits of genetic translocations (e.g. genetic rescue, heterosis) for revegetation. These issues apply to provenancing methods that recommend mixing material from a number of sources.

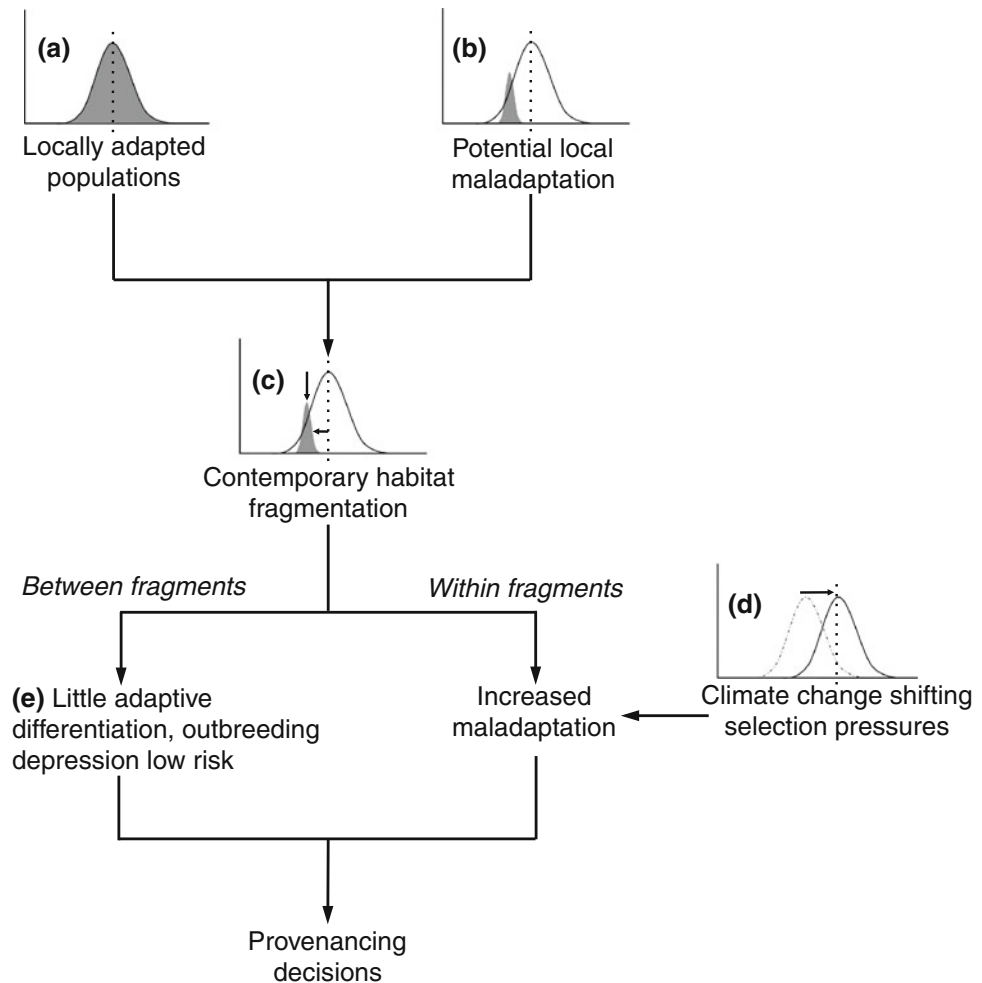
However, despite recent attention being paid to alternative seed-sourcing approaches, a current synthesis of these alternatives that integrates the issues raised by Byrne et al. (2011) and Weeks et al. (2011) is lacking. Here, we assess the relative strengths and weaknesses of current and proposed provenancing strategies with a synthesis of information on key underpinning evolutionary and population processes (Fig. 1). We discuss how these processes are likely to interact in contemporary landscapes with climate change pressures to impact provenance choices. We introduce a complementary strategy as part of this framework, termed 'admixture provenancing' (see 'Selecting a suitable seed-sourcing strategy' below for details), which aims to maximise adaptive potential and heterosis in revegetated populations. We hope to stimulate discussion around seed-sourcing techniques for long-lived perennials, and we identify experiments that should help test the outcomes of the different strategies and inform land managers to make decisions that drive resilience to habitat fragmentation and climate change—the major environmental challenges facing biodiversity today.

Evolution of local adaptation and maladaptation

Native populations are expected to be locally adapted, but may not universally be so (Gould and Lewontin 1979; Leimu and Fischer 2008; Hereford 2009), partly because organisms are adapted to at least one generation in the past, the time of their conception (Kawecki 2000). For example, a recent meta-analysis of local adaptation in plants (Leimu and Fischer 2008) reported that across 32 species, only 45 % of 1,032 paired population comparisons gave evidence for a genotype-environment interaction—classic evidence for local adaptation (Kawecki and Ebert 2004).

Hypothesised factors driving local adaptation are numerous. In the recent meta-analysis on local adaptation in plants, population size ($N > 1,000$) displayed a positive relationship

Fig. 1 Interaction of recent habitat fragmentation, climate change, maladaptation and outbreeding depression risks in relation to provenancing decisions. Naturally, populations may either be locally adapted (a) or maladapted (b) and may become increasingly maladapted due to the genetic effects of habitat fragmentation (c). Climate change is shifting population selection pressures (d). Adaptive differentiation is unlikely to have had sufficient time to cause high risks of outbreeding depression upon crossing of provenances isolated by contemporary habitat fragmentation (e). Simple fitness landscapes are used to visualise the relationship between a given environment's fitness optima (solid curve with dotted line indicating fitness peak), the fitness of a local population (shaded area), and the fitness optima of the recent past (dotted curve in d). Genotypes are represented on the x-axis, and the y-axis corresponds to fitness



with local adaptation (large populations were 27 % more likely to be locally adapted; (Leimu and Fischer 2008). Greater environmental differences between population pairs was also associated with greater local adaptation across all taxa, but with weak effect ($r^2 = 0.04$; Hereford 2009).

Conversely, maladaptation is a fitness difference between mean observed fitness of a population (or an organism) and the optimal phenotype in a given environment (Crespi 2000). It has many potential drivers with random genetic drift and inbreeding both potent and frequent causes (Crespi 2000; Lowe et al. 2005; Lopez et al. 2009). Maladaptation might have evolved in target revegetation species due to genetic drift being accentuated in small populations, and typically exhibited in remnant ecosystem patches in fragmented landscapes. Additional drivers of maladaptation include gene flow (e.g. homogenisation among-population allele frequencies or introducing a migration load; Lenormand 2002), temporal and spatial variation in natural selection resulting in confounding or opposing selection pressures (Kawecki and Ebert 2004) and genetic constraints (Weinreich et al. 2009).

Climate change and shifting selection pressures

A key assumption of local provenancing is that local genotypes are adapted to local environments, thus they should outperform exotic genotypes under local conditions. The distribution of plant species is often tightly linked with climate, as demonstrated by past range shifts in response to climatic changes across many species (Davis and Shaw 2001). However, there is unequivocal evidence that long-lived perennial plants are being forced to adapt or migrate due to contemporary climate change (Parmesan 2006). Therefore, selection pressures are changing over short periods of time (North et al. 2011; Bellard et al. 2012), introducing the risk that local seed is not best suited to local conditions—i.e. that local seed has increased genetic load.

There is growing evidence that many species may not have the migrational capacity to keep pace with current and future predicted climatic changes (Breed et al. 2011; Nathan et al. 2011; Zhu et al. 2011), and the selection pressures generated are predicted to be unprecedented (Beaumont et al. 2011; Hoffmann and Sgrò 2011).

Accordingly, many local genotypes are at risk of being maladapted or unable to adapt in situ to future conditions. As such, to help facilitate rapid evolution of populations to novel or rapidly changing conditions, revegetation projects could actively encourage novel gene combinations by admixing individuals from different populations (North et al. 2011). However, by admixing, outbreeding depression is introduced as a serious risk.

Outbreeding depression risks and genetic rescue

Concern about outbreeding depression, resulting from crossing local and non-local provenances, is a central supporting argument for local provenancing (Montalvo et al. 1997; Hufford and Mazer 2003; Kramer and Havens 2009). Outbreeding depression can result from the disruption of gene–gene (e.g. co-adapted gene complexes) or gene–environment interactions (e.g. maladapted gene introduction; Edmands 2007; Frankham et al. 2011). Outbreeding depression risks are expected to increase with greater adaptive differentiation or fixed chromosomal differences between provenances (Edmands 2007; Byrne et al. 2011; Frankham et al. 2011). Indeed, a recent study by Forrest et al. (2011) investigated optimal outcrossing distances in *Grevillea mucronulata* and reported that inbreeding and outbreeding depression was a function of geographic (and genetic) distance. Crosses of plants separated by intermediate distances (>20 m but <5 km) resulted in highest fitness offspring, with outbreeding depression observed in crosses beyond 5 km.

However, in contemporarily fragmented landscapes (<200 years), neither adaptive differentiation nor fixed chromosomal differences are likely to have evolved (Frankham et al. 2011). Consequently, crossing provenances that were genetically connected prior to fragmentation is predicted to have a low risk of outbreeding depression. Nonetheless, a cautious approach is still warranted for species that exhibit strong historical subdivision, when considering mixing seed provenances over strong environmental gradients or over distances greater than historical gene flow (Byrne et al. 2011; Weeks et al. 2011). In these cases, experimental investigations are warranted (see ‘[Transitioning to evidence-based revegetation](#)’ section below for details).

Novel gene combinations are powerful tools when future environmental uncertainty is high, but generating them needs to be balanced with risks of outbreeding depression and creating invasive genotypes must be avoided (Prentis et al. 2008; Byrne et al. 2011). However, of potentially greater concern is the effect that contemporary fragmentation has on plant mating patterns—these mating patterns directly impact the fitness of future generations (Breed et al. 2012; Breed et al. in press).

Fragmentation increases maladaptation and decreases adaptive potential

Since revegetation generally occurs in fragmented areas (Vesk and Mac Nally 2006; Broadhurst et al. 2008) it is important to integrate plant responses to fragmentation with seed-sourcing strategies. In a fragmented landscape, population size is decreased and pollination dynamics are disrupted (e.g. by disrupting plant–pollinator mutualisms; Vranckx et al. 2011; Breed et al. 2012). Disruption of pollination dynamics often leads to mating pattern shifts within fragments, which can have strong fitness impacts leading to maladapted offspring (Lowe et al. 2005; Breed et al. 2012; Breed et al. in press). Reproductive failure can occur if insufficient compatible pollen is deposited (Cheptou and Avendaño 2006). A reduction in pollen diversity can reduce progeny fitness by increasing the probability of unfit combinations of pollen and ovules (Breed et al., in press).

Probably the most detrimental impact to plants inhabiting a fragmented landscape is that inbreeding generally increases in sexual species, either through increased self-pollination or breeding between related parents (Lowe et al. 2005; Eckert et al. 2010; Breed et al. 2012). Indeed, Breed et al. (2012) showed that fitness of *Swietenia macrophylla* offspring sourced from populations in mesic provenances was directly impacted by reduced outcrossing rate (i.e. increased inbreeding). Outcrossing rate declined as a result of changes to pollination dynamics in fragmented stands.

These fitness impacts of increased inbreeding are likely to be most severe in species that primarily outcross (outcrossing is the predominant character of long-lived perennials; Petit and Hampe 2006), since it is outcrossing species that generally carry high genetic loads, which following inbreeding, can cause significant inbreeding depression (Crnokrak and Barrett 2002). Regardless of mating system, the expression of inbreeding depression is expected to be higher in stressful environments (Cheptou and Donohue 2010) and is likely to become more severe given an increase in environmental stress with climate change (Beaumont et al. 2011). Consequently, it would be preferable to mitigate against inbreeding depression by minimising collection of progeny from fragmented populations.

Selecting a suitable seed-sourcing strategy

Each provenancing strategy varies in its suitability to provide cost-effective and positive outcomes in the face of environmental change (Fig. 2). Selecting an appropriate strategy is determined by its likelihood of avoiding maladaptation, inbreeding depression and outbreeding

depression while integrating the need to facilitate genetic rescue and ensure adaptive potential where appropriate (each described above). Uncertainty surrounding climate change predictions at regional and local scales (Wiens et al. 2009; Buisson et al. 2010; Beaumont et al. 2011) imposes a restriction to strategies that rely on these data.

Local provenancing generally prescribes **strict collection of seeds located physically very close to the revegetation site** (e.g. English Nature, United Kingdom: 5 miles; Western Australian Forest Management Plan 2004–2014: 15 km; Broadhurst et al. 2008). A more relaxed local provenancing prescribes collecting seeds in a fashion that is biased towards certain ecological criteria and avoids small population fragments (e.g. Australian FloraBank: soil type, altitude and climate; Broadhurst et al. 2008). Thus, local provenancing is well suited to avoid maladaptation and outbreeding depression. Failure rates are expected to be low under current climate conditions as long as seed is collected from genetically healthy populations. However it does come with a number of limitations that risk undermining these benefits in the long-term.

Local provenancing risks facilitating strong genetic drift since sampling from narrow genetic bases is encouraged (small, fragmented and/or few populations; Broadhurst

et al. 2008), compromising the future adaptive potential of revegetation populations. Additionally, this strategy does not encourage generating novel genotypes through genomic admixture, limiting a potentially important way of overcoming future environmental uncertainty. Furthermore, if seed is collected from fragmented populations local to the revegetation site, there is also a risk of introducing offspring suffering from inbreeding depression. However, collecting seeds from large local populations should avoid creating populations with low adaptive potential and a high risk of inbreeding depression. Strict local provenancing will not account for shifting selection pressures due to climate change, which risks using genotypes that are genetically maladapted to local conditions.

By avoiding small, fragmented populations, local provenancing still has great utility. Clearly, a local provenancing approach would be most suitable in situations where only local populations remain (Fig. 2a) or if no significant range shifts are confidently predicted under climate change (Fig. 2b). Additionally, as a precautionary step, it would be best suited where it is unfeasible to assess genetic or environmental differences of possible source populations to avoid risking the introduction of invasive genotypes and excessive outbreeding depression (Fig. 2c).

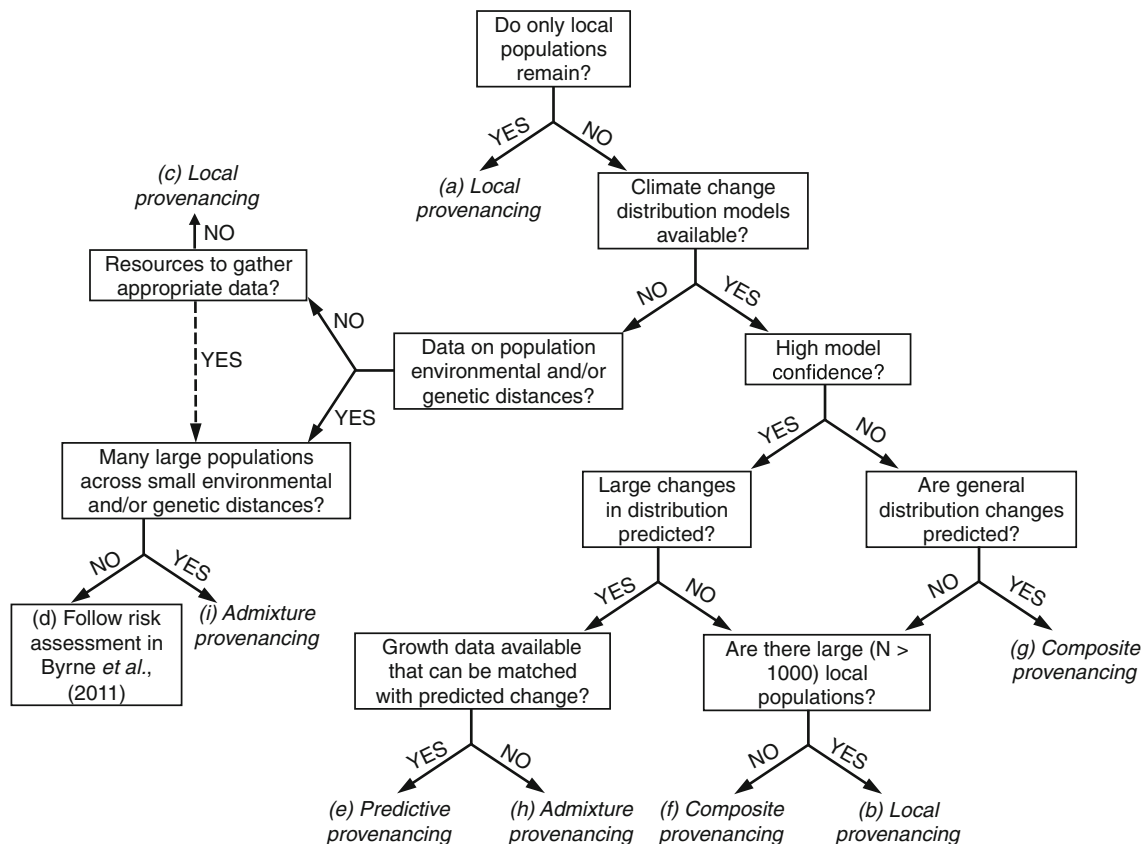


Fig. 2 Provenance strategy decision tree. Decisions are based on evidence and confidence surrounding climate change distribution modelling and the degree of population genetic and/or environmental difference between populations

It would also be suitable where only local populations and strongly genetically or environmentally divergent populations exist (see Byrne et al. 2011; Fig. 2d). However, alternative strategies are better placed than local provenancing when these factors are of serious concern.

Predictive provenancing (Crowe and Parker 2008; Wang et al. 2010; Sgrò et al. 2011) prescribes the use of naturally occurring genotypes that are experimentally determined to be adapted to projected conditions. This technique requires data on local adaptation of many populations (e.g. by reciprocal transplant experiments) as well as climate projections for the target species including the revegetation site (e.g. by bioclimatic modelling; Fig. 2e). Sgrò et al. (2011) suggested matching seed stock with 2050 projections.

While this strategy seems to deal directly with changing climatic conditions, there still remains high uncertainty surrounding climate modelling (Wiens et al. 2009; Buisson et al. 2010; Beaumont et al. 2011). If climate predictions are incorrect (e.g. caused by unforeseen synergies; Brook et al. 2008), then there is a high risk of failure since the selected genotypes are likely to be adapted to a narrow range of conditions. Additionally, since for most species provenance growth trial and population genetic data are not available, it is problematic to match provenances with future conditions without significant investment in gathering these data. Thus, since this provenancing method relies on these data streams it will have limited use due to lack of these data or budget limitations.

However, this strategy is positioned well to avoid maladaptation, inbreeding depression and outbreeding depression if matching seed source with future environments is done correctly. **Predictive provenancing will require significant investment into developing robust supporting datasets (e.g. local adaptation data for many genotypes/provenances).** However, if successful, this strategy should produce low failure rates and require little ongoing maintenance, recouping the costs of initial investment in data collection. Because of its high cost, predictive provenancing is likely to have greatest utility for high value species (e.g. forestry and threatened species) and where there is high confidence in future climate predictions. Thus, predictive provenancing is a strategy that is most applicable for species expressing local adaptation to environmental variables likely to undergo predictable and significant shifts in climate (Fig. 2e).

Wang et al. (2010) proposed a novel approach of predictive provenancing that integrated both the genetic and environmental effects of climate on phenotypes. They developed this method utilising phenotypic data from 140 populations of *Pinus conectora* planted in 62 growth trials monitored for over 20 years—the Illingworth lodgepole pine provenance trial. This extensive dataset was used to

match *P. conectora* provenances with various climate scenarios, which effectively matched the phenotype of a provenance with climate predictions at 2050 and 2080. Thus, this species was a good candidate for predictive provenancing because extensive phenotypic and climate modelling data were available.

Composite provenancing (Broadhurst et al. 2008) prescribes collecting a mixture of seed from populations of increasing distance that attempts to mimic natural gene flow patterns. However, for most species, population genetic or gene flow data are not available, making it problematic to delineate local, intermediate and distant provenances. Local, intermediate and distant distance-classes could be determined by identifying areas of population genetic differentiation. For example, it would be possible to use neutral genetic markers (e.g. microsatellites or AFLPs) and follow suggestions by Krauss and Koch (2004) to delimit genetic seed zones (i.e. within distances of positive spatial genetic structure) or by determining distance categories based on estimates of historical gene flow (e.g. local $F_{ST} < 0.05$; intermediate $F_{ST} > 0.05 < 0.1$, distant $F_{ST} > 0.1 < 0.2$).

Targeting seed collection to larger populations addresses genetic resource problems associated with small populations, thus avoiding inbreeding depression and capturing adaptive potential. Since this strategy encourages collection of seed over broad areas, the generation of novel gene combinations is increased, potentially facilitating rapid adaptation to novel conditions. However using seed from broad areas comes with risks, as seed may be maladapted to local conditions and crossing could result in outbreeding depression. These effects would reduce planting success. As such, increased sowing/planting density or follow-up plantings may be required, but the cost of doing so should be offset by strong recruitment of high fitness genotypes from the remaining stock, leading to low ongoing maintenance costs.

Thus, composite provenancing would be most suitable in situations where no significant range shifts are predicted under climate change but only small local populations remain (Fig. 2f) or where only general trends are attainable about range shifts under climate change scenarios (Fig. 2g). In the latter case, seeds should be collected in a fashion that is biased to the direction of predicted environmental change.

Using herbarium data, Guerin et al. (2012) linked *Dodonaea viscosa* subsp. *angustissima* leaf shape with contemporary climate change in the Adelaide Geosyncline region, South Australia. This region is highly fragmented due to urban and agricultural development and climate modelling predicts that plant distributions will generally shift in a southerly and up-altitude direction (Guerin and Lowe, in press). However, no published bioclimatic

modelling has been performed on *D. viscosa* subsp. *angustissima*. Thus, with the current extent of knowledge, composite provenancing is most suitable because: (1) it is likely that climate change is shifting selection on traits with adaptive significance; (2) general directional changes in climate are predicted; (3) regional populations are mostly fragmented, which is likely to impact seed quality; and (4) the taxonomy of *D. viscosa* subsp. *angustissima* is well resolved in the study region (Harrington and Gadek 2009).

Admixture provenancing, as proposed in this study, is similar in approach to composite provenancing whereby seed is collected from large populations, but is focused on capturing a wide selection of genotypes from various environments with no spatial bias towards the revegetation site and, as opposed to composite provenancing, has no regard to gene flow dynamics. Collected seeds are admixed for sowing/planting, generating a population with a mixture of genotypes from a wide array of provenances. Environmental differences between seed source and revegetation site (e.g. soil) should not be maximised, since environmental differences tend to predict revegetation success today (Hereford 2009; Noël et al. 2011). However, collecting seeds from across different environments is important to build evolutionary resilience into the plantings, as more additive genetic variation would be introduced, which would give more opportunities for the population to successfully adapt to novel conditions. Accordingly, this strategy would be useful in systems where drastic changes in conditions are confidently predicted but it is not feasible to collect sufficient growth data (Fig. 2h). In this case, seed should be collected from populations in the general direction of climate change predictions. It would also be suitable where it is not feasible to generate distribution models under climate change scenarios and many large populations exist across only minor genetic or environmental differences (Fig. 2i).

However, translocating novel genetic variants presents a risk of introducing invasive genotypes (or even species), which may outcompete local genotypes and potentially disrupt ecological processes (e.g. pollination via changes in flowering time; Byrne et al. 2011; Weeks et al. 2011). Therefore, we recommend that if taxonomic relationships have not been resolved, or if seed movement is planned over large eco-geographic distances (e.g. > 500 km, over strong environmental gradients or known biogeographical boundaries), that the genetic distance or chromosome compatibility between ecotypes should be estimated or tested first. If large genetic or environmental differences are present, we recommend following an assessment of genetic risk as outlined by Byrne et al. (Byrne et al. 2011; Fig. 2d).

This strategy has high risks of introducing maladapted seed and crossing between divergent genotypes that could

result in outbreeding depression. However, since the majority of these maladapted genotypes will likely be purged during the establishment phase, ongoing maintenance costs would be low as strong recruitment of advantageous genotypes from the remaining genetic stock negates the need for infill plantings.

A case where admixture provenancing may be well suited was presented by Breed et al. (in press). The authors studied *Eucalyptus socialis*, a long-lived tree from southern Australia (Clarke et al. 2010). There are only weak environmental differences across the region (e.g. soil, climate, vegetation communities; Jennings 2009), many *E. socialis* populations are highly fragmented (Breed et al. in press), weak population genetic differentiation was observed across the region ($G_{ST_est} < 0.01$; Breed et al. in press) and its taxonomy is well resolved (Slee et al. 2006). However, fragmentation was shown to drive negative shifts to the seed quality of *E. socialis* but the influence of climate change on the species and region is not well studied. Thus admixture provenancing is suitable because: (1) only weak environmental differences are present across the region, thus it is unlikely that *E. socialis* expresses strong local adaptation; (2) genetic and taxonomic evidence suggests that mixing *E. socialis* seed from across the region poses a low risk of introducing invasive genotypes and outbreeding depression; (3) there are insufficient data on climate predictions to bias the directionality of seed collections; and (4) fitness impacts of habitat fragmentation were demonstrated.

Transitioning to evidence-based revegetation

Facing significant environmental change, revegetation needs to transition from the *status quo* to a more scientifically informed practice. While we have reviewed four different provenancing strategies and their ability to deal with climate change and account for fragmentation, a useful exercise would be to look back at records of established plantings and judge revegetation success on the eco-geographic distance seeds were moved and size of source populations. The genetic origin and vigour of recruits into these established plantings could be monitored, particularly where mixing provenances has been performed. However, it is likely that these established plantings were initiated without an experimental design in mind, so special attention must be given to assess the quality of data collected. Thus, it is also crucial to establish long-term experiments to fully assess the practical feasibility and success of the different provenancing strategies. As environmental change is occurring rapidly, it is essential that these experiments are started now and their

progress monitored with feedback into management frameworks.

A knowledge gap that has direct relevance to revegetation is the balance between benefits and costs of genomic admixture (i.e. genetic rescue, adaptation to environmental change and heterosis versus outbreeding depression, risk of invasive genotypes/species). Investigating the relative impacts of inbreeding and outbreeding depression is important to revegetation, particularly in stressful/novel environments or across increasing degrees of population genetic differentiation. To address these issues a variety of genetically related individuals need to be crossed and grown in growth experiments (i.e. optimal outcrossing experiments). Crosses could range from fully selfed and close relatives (i.e. to produce full- and half-siblings) to a variety of more distantly related individuals (e.g. individuals from populations along an increasing genetic and/or environmental gradient). The example presented above by Forrest et al. (2011) provides a good case of where optimal outcrossing has been estimated for the bird-pollinated shrub *Grevillea mucronulata*. These types of experiments need to be located not only in 'local' environments but also in areas predicted to be suitable under climate change scenarios. For individual species, iterative refinement of relative risks and benefits of outcrossing could then be performed. This would allow honing in on species-specific optimal outcrossing levels. Additionally, with data collected from replicated optimal outcrossing experiments it would be possible to assess the average risk of outbreeding depression given a genetic (e.g. F_{ST}) or environmental difference (see Forrest et al. 2011 for an example of where this assessment was done). However, more studies on optimal outcrossing rates, bioclimatic distribution modelling and local adaptation are clearly needed to shift revegetation strategies from focussing on accounting for uncertainty (i.e. admixture and composite provenancing) to confidently match genotypes with future environmental conditions (i.e. predictive provenancing).

Many large revegetation projects are being initiated (Chazdon 2008; Galatowitsch 2009). Integrating an experimental component into these projects (e.g. as described above), by developing partnerships with scientific institutions, would benefit both parties and would assist in generating the scientific evidence required for best-practice revegetation under future conditions. To facilitate adaptive management, we recommend that projects have detailed records of provenance source and long-term monitoring of establishment outcomes, with an absolute minimum being provenance information (e.g. location; size of population), planting scheme (e.g. density; numbers planted), planting location (e.g. climate data; aspect; site preparation), as well as regular assessments of survival and recruitment. This information could be easily

integrated into established revegetation databases (e.g. Zerger et al. 2009).

Conclusions

Interest in carbon and biodiversity credits is rapidly growing and has produced great demand for revegetation (Galatowitsch 2009). With such economic stimuli, a great opportunity has arisen to revegetate large areas of cleared land with planted habitats that are resilient to climate change. However, efficient and effective provenance sourcing strategies need to be developed to help maximise the successes of revegetation programs, particularly due to the threats posed by environmental change. Projects must move beyond attempting to recreate pre-clearance ecosystems, as this does not acknowledge that evolution and environmental change are ongoing processes that can occur rapidly with large effect (Thomas 2011). Genetic rescue effects (Weeks et al. 2011) may be the solution to achieving immediate success (i.e. high establishment rates) and augmenting adaptive potential (Willi et al. 2006) may be key to maximising long-term success (i.e. evolutionary resilient populations; Sgrò et al. 2011; Weeks et al. 2011). The current predominant seed-sourcing strategy, local provenancing, is probably not the best approach to achieve this aim in all cases. We have presented a guide to selecting seed-sourcing strategies that should maximise establishment given the conditions of the species and landscape, and by acknowledging that evolution and environmental change are ongoing and can occur rapidly. While there is compelling evidence to change current local provenancing practises, some mistakes will inevitably occur. However, this only means that we need to adopt an evidence-based approach, and a preferred starting-point would be to establish long-term experiments to fully assess the practical feasibility and success of different provenancing strategies.

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