## Composite provenancing – progressing the 'local is best' paradigm for seed sourcing

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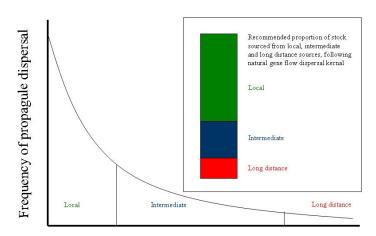
The use of local seed is widely advocated for restoration and is based on the premise that locally sourced seed will be the best adapted for restoration projects (Callaham, 1964; Keller, Kollman & Edwards, 2000; McKay *et al.*, 2005; O'Brien, Mazanec & Krauss, 2007). Despite evidence for local adaptation, a 'local is best' sourcing practise misses two important points, which may be seriously impacting on restoration outcomes, particularly resilience in the face of future environment changes. This paper identifies these issues and suggests a new and improved approach to seed sourcing – composite provenancing.

The first potential problem with 'local is best' recommendations is that there is a serious risk of encouraging the establishment of populations that will not harbour sufficient evolutionary potential for future environmental change (i.e. establish genetic ghettos, (Moritz, 1999). In addition, strict adherence to 'local is best' protocols may encourage the selection of inbred or genetically depauperate seed sources, when genetically healthier sources further a field may produce a more efficacious restoration result. This may serve to perpetuate the number of small inbred populations across highly degraded landscapes that are unlikely to persist in the long term.

The second issue is that particular environmental conditions that drive local adaptation can change very rapidly. The environment is continually changing at different rates and scales, from annual to 1,000 and 100,000 year time scales (Wilkinson, 2001). The most notable recent environmental change has been the emergence from the last ice age ~10,000 years ago when the atmosphere was significantly cooler and dryer than it is today. Following postglacial warming, species (and their genes) have redistributed across the landscape, some over thousands of kilometres and at exceptionally rapid rates (Lowe et al. 2006). In addition, recent anthropogenic influences are expected to have dramatically changed selection pressures; for example, variability in temperature and rainfall distribution associated with anthropogenically-forced climate change, and other environmental changes due to habitat fragmentation, increased salinity, irrigation, and heavy metal deposition. In the face of rapidly changing environments it is pertinent to ask how "local environments" should be defined in contemporary landscapes, especially for long-lived species such as trees (Wilkinson, 2001). In many regions of the world the conditions under which a 200-year-old tree was established are now very different to those existing today, and it could be legitimately argued that source material from more distant (geographically and ecologically) populations may harbour adaptations that more closely match the environment of the focal restoration site today.

So can we improve the selection of seed provenances to maximize evolutionary potential in restoration plantings? And can we facilitate long-term adaptive response to contemporary and future selection pressures (Ennos, Worrell & Malcolm, 1998; McKay et al., 2005; Moritz, 1999)? In answering this question it is informative to note two main processes, the redistribution of standing genetic adaptations (through gene flow) and the evolution of new adaptive variants, which have allowed species to keep pace with environmental change naturally. The answer to provenance selection for future adaptive potential surely then lies in mimicking these natural gene flow and evolutionary dynamics.

For some species gene flow via pollen and seed has been documented to occur over tens, and in some cases hundreds of kilometres (Bacles, Lowe & Ennos, 2006; Dick, 2001; Nathan, 2006; Ward *et al.*, 2005), but many species are now limited in their capacity to disperse propagules (both pollen and seed), following habitat alteration and fragmentation. Gene flow in most species is leptokurtic, with most propagules dispersing proximally, but with a significant proportion moving over longer distances (Fig. 1). To simulate gene flow during a restoration programme, it would be necessary to restore populations using a mixture of material sampled at different distances from the focal site, a practise defined here as composite provenancing. This 'composite provenance' would be predominantly composed of locally sourced material, taken from genetically healthy stock, but would also incorporate proximate and ecogeographically matched sources. In addition, a smaller proportion of material, depending on the natural gene flow dynamics of the focal species (somewhere between 10 and 30% depending on the inferred gene flow dynamics of the species), should be comprised of material from much further afield (Fig 1).



Distance from parent plant

Whilst this composite provenancing approach may risk introducing some maladapted germplasm, it crucially provides an opportunity for redistribution of preadapted genes

and the evolution of new adaptive gene combinations through mixture of multiply sourced stocks, a key driver of evolution. For restoration plantings, we need to be initiating plantings that will allow natural selection to act to produce a suitable and adaptively fit restored stand.

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