

SYNTHESIS

Seed supply for broadscale restoration: maximizing evolutionary potential

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Abstract

Restoring degraded land to combat environmental degradation requires the collection of vast quantities of germplasm (seed). Sourcing this material raises questions related to provenance selection, seed quality and harvest sustainability. Restoration guidelines strongly recommend using local sources to maximize local adaptation and prevent outbreeding depression, but in highly modified landscapes this restricts collection to small remnants where limited, poor quality seed is available, and where harvesting impacts may be high. We review three principles guiding the sourcing of restoration germplasm: (i) the appropriateness of using 'local' seed, (ii) sample sizes and population characteristics required to capture sufficient genetic diversity to establish self-sustaining populations and (iii) the impact of over-harvesting source populations. We review these topics by examining current collection guidelines and the evidence supporting these, then we consider if the guidelines can be improved and the consequences of not doing so. We find that the emphasis on local seed sourcing will, in many cases, lead to poor restoration outcomes, particularly at broad geographic scales. We suggest that seed sourcing should concentrate less on local collection and more on capturing high quality and genetically diverse seed to maximize the adaptive potential of restoration efforts to current and future environmental change.

Introduction

Negative environmental impacts associated with vegetation clearing have precipitated a significant increase in the restoration of degraded landscapes around the globe. The scale of these restoration projects varies from small, local initiatives (ca. 1–10 ha) that aim to re-establish historic community composition, to extremely large projects that concurrently plant several key species across broad geographic scales (ca. 10²–10⁶ ha). Irrespective of the restoration scale, however, access to high quality and appropriately sourced germplasm is a primary consideration to

improve planting success and ensure that new populations become functional, self-sustaining and resilient to environmental challenges. As restoration targets continue to grow, however, it is timely to review the state of knowledge underpinning the major paradigms that drive seed sourcing guidelines. This is particularly important since many guidelines were developed in the 1990s, and our understanding of the demographic and genetic effects associated with landscape fragmentation, evolutionary and population genetic patterns, small population theory and effects, and gene flow have increased significantly. For example, despite negative genetic and demographic effects

being clearly demonstrated for small fragmented plant populations, using 'local' seed remains the primary focus of restoration projects. Little consideration has also been given as to where the large volumes of seed required for restoration will be sourced (Mortlock 2000a). Restoration will also involve significant financial investment over the coming decades and it is imperative that these efforts are cost-effective. Rationalizing seed collection is likely to aid in this regard.

This review will assess the following three major concerns that direct seed sourcing guidelines:

- 1 the appropriateness of using 'local' seed,
- 2 the sample size and source population characteristics required to capture high quality and genetically diverse seed to establish self-sustaining and evolutionarily adaptive populations and
- 3 the impact of over-harvesting source populations.

Within each of these topics the review addresses (i) current collection guidelines, (ii) the scientific evidence supporting these guidelines, (iii) whether the guidelines can be modified in light of more recent evidence and (iv) the consequences of not modifying the guidelines. To maintain focus, we have constrained the review within the following boundaries:

- 1 We consider restoration to be the maintenance or restoration of evolutionary potential (future-focussed) while acknowledging the evolutionary heritage of the resident flora within degraded landscapes (past-focussed). However, a range of new environments now exists to which local species may not be adapted and where restoration efforts may never reflect historic community structure. Restoring these landscapes may require fundamentally different, yet functionally similar species and even the introduction of specific genotypes capable of dealing with these new habitats (Fenster and Dudash 1994; Falk et al. 2001). This review assumes that the selection of species to meet these various restoration challenges has been completed.
- 2 This review focuses on the practicalities of seed collection and does not address restoration methods as these warrant separate examination.
- 3 The review primarily targets seed sourcing for broadscale restoration. However, many of the issues discussed are relevant to smaller scale projects as while these are sometimes conducted in isolation, the net effect of a large number of small projects can be viewed in a regional context and in this sense, converge with the broadscale.
- 4 The review is principally concerned with common and abundant species, although many of the points discussed are equally applicable to rare species.

- 5 We also acknowledge that our understanding is primarily with broadscale Australian restoration; however, the review has been globally focussed as restoration across broad geographic scales occurs in other regions of the world including Europe, Asia and North America.

Using local seed

'Local' seed is widely advocated for restoration and is based on the premise that locally adapted seed will deliver superior restoration outcomes (Callaham 1964; Keller et al. 2000; McKay et al. 2005; O'Brien et al. 2007). Proposed benefits include better survival and growth (Mortlock 2000a), reduced risk of restoration failure due to maladaptation to local conditions (McKay et al. 2005), limiting 'pollution' of local gene pools and outbreeding depression (Templeton 1986; Potts et al. 2003), and avoiding resource provisioning at inappropriate times (Jones et al. 2001).

Current guidelines

Recommendations to use local seed are rooted in scientific literature (Brown and Marshall 1995; McKay et al. 2005), but the practical translation of these data is highly variable and occasionally so restrictive that projects have been cancelled due to a lack of 'appropriate' seed (Wilkinson 2001). Some guidelines are spatially explicit with respect to the scale of germplasm collection. For example, English Nature in the United Kingdom specifies that species can only be established if they occur within 5 miles of the restoration site, whereas the Western Australian Forest Management Plan 2004–2014 (Conservation Commission of Western Australia 2004) advocates collection within 15 km of the rehabilitation site. In contrast, Australian FloraBank guidelines are less spatially prescriptive, recommending that environmental variables such as soil type, altitude and climatic conditions be considered (Mortlock 2000b). The U.S. Forest Service uses genetically delineated *seed zones* where possible, but incorporates topographic, climatic and edaphic data when genetic information is limited (Knapp and Dyer 1998 and references therein). Seed sourcing can be further complicated by the apparent distinction between *provenances*, that restricts germplasm to a specific population or ecogeographic source region, and *seed zones* (seed transfer zones) which describe an area or region within which germplasm can be transferred but defines the limit of transfer between zones (Buck et al. 1970; Parker 1992; Parker and van Niejenhuis 1996; Ennos et al. 1998; Randall and Berrang 2002). Most *seed zone* research has occurred in the northern hemisphere (Hufford and Mazer 2003) and despite these operating at regional scales, these

data continue to drive the ethos underlying that *local is best* paradigm. For most restoration species, however, little is known of the spatial or ecological scale over which seed can be moved, and boundaries are often a 'best guess' in the absence of any real understanding of adaptive variation.

Evidence supporting the current guidelines

Local adaptation and maladaptation

Local adaptation was first observed by Turesson in 1925 and has since been demonstrated in several species (Montalvo and Ellstrand 2000; Joshi et al. 2001; Hufford and Mazer 2003). In reviewing the northern hemisphere forestry literature, Ennos et al. (1998) found a home-site advantage in reciprocal transplant experiments across latitudinal and/or altitudinal gradients for a range of species, but also concluded that transfers between coastal and interior sites, high and low rainfall zones, valley and hill-top aspects can influence plant performance. Local adaptation is also evident between extreme habitats for species other than trees, but may only be apparent in a relatively few traits, the importance of which remains unknown (Rapson and Wilson 1988; Rice and Mack 1991; Galloway and Fenster 2000; Sambatti and Rice 2006). Evidence also suggests that local seed can be important for maintaining a range of biotic interactions including pollinators and pathogen resistance (reviewed by Linhart and Grant 1996; Jones et al. 2001; Cunningham et al. 2005).

The scale of local adaptation is also highly variable among species (Ennos et al. 1998; Bischoff et al. 2006). For example, Douglas fir and Scots pine were very sensitive to site transfer, whereas some collections of western white pine and oaks have broadscale success. Species and/or environmental characteristics including range, environmental gradients, time since colonization, generation time and gene flow can promote or reduce adaptive variation. Selfing, gravity-dispersed, herbaceous annuals that are widespread and long-term occupants across a range of habitats are expected to be more locally adapted and be more prone to maladaptation following transplantation. In contrast, wind-pollinated and seed-dispersed trees with recent range expansion into a relatively uniform habitats are expected to be more robust to transplantation. These expectations are largely borne out by evidence (Ennos et al. 1998; Hufford and Mazer 2003).

Outbreeding depression

Mixed evidence for outbreeding depression ranging from poor progeny fitness to heterosis in F1 crosses exists, although this may primarily reflect the paucity of these types of studies in the scientific literature

(Hufford and Mazer 2003; Edmands 2007). The effects of outbreeding depression in generations beyond initial crosses also varies from strong hybrid breakdown to progeny being as fit as parental types (Hufford and Mazer 2003; Edmands 2007). Crossing divergent populations for six generations has demonstrated that while some later-generation hybrids have lower mean fitness than parental populations, others can outperform parental types (Erikson and Fenster 2006; Johansen-Morris and Latta 2006), illustrating that new gene complexes established through divergent population crosses may prove to be better adapted than the original parental genetic combinations.

Improving the current guidelines

Clearly local adaptation and outbreeding depression do exist, but we challenge the recommendation that 'local' seed should continue to drive restoration efforts simply because too little information is available to support an alternative approach. Indeed, the contrary position that this lack of information does not justify such a precautionary approach could be equally argued. Strong adaptive signals do characterize some populations, but the underlying premise that all populations are highly (and equally) adapted ignores the reality that populations exist along a continuum with some being more locally adapted than others (Raabova et al. 2007). Constraining restoration programmes on the possibility that a minority of populations will be negatively impacted is undesirable as land degradation continues to erode agricultural sustainability and biodiversity values. Other environmental challenges including climate change, increased salinity levels, vegetation redistribution due to habitat conversion, and deposition of fertilizers and heavy metals will also impact on seed sources and restoration sites over the coming decades. Climate change is perhaps the most globally significant of these, and it is questionable whether defining 'local environments' in contemporary but increasingly unpredictable landscapes is appropriate. While the issues surrounding ecological restoration in relation to climate change were recently articulated (Harris et al. 2006), little empirical understanding of how to select seed to meet these challenges is available (Bower and Aitken 2008).

Maintaining adaptive potential in environments where new or more intense selection pressures exist may be possible by mimicking natural gene flow thereby providing opportunities for genes capable of persisting in both established and new environments to disperse. Gene flow dynamics suggest while most propagules fall locally, dispersal over large distances does occur (Dick 2001; Ward et al. 2005; Bacles et al. 2006; Nathan 2006).

Restoration can mimic this process by differentially sampling populations at various distances to the focal site, and could even include the generation of 'regional' seed mixes (Knapp and Dyer 1998) for more broadscale projects. This 'composite provenancing' would primarily source seed from genetically healthy stock near the target site, but would also include other more distant but ecogeographically matched sources. While this approach may lead to some seedling failure if the more distant material is maladapted, composite provenancing facilitates the production of new gene combinations potentially able to respond to environmental changes. Mitigation against potential failures may be overcome by sowing at higher densities, or by tolerating higher failure rates while accepting that natural selection is acting to produce a suitable and adaptively fit restored population.

Broadening seed sourcing guidelines that embrace environmental and climatic conditions will not only expand available seed sources, but will also provide a framework within which high quality, and hence more successful, seed sources will be targeted for restoration. In addition, we should be more focussed on how to use restoration to maintain processes that redistribute genes across landscapes, rather than concentrating on ways to constrain locally adapted genotypes in relatively unstable environments.

Consequences of not improving the guidelines

- 1 The continued emphasis on *local is best* risks establishing populations with insufficient evolutionary potential to meet environmental challenges. Continued adherence to *local is best* protocols may also promote the use of inbred or genetically depauperate seed when genetically healthier but more distant sources may produce a better restoration result. Re-establishment under these circumstances is unlikely to restore functional vegetation communities in regions where these are most urgently required.
- 2 Failure by scientists to recognize that many of the assumptions underlying the *local is best* paradigm are without a strong scientific basis serves to maintain misconceptions among practitioners. Given that we do not yet (and may never) understand the scale and importance of local adaptation, and yet alone be able to predict populations that show strong local adaptation (Murren et al. 2006), adopting a precautionary approach is misguided and likely to constrain restoration efforts in those regions most in need of rehabilitation.
- 3 The use of generalized guidelines for seed movement without reference to life-history traits, spatial

distribution and historic factors will continue to restrict restoration success through poor management decisions with respect to seed collection and deployment.

Sampling to maximize genetic diversity and seed quality

Seed collecting guidelines primarily follow those developed for the conservation and management of rare taxa, which are often characterized by a few, small and highly fragmented populations with limited seed crops. Consequently, rare taxa guidelines were built around sampling to conserve depauperate field genetic resources so as to preserve as much diversity as possible for the future. These ideals, however, are not necessarily appropriate for restoring widely distributed abundant taxa. Much of the scientific information surrounding the development of rare taxa guidelines is also derived from short-lived herbaceous species, which cannot necessarily be extrapolated to long-lived woody taxa. Strong evidence highlighting negative genetic and demographic effects associated with population fragmentation exists, but there has been little translation of this information to improving seed sourcing guidelines. Seed quality assessment has largely focussed on measures of genetic diversity and inbreeding as influenced by the small population paradigm in conservation genetics (see Barrett and Kohn 1991; Ellstrand and Elam 1993), but a range of other factors including maternal effects, phenotypic plasticity and population-specific environmental effects are also important influences (Dudash et al. 2005).

Current guidelines

Several guidelines seek to ensure that representative levels of genetic variation are collected (e.g. Center for Plant Conservation 1991; Guerrant et al. 2004; Touchell et al. 1997), but these often provide only the broadest recommendations regarding the number of plants and populations required. Based on a review of rare and endangered plants, Guerrant et al. (2004), considered 50 randomly selected individuals per population and up to 50 populations per species as adequate. The Center for Plant Conservation (1991) suggested 10–50 plants per population while FloraBank guidelines (Mortlock 2000b), which drive most Australian seed collection, recommend sampling from 10 to 20 widely spaced, plants from 'healthy and viable populations' without any specific information as to how these parameters should be defined in the field. Other guidelines leave sample size to the practitioners discretion, thus relying on experience, enthusiasm and financial considerations.

Evidence supporting the current guidelines

Current collection strategies are primarily based on adequately sampling allelic richness, although Brown and Briggs (1991) also argued that heterozygosity and genet (genotype) richness are important for self-pollinated, clonal or apomictic species. Marshall and Brown (1975) suggested that at least one copy of 95% of all alleles with a frequency >5% should be collected and considered that a random sample of 50–100 plants to be appropriate with additional collecting efforts being directed towards visiting ecologically diverse sites. The overriding emphasis for these guidelines, however, is on germplasm ‘conservation’, not restoring functional and resilient populations, and not for broad spatial applications. In addition, ‘genetic variation’ is an inclusive term variously interpreted with respect to assessing germplasm quality. For example, quantitative (continuous) characters such as seed set, growth rate and time to flowering are under polygenic control with each gene characterized by multiple loci and interactions between these genes and the environment largely unknown. Single genes of major effect, such as those controlling self-incompatibility, can also influence fecundity and seed quality (Fenster and Dudash 1994). Both polygenic inheritance and genes of major effect are important to population viability and long-term evolutionary persistence but are generally ignored by collection protocols.

Improving the current guidelines

Genetic variation is the basis of evolutionary adaptation to changing environments (Gordon and Rice 1998) and theoretically, restoring populations with greater genetic diversity will promote adaptive potential for evolutionary change and avoid the creation of small, inbreeding populations. Identifying high quality seed sources, however, is one of the most crucial, yet inherently difficult, issues for restoration in highly degraded landscapes. Many remnant populations in these regions are small and isolated, harbouring lower levels of genetic variation and more likely to be affected by nonadaptive evolution through random genetic drift at the expense of adaptive change by natural selection (Ellstrand and Elam 1993). Consequently, the utility of these to act as major seed sources may be limited with negative genetic and demographic consequences emerging as populations fall below 100–200 reproductive plants (Young et al. 2000; Lienert 2004; Lowe et al. 2005; Broadhurst and Young 2006; Yates et al. 2007). Despite life-history traits playing a major role in the manner in which species respond to fragmentation, little of the information now available has been incorporated into collection guidelines. For example, wind pollinated trees that maintain high genetic loads and are more at risk from inbreeding depres-

sion, may require quite different sourcing protocols than predominately selfing species that have purged their genetic load through selection against deleterious recessives.

Altered gene-flow patterns associated with increased isolation in fragmented ecosystems (Lowe et al. 2005; Ward et al. 2005) will also influence seed collection. Genetic ‘rescue’ of small fragmented populations (Dick 2001; Hoebee and Young 2001; Keller and Waller 2002; Hedrick 2005; Lowe et al. 2005; Bacles et al. 2006) suggests that these may be suitable seed sources for restoration although emerging evidence suggests that long distance gene flow is not necessarily commensurate with improved demographic responses (Byrne et al. 2007; Yates et al. 2007). Further study is required to determine the scale and intensity of gene flow required to mitigate against negative genetic and demographic effects in fragmented ecosystems. Perhaps more importantly, altered gene flow patterns in fragmented landscapes may render moot any considerations regarding local adaptation and outbreeding depression, as plant populations may already be interacting over broader spatial scales than that operating prior to fragmentation. Habitat quality and maternal effects can also play a role in seed quality. Fragmentation can influence pollinator abundance and behaviour, leading to reduced outcrossing and higher inbreeding (Sampson et al. 1996; Armbruster and Reed 2005; Ward et al. 2005; Coates et al. 2007) while resource provisioning to developing seed can influence early acting traits such as seed size, germination characteristics and seedling growth (Ouborg and van Treuren 1995).

While some seed collection protocols include consideration of a species’ life history, distribution, population size and isolation, very few make definitive statements as to how this should be incorporated into collection procedures. Given that more successful restoration programmes, at least in terms of ecological establishment, are likely to result from material sourced from large healthy patches that do not necessarily local, the *local is best* paradigm clearly conflicts with the benefits of collecting for genetic diversity. Restoration guidelines therefore need to emphasize the problems associated with sourcing local and distant material, and should encourage decisions that balance these issues with the genetic quality of sources and consideration of the focal species characteristics. The health of source populations should also be included in guidelines.

Consequences of not improving the guidelines

The continued acceptance of *local is best* as a guiding principle for seed sourcing is likely to contribute to significant restoration failure over the coming years through the use of poor quality seed. Elevated inbreeding is known to affect a range of seed and seedling fitness components as well as

seed crop production, constraining both the initial and long-term performance of restored populations. Restoring with a low genetic base will fail to ensure that populations have the functionality and resilience necessary to become self-sustaining in the face of environmental change.

Over-harvesting source populations

In heavily modified landscapes most in need of ecological restoration, seed is commonly collected from remnant vegetation fragments already threatened by a range of altered ecological, demographic and genetic processes (Hobbs and Yates 2000). In these landscapes, the demand for locally collected seed often exceeds supply, and seed harvesting to meet growing restoration targets may impact further on remnant vegetation viability by reducing seed availability for natural population turnover, or reducing plant vigour through collateral collection damage (Lamont et al. 2001; Peres et al. 2003). Concerns associated with over-harvesting in a restoration context have probably arisen from the history of extractive utilization of natural resources such as fisheries and forestry. However, seed harvesting for ecological restoration differs from extractive harvesting in that it is planted back into the landscape where the collections were undertaken. Through these practices, the rate at which collected seed becomes established will generally be much greater than if the seed were left *in situ*, and therefore population growth of the collected species is increased. Generally, confidence in the success of active regeneration is higher than for natural regeneration (Vesk and Dorrrough 2006). Moreover, for many species the seed produced over a life-time far exceeds the number required for self-replacement and some harvest should be possible without negative impacts (Harper 1977; Crawley 1992).

Current guidelines

As restoration targets grow and if the emphasis on local seed sources remains a priority, localized negative impacts through unsustainable practices may occur. Unfortunately, very few guidelines provide advice regarding sustainable harvesting or ensuring minimal damage to plant canopies to minimize these effects on local population dynamics. FloraBank guidelines, for example, do recommend collecting not more than 20% of the seed crop or fruit of any individual plant (Mortlock 2000b) but it is unclear whether such a generalized approach is appropriate.

Evidence supporting the current guidelines

The information in this section is drawn from three sources: (i) studies that directly investigate the impact of removing seed from a population, (ii) those that indi-

rectly investigate the impact of removing seed using population viability analysis and (iii) those that investigate the relative importance of seed and safe site limitation on seedling recruitment.

Seed harvesting

Few studies have directly investigated the seed harvesting impacts on local population dynamics. Murali et al. (1996) found that harvesting intensity on three tree species (*Phyllanthus emblica*, *Terminalia bellirica*, *Terminalia chebula*) significantly impacted on population age structure with fewer juveniles in intensively harvested stands than in those where harvesting was considerably lower. The best documented case of seed harvesting impacts is the Brazil nut tree (*Bertholletia excelsar*), which is harvested entirely from wild populations in the Amazon basin (Peres et al. 2003). Peres et al. (2003) found that the history and intensity of exploitation of this species were major determinants of population size and age structure with persistently harvested populations lacking juvenile trees in contrast with those with a history of either light or recent exploitation. Modelling these data indicated that reduced juvenile recruitment associated with intensive exploitation will limit long-term population persistence (Peres et al. 2003). These studies suggest that over-harvesting can affect natural replacement in exploited populations, but extrapolation beyond species with similar life-histories in similar ecosystems is not possible without further research.

Population viability analyses

Population viability analyses using empirically derived, stochastic, stage-based transition matrix models have investigated harvesting impacts on the extinction risk for a variety of life-forms including perennial herbs, palms, woody shrubs and trees (Bernal 1998; Lamont et al. 2001; Menges et al. 2004). Bernal (1998) found that up to 86% of seed could be harvested from an ivory palm population (*Phthelephas seemannii*) before negatively impacting on population growth rates. Modelling the intensity and frequency of seed harvest on the extinction probability for 22 perennial species, Menges et al. (2004) found that the species fell into one of three groups. In the first group, models predicted that short-term harvesting of any intensity and frequency was unlikely to cause extinction with the caveat that relatively short simulation times (<100 years) may not detect extinction risks in trees and shrubs that are longer-lived and have low mortality rates in later life-stages. In the second group, species exhibited variable sensitivities but a harvesting regime of 10% of seed in 10% of years had little impact on their extinction risk. Extinction probability was highest in the third group, irrespective of seed harvesting levels and while this

risk declined as population size increased, populations of 500 were generally unable to sustain more than 50% harvest in 50% of years. Hence, seed harvesting can reduce population viability, but sensitivity is species-specific. Most species, except those that are highly endangered with extremely small populations, will tolerate some level of harvesting, but this may range from 10% of seeds in 10% of years to 86% of seeds in most years.

Seed or safe site supply

The utility of populations to act as seed sources is also dependent upon whether plant population growth is limited by seed supply (seed-limited) or by the abundance of safe sites (safe site-limited). In this context, safe sites are thought of as those opportunities in the environment that provide the necessary conditions for germination and seedling growth, and protection from pathogens, predators and herbivores (Harper 1977). If recruitment is seed-limited, then harvesting will impact on source population dynamics. Under safe site-limited recruitment, more seed are produced than are required for self-replacement, making these populations harvestable. Studies to determine relative importance of seed- and safe site-limitation indicate that seed-limitation is more prevalent, although this does appear to be influenced by life-history traits (Turnbull et al. 2000; Munzbergova and Herben 2005; Svenning and Wright 2005). Generally, however, environmental and disturbance effects that create safe sites for germination and establishment are far more important for recruitment limitation than are species traits (Turnbull et al. 2000).

In many ecosystems where natural recruitment is strongly associated with frequent disturbance creating small gaps, over-harvesting may have detrimental impacts on persistence. For example, in ecosystems where dynamics are driven by stand scale disturbances such as fire at irregular intervals, many species have canopy- or soil-stored seed banks to take advantage of unpredictable recruitment opportunities (Whelan 1995; Bond and van Wilgen 1996). In periods between fires, canopy-stored seeds may be released and soil-stored seed may germinate in relatively small numbers, often contributing little to recruitment (O'Dowd and Gill 1984; Wellington and Noble 1985; Andersen 1989; Enright and Lamont 1989; Lamont et al. 1993; Yates et al. 1994, 1995, 1996) while postfire seed may not reach safe sites and there can be strong intra-specific seedling competition and mortality (Keeley 1977; Wellington and Noble 1985; Cowling and Lamont 1987; Lamont et al. 1993). Theoretically, some proportion of seed from these species could be harvested without affecting population replacement and studies indicate that up to 50% of cones from *Protea repens* and up to 85% for *Protea neriifolia* can be harvested without

detrimental effects (Maze and Bond 1996). But modelling of harvested *Banksia hookeriana* populations indicate that plant age, growing conditions and harvest intensity also influence populations persistence (Lamont et al. 2001).

Improving the guidelines

The potential negative consequences of over-harvesting must be balanced with the broader positive outcomes for native vegetation that can be achieved by ecological restoration. While evidence that seed collection can harm local population viability exists, species vulnerability varies greatly from those capable of sustaining very high levels of harvesting, to those for which relatively small collections will have negative impacts. Generalizations aimed at improving seed sourcing guidelines can already be made at the habitat level about the relationship between propagule supply and recruitment. Unfortunately, for habitats in which infrequent major disturbance (such as fire) drives recruitment, our ability to adjust harvest accordingly is limited by the inherent unpredictability of these disturbance events. Harvest frequency (see Menges et al. 2004) is particularly important in these habitats, because recruitment failure could occur if a site was collected heavily just prior to a major recruitment opportunity. In these environments, the focus should be to maintain a sufficient seed bank for populations to exploit unpredictable disturbance opportunities which could be achieved by favouring smaller, repeated collections, rather than mass, infrequent collections.

Consequences of not improving the guidelines

The risk that seed collection will have a negative effect exceeding the benefits gained through directed dispersal of seed and facilitated establishment of seedlings is of concern only for some species, particularly those with small populations.

Concluding remarks

The success of restoration efforts rests on many biotic and abiotic factors including the appropriate collection and deployment of germplasm as well as the selection, preparation and management of target sites. The continued insistence on using local seed sources clearly needs revision, particularly given the strong links between altered ecological, demographic and genetic processes associated with habitat fragmentation and seed quality. Failure to do so ignores that inbreeding and inadvertent genetic bottlenecks can be just as potent as maladaptation and outbreeding depression in determining the ecological success of restoration plantings. Not only does

this waste precious resources, but also as restoration efforts begin to fail over time, community and government confidence in restoration programmes will be eroded. Broadscale restoration in particular must choose between rapid and large-scale establishment to ameliorate immediate risks, as opposed to a slower, smaller scale approach that includes consideration of local adaptation. While we agree that using the local gene pool is an excellent starting point for any restoration project as it presumably already encapsulates the evolutionary processes defined by the local environment, clearly the continued use of local seed sources has its limits for all types restoration, especially those across broad geographic scales. This is particularly relevant to ensure the restored vegetation is resilient, ecologically competent and possesses the evolutionary potential required to meet changing and challenging environments.

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