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*Review*

# Guidelines for genetic monitoring of translocated plant populations

Fabienne Van Rossum [1,2] and Olivier J. Hardy[3]

[1]Meise Botanic Garden, Nieuwelaan 38, Meise, 1860, Belgium, email fabienne.vanrossum@botanicgardenmeise.be
[2]Service général de l'Enseignement supérieur et de la Recherche scientifique, Fédération Wallonie-Bruxelles, rue A. Lavallée 1, Brussels, 1080, Belgium
[3]Unit of Evolutionary Biology and Ecology, Université Libre de Bruxelles, Avenue F.D. Roosevelt 50, CP 160/12, Brussels, 1050, Belgium

**Abstract:** Plant translocation is a useful tool for implementing assisted gene flow in recovery plans of critically endangered plant species. Although it helps to restore genetically viable populations, it is not devoid of genetic risks, such as poor adaptation of transplants and outbreeding depression in the hybrid progeny, which may have negative consequences in terms of demographic growth and plant fitness. Hence, a follow-up genetic monitoring should evaluate whether the translocated populations are genetically viable and self-sustaining in the short and long term. The causes of failure to adjust management responses also need to be identified. Molecular markers and fitness-related quantitative traits can be used to determine whether a plant translocation enhanced genetic diversity, increased fitness, and improved the probability of long-term survival. We devised guidelines and illustrated them with studies from the literature to help practitioners determine the appropriate genetic survey methods so that management practices can better integrate evolutionary processes. These guidelines include methods for sampling and for assessing changes in genetic diversity and differentiation, contemporary gene flow, mode of local recruitment, admixture level, the effects of genetic rescue, inbreeding or outbreeding depression and local adaptation on plant fitness, and long-term genetic changes.

**Keywords:** admixture, contemporary gene flow, genetic rescue, genetic restoration, inbreeding depression, outbreeding depression, quantitative genetics, reinforcement

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**Resumen:** La translocación de plantas es una herramienta útil para implementar el flujo génico asistido en los planes de recuperación de especies de plantas en peligro crítico. Aunque ayuda a restaurar poblaciones genéticamente viables, no está exento de riesgos genéticos, como la baja adaptación de los trasplantes y la depresión por exogamia en la progenie híbrida, que pueden tener consecuencias negativas en términos de crecimiento demográfico y adaptabilidad de las plantas. Por tanto, un monitoreo genético de seguimiento debería evaluar si las poblaciones translocadas son genéticamente viables y autosustentables en el corto y largo plazos. Las causas del fracaso al ajustar respuestas de manejo también deben ser identificadas. Se pueden utilizar marcadores moleculares y atributos relacionados con la adaptabilidad para determinar si una translocación de plantas aumentó la diversidad genética, incrementó la adaptabilidad y mejoró la probabilidad de supervivencia a largo plazo. Diseñamos directrices y las ilustramos con estudios en la literatura para ayudar a que los practicantes determinen los métodos de monitoreo genético adecuados para que las prácticas de manejo integren procesos evolutivos de mejor manera. Estas directrices incluyen métodos para muestrear y evaluar cambios en la diversidad y diferenciación genética; el flujo génico contemporáneo; la forma de reclutamiento local; el nivel de mezcla; los efectos del rescate genético, la depresión por endogamia o exogamia y la adaptación local sobre la adaptabilidad de las plantas y los cambios genéticos a largo plazo.

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**Palabras Clave:** depresión por endogamia, depresión por exogamia, flujo génico contemporáneo, genética cuantitativa, mezcla, reforzamiento, rescate genético, restauración genética

## Introduction

Plant translocations are intentional introductions of living organisms from one area to another, usually as spores, seeds, or plug plants (Menges 2008; Weeks et al. 2011). Translocation is useful for implementing assisted gene flow in recovery plans of critically endangered plant species; bringing new, genetically diverse material allows for genetic restoration or rescue. Genetic restoration refers to the recovery of genetic diversity and evolutionary resilience of the population (Weeks et al. 2011), whereas genetic rescue aims to counteract the expression of genetic load (deleterious genes) to improve plant fitness (Bell et al. 2019). Accordingly, plant translocations can be used for population reinforcements, reintroductions, and introductions. Reinforcements (also called augmentations) consist of translocating additional plants in small and isolated endangered populations (Betz et al. 2013; Ottewell et al. 2016), allowing for genetic restoration or rescue when populations are depauperate or inbred (Weeks et al. 2011; Zavodna et al. 2015). However, when populations have been extirpated and when a persistent seed bank in the soil or seed recolonization from neighboring sites cannot be relied on, it is necessary after habitat restoration to recreate new populations by reintroducing plants (Menges 2008; Weeks et al. 2011). If the original sites cannot be restored to suitable conditions, introductions may be considered at other sites, possibly after ecological restoration (Colas et al. 2008).

Although plant translocations aim to restore genetically viable populations, they may be associated with genetic risks, which may have negative consequences in terms of demographic growth, plant fitness, or conservation of local genetic diversity. When local populations are too depauperate or inbred, the translocation of a highly diverse genetic pool, possibly with nonlocal or mixed source populations, can maximize evolutionary resilience, counteract the detrimental effects of inbreeding depression, and increase the number of compatible mates (Weeks et al. 2011; Maschinski et al. 2013; Zavodna et al. 2015). However, the introduced and local genotypes may be genetically very different from each other, such that the new transplants and their progeny may be poorly adapted to the translocated sites and local genetic variability may be lost. Outbreeding depression (i.e., lower fitness of hybrid offspring) may be expressed in terms of seed germination, plant growth, and survival because of the breakdown of positive epistatic interactions in local co-adapted gene complexes. Hybrid generations may also display intermediate phenotypes that are less adapted than the parental ones (Edmands 2007; Frankham et al. 2011; Weeks et al. 2011). Nevertheless, the risk of outbreeding depression after a few generations of cross mating may be compensated by an increase in plant fitness expected with heterosis (Willi et al. 2007). Moreover, natural selection will favor the best adapted genotypes in the long term (Sgrò et al. 2011).

To maximize the ability to recover demographically sustainable and evolutionary resilient populations, the following should occur prior to implementation of translocations: estimate the genetic and demographic status of the populations to reinforce; carefully select appropriate target sites and source populations for translocation; design appropriate plant propagation protocols; and carefully prepare the transplantation site (Menges 2008; IUCN/SSC 2013; Basey et al. 2015; Godefroid et al. 2016; Ottewell et al. 2016; Maschinski & Albrecht 2017; Commander et al. 2018). Based on prior evaluations (cited in the previous sentence), it is important that recovery planners first determine what the goals of the translocation are: restoration of demographically viable populations; genetic restoration or rescue of genetically depauperate or inbred populations; or creation of additional populations (Weeks et al. 2011). Furthermore, to assess whether the targeted goals are achieved, planners must select appropriate success criteria (i.e., measurable population parameters that estimate whether translocation improves long-term population viability [Menges 2008]). After the translocation, it is necessary to implement follow-up demographic and genetic monitoring to evaluate these success criteria. The causes of failure also need to be identified so that management responses can be adjusted (Schwartz et al. 2007; Menges 2008; Godefroid & Van Rossum 2018).

Demographic monitoring is very useful for assessing population growth based on recruitment, plant survival, and reproductive success (Godefroid et al. 2011; Commander et al. 2018; Albrecht et al. 2019; Fenu et al. 2019). However, it cannot provide insights into the evolutionary potential of translocated populations or the detailed reproductive processes occurring after translocation, which are key determinants of the success or failure of the translocation (Schwartz et al. 2007; Van Rossum et al. 2020). For instance, genetic monitoring allows quantification of gene flow, degree of admixture between local and introduced gene pools, and inbreeding or outbreeding depression. Moreover, many perennial plant species can also propagate asexually, so population census size may increase while genotypic diversity remains low or decays (Menges 2008; Becheler et al. 2017; Van Rossum & Raspé 2018). Recruitment from

sexual reproduction, an important indicator of translocation success (Menges 2008; Albrecht et al. 2019), can be distinguished from clonal propagation with molecular markers (Peakall & Smouse 2006), but not by demographic measures. Therefore, genetic monitoring is an important tool for evaluating translocated population sustainability.

It is only recently that recovery plans have begun to incorporate thorough genetic monitoring of plant populations restored or rescued through reinforcements, introductions, or reintroductions (e.g., Zavodna et al. 2015; Rodríguez-Rodríguez et al. 2018). Practical information and a framework for implementing genetic surveys of threatened animal and plant species are available (e.g., Schwartz et al. 2007; Menges 2008; Flanagan et al. 2018; Godefroid & Van Rossum 2018). However, they are incomplete for translocated plant populations or are lost in more general reviews. Plants have particular characteristics relative to most animals, such as the inability to escape unsuitable conditions, gene dispersal mediated by pollen and seeds, and often the ability to propagate asexually. Plant translocations also have some specificities, such as the need to transplant a large number of individuals, often of a single founder stage (seeds or juveniles), which creates a population with an even age or stage structure (Godefroid et al. 2011; Maschinski & Albrecht 2017). When transplants are previously grown in ex situ conditions, selective conditions may differ from the field, possibly leading to differential survival and genetic variation (Alonso et al. 2014; Basey et al. 2015; St. Clair et al. 2020). Therefore, guidelines for monitoring translocations of plant species differ somewhat from animal species.

We reviewed the existing literature on genetic monitoring of translocated plant populations and based on our findings we devised practical genetic monitoring guidelines for evaluation of plant translocations. The guidelines include methodological aspects and genetic data analyses and are organized according to goals of the translocation, sources used, and possible questions to address (success criteria).

## Evaluating Success of Plant Translocation via Genetic Monitoring

Genetic monitoring is used to evaluate whether plant translocation has been successful, that is, whether it has led to genetically viable and self-sustaining populations, and identify the causes of failure. Based on molecular markers and fitness traits, different questions are asked in the evaluation of translocation success over short (over a few generations) and long terms. The questions asked depend on the predefined goals of the translocation (i.e., whether the translocation is a reinforcement of depauperate or inbred populations, an introduction, or a reintroduction) and the sources of transplants (local, nonlocal, mixed) (Fig. 1).

First, is genetic diversity sufficient to ensure population evolutionary resilience? This question applies when genetic diversity has been enhanced or is higher or comparable to functioning natural (reference) populations. The extent of genetic differentiation between generations and between translocated populations is expected to be lower or comparable to reference populations. Successful genetic restorations have contemporary gene flow and sufficient gene dispersal in the translocated populations to maintain low inbreeding levels; for clonally propagating species, sexual reproduction (not only clonal propagation) contributes to recruitment; and for mixed or nonlocal source populations, progeny result from admixture between sources and local genetic diversity is represented in the offspring.

Second, is adaptive variation sufficient to ensure population growth and survival? This question applies when the fitness of plants detrimentally affected by genetic effects has been increased through the introduction of new genetic variation or through heterosis and when inbreeding depression has been alleviated. In case of mixed or nonlocal sources, the question applies when local adaptation has been maintained, transplants have no maladaptation issues, and there is no outbreeding depression in the cross progeny.

Finally, in the long term, do the recovered populations show effective population size high enough to be viable?

## Guidelines for Genetic Monitoring of Translocated Plant Populations

### Sampling Methods for Assessing Translocation Success

To evaluate translocation success, the first step is to design appropriate sampling methods and choose the appropriate markers (Fig. 1). Specific expertise and equipment may be required, so collaborative work between conservation practitioners and evolutionary geneticists is encouraged.

Genetic data should be obtained for the populations used as sources for translocations and for several generations of the translocated populations (transplants and newly established individuals and their seed progeny). For some species, long recruitment time lags constrain monitoring of new generations (Bowles et al. 2015; Fotinos et al. 2015; Rodríguez-Rodríguez et al. 2018). Natural functioning populations may serve as reference populations (Menges 2008). Sample sizes—number of individuals and number of seeds per maternal plant for examining seed progeny—depend on the questions addressed and on the analyses to be performed (e.g., Basey et al. 2015; Godefroid & Van Rossum 2018). Mapping individuals in

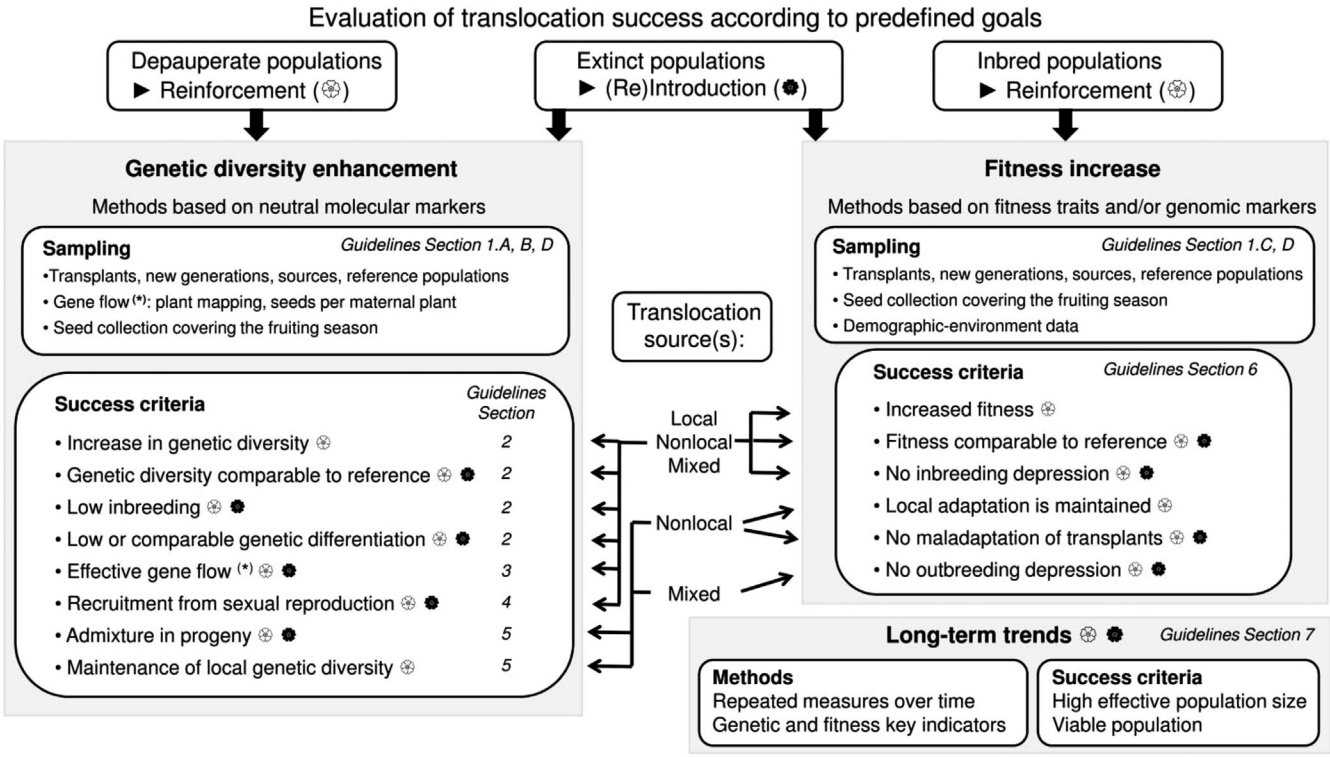


*Figure 1. Summary of the guidelines for implementing genetic monitoring to evaluate the success of plant translocations organized by population status (depauperate, inbred, or extirpated), translocation goal (white flower, reinforcement; black flower, introduction or reintroduction), and sources used to produce transplants (local, nonlocal, mixed).*

the field can be required for estimating pollen and seed dispersal distances (see "Contemporary Gene Flow" below).

Suitable molecular markers (DNA fragments) for quantifying genetic diversity and structure should be highly polymorphic (variable), such as microsatellites, or numerous (many loci), such as single-nucleotide polymorphisms (SNPs). Preferable, they should be codominant, meaning that distinct alleles (variants for a gene) can be distinguished in heterozygotes (Peakall & Smouse 2006; Flanagan & Jones 2019). Dominant markers, such as amplified fragment-length polymorphisms (AFLPs) or inter-simple sequence repeats (ISSRs), for which heterozygotes cannot be distinguished from homozygotes for the dominant allele can be useful, but such binary data (presence–absence scores) are not suitable to infer inbreeding, a key factor in assessing the success of the translocations (Schwartz et al. 2007; Weeks et al. 2011). Investing in laboratory equipment (e.g., extraction tools, PCR devices, and a capillary sequencer) may be very expensive (several tens of thousands in U.S. dollars), so that it may be best to outsource molecular analyses to external firms or academic laboratories.

The variation in molecular markers, such as microsatellites or AFLPs, is usually representative of neutral genetic processes; thus, they are not related to fitness, although any marker can potentially be linked to a selected gene. Therefore, they are very useful to quantify overall genetic diversity, genetic differentiation, and gene flow and to infer admixture or recruitment mode. However, they may not provide insight into inbreeding or outbreeding depression and adaptation-related genetic diversity (Leinonen et al. 2008). The genomic approach of using next-generation sequencing technology, by screening large regions of the genome and developing a large number of markers, is a promising tool to facilitate identification of putatively adaptive or detrimental genes and of the breakdown of co-adapted gene complexes (Angeloni et al. 2012; Benestan et al. 2016; Flanagan et al. 2018). Most molecular data analyses can be performed using freely available software (Appendix S1).

Quantitative genetics, which is based on continuously varying phenotypic character measurements (Table 1), especially in standardized environmental conditions, can provide insight into the genetic variability of traits under selection and into heterosis and inbreeding and outbreeding depression (Edmands 2007; Sgrò et al. 2011; Zavodna et al. 2015; Barmentlo et al. 2018). Getting enough data for statistically sound analyses can be time-consuming, but usually does not require buying expensive equipment. Low fitness, expressed through a reduced growth, seed abortion, seedling chlorosis, and

**Table 1. Quantitative traits used to measure plant fitness at the individual level.*.**

| *Fitness trait* | *Variable to measure* |
|---|---|
| Health | seedling chlorosis |
| | plant mortality |
| | disease |
| | herbivory |
| Vegetative performance | plant size and height |
| | growth (including clonal production) |
| | number of leaves |
| Reproductive performance | floral display |
| | pollen viability |
| | seed set |
| | seed weight |
| | seed abortion |
| | seed germination |
| Phenotypic plasticity | variance in the measured characters |
| Cumulative fitness performance | seed yield (fruit set × viable seed set × mean seed weight) |
| | sexual fitness (viable seed set × germination rate × survival × number of flowers, flowers buds and fruits) |
| | leaf area index (number of leaves × leaf length × leaf width) |

**From Willi et al. (2007), Menges (2008), Angeloni et al. (2011), Bowles et al. (2015), Zavodna et al. (2015), Barmentlo et al. (2018), and Godefroid and Van Rossum (2018).*

low pollen viability, may indicate inbreeding or outbreeding depression (Edmands 2007; Godefroid et al. 2016). High plant fitness expressed through higher seed weight, germination rate, growth rate, or reproductive success may indicate heterosis and genetic rescue or local adaptation if it concerns only local genotypes (Willi et al. 2007; Bell et al. 2019).

Sites targeted for plant translocation may vary in ecological conditions (e.g., in vegetation composition, edaphic conditions, management interventions, competition with other species, herbivory pressure). Ecological conditions, such as climatic conditions and disturbance regimes related to management interventions, may also vary from year to year (Menges 2008; Reckinger et al. 2010; Albrecht & Long 2019). The number of sown seeds or translocated plants and demographic dynamics (survival, flowering, and recruitment) may also vary among translocated sites (Colas et al. 2008; Fant et al. 2013; Bowles et al. 2015; Fenu et al. 2019). Therefore, these data should be integrated in the genetic data analyses to disentangle environmental and population demographic effects from genetic restoration and rescue effects (Menges 2008; Godefroid & Van Rossum 2018).

### Changes in Genetic Diversity and Differentiation

Genetic monitoring should assess whether genetic diversity (on which evolutionary resilience depends) has increased, if the translocation is a reinforcement, or is comparable to reference populations, if the translocation is an introduction or a reintroduction. To control for genetic drift and inbreeding, it is important to verify that the genetic restoration is maintained across generations and whether genetic differentiation within and between translocated populations is low or comparable to reference populations.

We found 16 studies on plant translocations in which genetic monitoring of translocated plant populations (Table 2) was conducted, a low number relative to the numerous demographic studies performed (e.g., Godefroid et al. 2011; Albrecht et al. 2019). A majority of studies showed that genetic diversity is higher in reinforced populations and higher or similar in reintroduced populations compared with natural populations. Genetic differentiation is low to moderate in the new generations or between populations. In these studies, success was attributed to the large number of transplants planted at high density and to the mixing of multiple, sometimes nonlocal, seed sources (Ritchie & Krauss 2012; Fant et al. 2013; Alonso et al. 2014; Zavodna et al. 2015; St. Clair et al. 2020). When a small number of individuals are translocated or when there is a high mortality of the transplants and reduced flowering rate, evidence of inbreeding appears in subsequent generations (Krauss et al. 2002; Aavik et al. 2012; Fant et al. 2013; Fotinos et al. 2015). The small population sizes reported for many restored populations (Table 2) may challenge their long-term viability. Transplant survival, seed germination, and establishment of new recruits may be compromised by poor habitat quality or by a lack of follow-up habitat management (Godefroid et al. 2011; Albrecht & Long 2019). Pre- and posttranslocation management interventions in the sites of translocation favor genetic restoration and recruitment for *Pulsatilla vulgaris* (Betz et al. 2013) and *Arnica montana* (Van Rossum et al. 2020).

To estimate the amount of genetic variation within a population, the most popular variables are allelic richness, proportion of polymorphic loci, observed heterozygosity, and genetic diversity sensu stricto (expected heterozygosity) (Schwartz et al. 2007). Departure from

**Table 2. Studies in the literature involving genetic monitoring of translocated populations of critically endangered plant species.[a].**

| *Study species* | *No. of translocations (*n*), markers traits* | *Main results of genetic monitoring* | *Reference* |
|---|---|---|---|
| *Arenaria grandiflora* | 3 (440 plants from 9 local and 11 nonlocal cuttings); 10 microsatellites, flower number/plant | higher genetic diversity in reintroduced populations (mixed sources) than in natural populations maintained over 12 years; 80% of admixed individuals and local genetic pool maintained after 12 years; conflicting effects of heterosis, inbreeding, and outbreeding depressions and local adaptation on plant fitness | Zavodna et al. 2015 |
| *Argyroxiphium sandwicense* ssp. *Sandwicense* | 1 (450 plants from seeds from 2 maternal plants), 11 RAPD | lower genetic diversity in the reintroduced than in the natural population due to the small number of plants used as seed sources; manual pollen transfer from the natural to the reintroduced population recommended to incorporate additional genotypes, followed by natural recruitment | Robichaux et al. 1997 |
| *Arnica montana* | 3 (700 plants from 2 seed sources), 9 microsatellites, seed fitness performance, plant size | high levels of genetic variation; random contemporary pollen flow but spatial genetic structure (SGS) in recruits as a result of restricted seed dispersal; admixture (25–68%) in the first generation of seed progeny and newly established recruits | Van Rossum et al. 2020 |
| *Asclepias meadii* | 7 (30–180 plants and 35–135 seeds, 20–71 plants and 18–66 seedlings after 1 year), leaf area index | after 10 years, heterosis at seedling establishment and outbreeding depression expressed at older stages and under more stressful conditions, but multiple seed sources needed for maximizing self-incompatible allele diversity | Bowles et al. 2015 |
| *Banksia attenuata* | 1 (seeds of local provenance, 200 trees after 13 years), 7 microsatellites, germination, survival, leaf and root traits | similar high genetic diversity and offspring fitness performance; low differentiation and inbreeding in restored and natural populations; low SGS; extensive pollen dispersal within and between populations | Ritchie & Krauss 2012 |
| *Castilleja levisecta* | 11 (seeds or plants from 4 seed sources), 7 microsatellites | higher genetic diversity and lower inbreeding and relatedness in reintroduced (mixed sources) than in source populations; indication of admixture; better to directly use seeds from sources than produce them by nursery beds | St. Clair et al. 2020 |
| *Cirsium pitcheri* | 2 (6 seed sources, 100–500 plants 8–15 years after last translocation), 6 microsatellites | higher genetic diversity in reintroduced (mixed sources) than in natural populations, but higher $F_{IS}$ values as a result of inbreeding and spatial substructuring (so limited contemporary gene flow), and small flowering- and effective-population sizes. | Fant et al. 2013 |

*Continued*

**Table 2. (Continued).**

| *Study species* | *No. of translocations* (n), *markers traits* | *Main results of genetic monitoring* | *Reference* |
|---|---|---|---|
| *Cochlearia polonica* | 1 (14 plants, 30,000 after 30 years), 3 AFLPs | fine-scale SGS within the population due to nonrandom gene flow; seed sampling to create new populations must be done on the whole population | Cieślak et al. 2007 |
| *Grevillea scapigera* | 2 (hundreds of clones from 10 plants, 266 plants survived), 3 AFLPs | low genetic diversity and high inbreeding in the F1 generation (seed progeny); $N_e$ approximately 2 due to small number of genotypes used as source for translocation and variance in reproductive success; to increase $N_e$, use offspring of founders and stimulate germination through disturbance | Krauss et al. 2002 |
| *Lasthenia conjugens* | 192 (3 × 100 seeds), 3 ISSRs | similar genetic diversity across 3 generations and among restored and natural populations | Ramp et al. 2006 |
| *Lychnis flos-cuculi* | 9 (commercial seed mixtures, 12–2050 plants after 3 or 8 years), 6 microsatellites | similar genetic diversity and allelic richness; inbreeding coefficients 3 times higher in sown than in natural populations; restricted contemporary gene flow among sown populations, depending on distance and population size | Aavik et al. 2012, 2013 |
| *Prostanthera eurybioides* | 2 (reinforced with local seeds) | similar genetic diversity between planted and natural subpopulations | Ottewell et al. 2016 |
| *Pseudophoenix sargentii* | 3 (3–119 plants, 0–63 plants after 20 years), 10 microsatellites | increased genetic diversity in 1 population but evidence of inbreeding in the other one, which needs additional reintroduction | Fotinos et al. 2015 |
| *Pulsatilla vulgaris* | 9 (1–380 plants after 3 years), 3 AFLPs, vegetative and reproductive performance | self-reinforcement after 3 years led to similar levels of genetic variation, fitness performance, and germination rates for natural and translocated individuals; population sizes increased (1- to 68-fold) | Betz et al. 2013 |
| *Sambucus palmensis* | 13 (cuttings from 3–129 plants), 30-year reintroduction program, 7 microsatellites | increased genetic diversity and high clonality due to propagation method; indication of natural regeneration by sexual reproduction; rare alleles maintained in natural populations but not present in translocated populations | Rodríguez-Rodríguez et al. 2018 |
| *Silene hifacensis* | 3 (4–14 plants, >10 years), 3 AFLPs | similar genetic diversity among restored and natural populations; inbreeding in 2 restored populations likely due to ex situ cultivation history, suggesting need for additional use of seeds with mixed origins | Alonso et al. 2014 |

[a] *Based on exhaustive searches in Web of Science, Google Scholar, and Google from 1955 up to 2020. Keywords: plant, conservation, genetic, population, restoration, rescue, translocation, reinforcement, augmentation, introduction, reintroduction, and genetic monitoring.*
[b] *Abbreviations: n, number of translocated individuals per population; markers traits, molecular markers and fitness traits investigated; RAPD, random amplified polymorphic DNA; AFLPS, amplified fragment-length polymorphisms; ISSRs, intersimple sequence repeats.*
[c] *For the cited literature, see Appendix S2.*

panmixia is usually estimated by calculating Wright's inbreeding coefficient ($F_{IS}$). When $F_{IS}$ is positive, it can indicate inbreeding from self-fertilization or assortative mating, but it can also result from the spatial structure of the population related to restricted seed or pollen dispersal (Van Rossum & Triest 2006; Fant et al. 2013). Heterozygosity can also be calculated at the individual level if many codominant markers are available (e.g., SNPs), potentially revealing inbred versus outbred individuals (Coulon 2010). Statistical analyses include comparisons between generations, between repeated measures through time, and between translocated and natural populations (e.g., Schwartz et al. 2007; Zavodna et al. 2015; Van Rossum et al. 2020). General or generalized linear models and multivariate analyses can also integrate demographic and environmental data (Rellstab et al. 2015).

To describe genetic divergence among generations and among translocated or natural populations, genetic distance and differentiation statistics (e.g., $F_{ST}$, $G_{ST}$, Jost's $D$) are usually combined with Bayesian clustering analyses or multivariate analyses (Appendix S1; Jombart et al. 2010; Alonso et al. 2014; Fotinos et al. 2015; Rodríguez-Rodríguez et al. 2018; Van Rossum et al. 2020). To distinguish between temporal (life stages, generations) or spatial (populations or subpopulations) components of the genetic differentiation, a hierarchical analysis of molecular variance can also be performed (Ramp et al. 2006; Van Rossum & Triest 2006; Van Geert et al. 2008).

#### Contemporary Gene Flow

Contemporary gene flow among populations and gene dispersal within populations are key factors for long-term population sustainability (Weeks et al. 2011; Ottewell et al. 2016). The translocation in the field must be designed to optimize random mating and cross-pollination by transplanting a large number of individuals. And, transplant density must be high and sources spatially randomized (Kirchner et al. 2006; Colas et al. 2008; Zavodna et al. 2015; Maschinski & Albrecht 2017). The patterns of gene dispersal in new recruits are expected to be reflected in the translocation design. However, different factors may influence gene dispersal, such as life history traits (e.g., seed and pollen dispersal abilities), pollinator service, management interventions, and population demographic dynamics, in terms of survival, flowering, and recruitment (Hardy et al. 2004; Raabová et al. 2015; Van Rossum et al. 2015; Benthien et al. 2016). Restricted seed or pollen dispersal may lead to spatial genetic substructuring of populations (individuals at close geographic proximity may be more genetically related) and to local (biparental) inbreeding (Vekemans & Hardy 2004; Van Rossum & Triest 2006).

Contemporary gene dispersal patterns have only been investigated for a few translocated plant populations (Table 2). Nonrandom gene flow resulting in spatial genetic structure (SGS) has been reported 30 years after translocation for *Cochlearia polonica* (Cieślak et al. 2007) and *Cirsium pitcheri* (Fant et al. 2013). Despite effective pollen dispersal in translocated populations of *Arnica montana*, some spatial structuring appears in the recruits due to restricted seed dispersal, allowing siblings and half-siblings to grow in close proximity (Van Rossum et al. 2020). This emphasizes the importance of maintaining extensive pollen flow, and thus pollinator services for animal-pollinated species, and of possibly increasing seed dispersal (e.g., by implementing grazing during the fruiting season [Benthien et al. 2016]).

A direct quantification of gene flow can be accomplished by genotyping offspring and their maternal plants to calculate outcrossing, biparental inbreeding, and selfing rates (Ritland 2002; McClure & Whitlock 2012). When plants are mapped and sampled exhaustively, paternity analyses can be performed on seeds collected directly from plants to identify pollen donors and distance of pollen dispersal and possibly to identify pollen migrants (Chybicki 2018). When the maternal plant is unknown (in the case of recruits), parentage analyses reveal pollen and seed dispersal. In the case of a large number of potential fathers or parents, high polymorphism of molecular markers is necessary to successfully determine parentage, so analyses can be expensive (Hardy et al. 2004; Chybicki 2018; Flanagan & Jones 2019). Bayesian clustering analyses or Bayesian assignment (Appendix S1) can also identify migrants when the geographic location of the individuals is known and the source populations are genotyped and well differentiated (Aavik et al. 2013).

Indirect methods, which require fewer molecular markers and nonexhaustive sampling, also allow for estimating gene dispersal. The most popular approach is the analysis of SGS at a fine geographic scale (Hardy & Vekemans 2002; Vekemans & Hardy 2004). The SGS analysis can give insight into gene dispersal patterns for the newly produced generations. The translocated generation is expected to be characterized by an absence of fine-scale SGS when the translocation protocol has led to randomization of the spatial distribution of seed sources. However, depending on plant mortality and on local selective processes, fine-scale SGS in the long term might appear in the transplants (Table 2) (Van Rossum et al. 2020). Separate spatial autocorrelation analyses can be performed within and between generations (Van Rossum et al. 2020). Indirect estimates of contemporary pollen dispersal can also be obtained from the pattern of pollen pool differentiation between maternal families (Robledo-Arnuncio et al. 2007).

When successful pollination depends on animal vectors, whether pollinator guilds might represent a limiting factor for gene flow can be evaluated by observations of abundance and movements of the visiting

pollinators (Pasquet et al. 2008; Brunet et al. 2019). Fluorescent powdered dye particles can be used as analogues for pollen and provide an estimate of pollinator movements and pollen dispersal distances (Van Rossum et al. 2011, 2015; Diniz et al. 2019). These low-cost methods can be convenient when populations are too large for paternity analyses.

### Mode of Local Recruitment

The establishment of new plants in the translocated populations can result from sexual reproduction. For many perennial plant species, it can also result from clonal (asexual) propagation. Sexual reproduction can facilitate gene exchanges and bring new genotypes that will increase mating opportunities and effective population size. It is therefore a good indicator of successful population restoration. Clonal propagation can rapidly provide new individual clones, allowing the maintenance of already existing genotypes and increasing census population size (Menges 2008; Becheler et al. 2017; Van Rossum & Raspé 2018). However, the clumping of clones of a same genotype can also increase self-pollination and the risk of inbreeding depression. Sexual versus asexual prevalence in recruitment has only been tested for translocated populations of the clonally propagating *Arnica montana*. The recruitment was mainly based on sexual reproduction, indicating successful population rejuvenation (Van Rossum et al. 2020).

Whether the recruits resulted from sexual reproduction or clonal propagation can be assessed by identifying the distinct multilocus genotypes and assigning each individual to these genotypes based on a probability estimator (Peakall & Smouse 2006). When only a subsample of the transplants is genotyped, the rate of clonality can be quantified using a Bayesian approach that compares transplants with the first new generation (Becheler et al. 2017).

### Population Integration Through Admixture

Genetic variability and fitness can be maximized by recombining genomes, thus by admixture between transplants (Maschinski et al. 2013; Zavodna et al. 2015; St Clair et al. 2020). Failure in admixture may indicate outbreeding depression or reproductive isolation (Edmands 2007). Therefore, when using nonlocal or several sources for reinforcement, introduction, or reintroduction, it is important to verify whether the genetic mixing is effective (i.e., successful mating between local and nonlocal or between mixed sources) and the local gene pool has been conserved.

The 12-year-old translocated populations of *Arenaria grandiflora* show 80% of genotypes resulting from admixed (nonlocal–local) crosses. The local genetic pool was preserved (Zavodna et al. 2015). In translocated populations of *Arnica montana*, 25–68% of the F1 generation resulted from admixture between differentiated seed sources, indicating extensive pollen flow (Van Rossum et al. 2020). In *Castilleja levisecta*, there was an indication of mixed parentage between seed sources in reintroduced populations (St. Clair et al. 2020).

The possibly admixed origin of newly established individuals can be estimated by performing Bayesian clustering analyses (Pritchard et al. 2000; St. Clair et al. 2020), by calculating a hybrid index for each individual (Zavodna et al. 2015), by performing a principal coordinate analysis (with axis values as estimators), or by conducting a parentage analysis (Peakall & Smouse 2006; Flanagan & Jones 2019). Bayesian clustering analyses can also be followed by a simulation that allows the assignment of offspring genotypes to one of the sources or to the first-generation hybrids (Van Rossum et al. 2020).

### Increase of Local Plant Fitness by Genetic Rescue and Indication of Inbreeding or Outbreeding Depression and Local Adaptation

When the plant translocation goal is genetic rescue, we expect an increase of plant fitness in reinforced, formerly inbred populations due to the introduction of new genetic variation or heterosis (increased vigor of the cross progeny) (Bell et al. 2019). For introduced and reintroduced populations, plant fitness should be higher or similar to reference populations (Weeks et al. 2011). It is also important to check for inbreeding and outbreeding depression (reduced fitness in inbred or admixed offspring) and for local adaptation (higher fitness of local genotypes) (Edmands 2007; Menges 2008). Up to now, these evaluations have been based on phenotypic traits, but the new genomic technological developments (see below) offer future perspectives in detecting heterosis, inbreeding, and outbreeding depression or selection processes.

Genetic rescue, as well as inbreeding and outbreeding depression, may be tested by experimental crosses (e.g., Edmands 2007; Willi et al. 2007; Bartmentlo et al. 2018) and local adaptation by reciprocal transplant experiments (Bowman et al. 2008; Reckinger et al. 2010). However, such experiments are not always possible to carry out before implementing plant translocations in species recovery plans because it may take several years to obtain new generations. Genetic rescue, with local or nonlocal source provenance, is usually successful (Table 2) (Wili et al. 2007; Betz et al. 2013; Zavodna et al. 2015; Bartmentlo et al. 2018). However, the effects of heterosis, inbreeding, and outbreeding depression and local adaptation on plant fitness may be complex and conflicting and may depend on life stages (Bowles et al. 2015; Zavodna et al. 2015; Bartmentlo et al. 2018). There was no sign of heterosis or outbreeding depression in the F1 generation of translocated populations of *Arnica montana*. Phenotypic plasticity and maternal effects were found (Van

Rossum et al. 2020). Phenotypic plasticity may increase transplant survival in spatially or temporally varying environments in the short term and favor adaptation and population evolutionary resilience to changing environmental conditions in the long term (Nicotra et al. 2015; Christmas et al. 2016). Maternal effects may favor adaptation in stable environments (Schuler & Orrock 2012). Differences in progeny fitness may also reflect genetic variability (Basey et al. 2015; Hamilton et al. 2017) and so contribute to population evolutionary potential.

Including molecular data in the analyses of individual phenotypic traits (Table 1) can make the inferences stronger (Zavodna et al. 2015; Bartmentlo et al. 2018). To avoid variation related to environmental effects and to examine possible maternal effects, measurements should preferably be carried out in standardized environments (Leinonen et al. 2008; Whitlock 2008) that are as close as possible to the environments of natural or translocated populations. It is also possible to measure traits in the field provided a large number of individuals have been translocated to a site and the population origin of the transplants is known (Savolainen et al. 2013). Defining the environmental conditions in controlled experiments may be important because inbreeding depression or heterosis effects are not always expressed when the conditions are optimal (e.g., in case of cultivation in common garden), but they may appear under stressful conditions, such as dryness or competition (Edmands 2007; Willi et al. 2007). Phenotypic plasticity may also not be expressed in a common-garden environment (Whitlock 2008). Phenotypic data can be analyzed in relation to molecular genotypes (local vs. introduced genotypes, individual heterozygosity, admixture level), source origin, and environmental characteristics of the sites, including management interventions, but can also be compared with data from natural (source, inbred, and healthy) populations (Bowman et al. 2008; Reckinger et al. 2010; Bowles et al. 2015; Zavodna et al. 2015).

When inbred and outbred (admixed or not) individuals can be clearly identified based on their molecular genotypes, inbreeding or outbreeding depression can be quantified by calculating a relative performance coefficient (Angeloni et al. 2011). Local adaptation can be quantified by calculating the relative fitness of translocated individuals compared with natural ones or by comparing different sources at a given translocation site and in a given year (Hereford 2009).

To detect evidence of local adaptation, different approaches may be used. First, a genome-wide selection scan analysis compares genetic variation among all genomic markers to build a neutral distribution. Markers deviating from this distribution are expected to be under selection (linked to candidate adaptive genes) (Angeloni et al. 2012; Benestan et al. 2016). Second, genotype–environment association methods consist of identifying candidate adaptive loci by associating their allele frequencies with environmental variables. These methods entail performing univariate, multivariate, or Bayesian analyses and can be combined with geographic information systems (Joost et al. 2007; Flanagan et al. 2018). Finally, genome-wide association studies test the association of genotypes with phenotypic data (Savolainen et al. 2013; Rellstab et al. 2015). The homozygosity or heterozygosity level of some genomic regions may also be associated with fitness traits and thus reveal major genes implicated in inbreeding or outbreeding depression (Angeloni et al. 2012).

### Long-Term Monitoring of Genetic Changes

Short-term monitoring over a few generations can reveal contemporary processes, such as pollination and seed dispersal, on yearly basis. However, long-term genetic monitoring is also necessary because the genetic composition of a translocated population can change through time. First, outbreeding depression can only be expressed in the progeny after 2 or 3 generations of admixture (Edmands 2007). Second, it can take time for natural selection to remove the poorly adapted genotypes (Week et al. 2011; Zavodna et al. 2015; Barmentlo et al. 2018). Finally, the temporal dynamics of the genetic composition can depend on species' life history traits (e.g., breeding system, growth form, plant longevity, recruitment time lag), translocated population demographic dynamics (e.g., census population size, plant density, sex or morph ratio, recruitment rate), and variation in local factors between translocated sites (e.g., management interventions, soil chemical composition, vegetation composition, grazing pressure, competition) (Van Rossum & Triest 2006; Bowman et al. 2008; Menges 2008; Weeks et al. 2011; Maschinski & Albrecht 2017; Albrecht et al. 2019). Therefore, measurements (possibly restricted to those identified as key indicators in the restoration of genetically viable populations) should be repeated over several generations and over a long period to detect possible changes in genetic diversity and structure, rescue status, and adaptive response.

Despite their importance in evaluating the success of plant translocations, long-term monitoring studies over 10–20 years are still rare for demographic surveys (Colas et al. 2008; Godefroid et al. 2011; Albrecht et al. 2019) and even rarer for genetic monitoring (Bowles et al. 2015; Zavodna et al. 2015; Rodríguez-Rodríguez et al. 2018). A long-term genetic survey may be difficult to implement for understandable reasons (limited budget and staff or other conservation priorities for practitioners). Given that plant translocations may be the last chance for preserving some populations and represent high financial and time investment (Fenu et al. 2019), it should be systematically considered in species recovery plans.

Repeated, long-term molecular data collection allows the calculation of 2 indicators of the long-term sustainability of the populations: effective population size ($N_e$) and population viability. To our knowledge, one attempt has been made to estimate these indicators on translocated plant populations, for the clonal *Grevillea scapigera* (Table 2). Despite demographic data indicating translocation success with thousands of *G. scapigera* seeds produced by a large census population size (266 plants), $N_e$ estimates were approximately 2 because only 10 plants were used as a source and there was large variation in reproductive success (Krauss et al. 2002). The $N_e$ can be estimated using the linkage disequilibrium estimator (comparison of $N_e$ over several years), temporal changes in allele frequencies, and sibship or parentage frequency (Appendix S1) (Luikart et al. 2010; Wang 2016). Population viability analyses (PVA) are used to estimate the population size needed for the long-term persistence and to estimate a population's risk of extinction (Menges 2008; Pe'er et al. 2013). When combining demographic, genetic, and environmental data through time and space, the PVA can take evolutionary potential into account (Kirchner et al. 2006; Pierson et al. 2015).

## A Tool for Conservation Practitioners

Genetic monitoring is a useful tool for evaluating whether species conservation plans have achieved the recovery of long-term sustainable translocated populations. However, the available genetic tools are often underused. Attention should be given to recruitment by sexual reproduction, contemporary gene flow, admixture between sources, and the maintenance of the local genetic pool. These factors are also important to consider if the translocated populations will be used as sources for further translocations. We believe best practices for monitoring conservation translocations should include both molecular and phenotypic approaches, given the potential roles of heterosis, outbreeding, adaptation, phenotypic plasticity, and maternal effects on population dynamics. Results of genetic monitoring studies (Betz et al. 2013; Van Rossum et al. 2020) emphasize the importance of implementing ecological management interventions. They stimulate flowering to optimize pollination and random mating, and thus reproductive success, and favor seed germination and recruitment. As a result, genetic dynamics can be initiated and further pursued with success to maximize evolutionary resilience. We hope our guidelines will help conservation practitioners find the appropriate genetic survey methods, depending on the goal of the plant translocation, so that they can adapt management practices to better integrate evolutionary processes.

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## Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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