



A long-term genetic study reveals complex population dynamics of multiple-source plant reintroductions



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ABSTRACT

A major challenge of using multiple-source populations in reintroductions for restoration and species conservation is to adequately assess the trade-off between the benefits of counteracting inbreeding depression via heterosis, and the risks of maladaptation and reduced fitness through outbreeding depression. In the 1990s, populations of the perennial plant *Arenaria grandiflora* rapidly declined and were nearing extinction in the Fontainebleau forest, France. This was likely due to inbreeding depression and/or fixation of deleterious alleles. To restore *A. grandiflora* in the Fontainebleau forest, a reintroduction experiment was conducted in 1999 using transplants from both local and non-local populations. Eight and twelve years later, we carried out a genetic study using microsatellite markers to assess the temporal dynamics of the genetic composition of reintroduced populations. We show that genetic diversity increased significantly in the reintroduced populations compared to the local-source population and that this increased diversity has been maintained for over ten years, highlighting the benefits of mixing individuals of multiple-source populations for restoration of small and inbred populations. Our results also suggest that the level of individual admixture between local and non-local genetic sources might affect individual fitness, which is influenced by the opposing effects of heterosis, inbreeding and outbreeding depressions and local adaptation.

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1. Introduction

Due to human-accelerated landscape fragmentation and habitat disturbance, natural populations may decline and become smaller and isolated. As a consequence, such populations experience a reduction in genetic diversity that is caused by genetic drift, limited gene flow (Frankham, 1996) and/or inbreeding (Kephart, 2004). To recover declining populations and restore their evolutionary potential in a long-term self-sustained manner, various re-establishment practices are used in conservation biology. These may include efforts to restore the habitat where endangered or threatened species occur. When habitat restoration is not sufficient or successful, species-focused restoration plans are undertaken. Among those are, for example, enhancement/reinforcement that refers to the addition of individuals into existing populations or reintroduction that implies re-establishment of a species within its historical range, where it had become locally extinct (IUCN, 1998).

Recent reviews on the success of reintroduction indicate that reintroduction plans are very complex and influenced by multiple factors that should be considered beforehand (Seddon et al., 2007; Menges, 2008; Godefroid et al., 2011; Breed et al., 2013). A successful reintroduction

requires a sufficient population size to avoid demographic stochasticity or Allee effect. The number of reintroduced individuals must exceed the population viability thresholds, which largely depend upon the mating system of the species. Demographic and genetic studies have demonstrated a positive relationship between founder population size and population fitness, where larger founding populations are likely to persist for longer (Reed and Frankham, 2003; Ottewill et al., 2014).

A successful reintroduction also requires a detailed knowledge of both the ecological needs of the species and the environmental characteristics of the reintroduction site. Generally, locally sourced individuals are preferred for the reintroduction (Breed et al., 2013; but see also Jones, 2013). If populations are locally adapted, then the introduction of individuals from elsewhere might introduce maladaptive genes into the restored populations and reduce their fitness. A number of studies have shown that the survival of reintroduced populations is higher for locally sourced than for non-local individuals (e.g. Montalvo and Ellstrand, 2000; McKay et al., 2005; Olsson, 2007; Vander Mijnsbrugge et al., 2010). If local individuals are not available, then introduced individuals should originate from populations of a very similar ecological habitat (Bottin et al., 2007).

Sufficient genetic variability is one of the key variables that influence the long-term survival of the species because it may increase the adaptive potential to face environmental changes and avoid inbreeding depression (Booy et al., 2000; Jones, 2003). If declining populations have lost genetic diversity due to genetic drift and suffered from inbreeding depression,

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reintroduction should not be limited only to material from a single, local population (Smulders et al., 2000). Mixing genetically divergent source populations and subsequent admixture might reinforce the genetic variability and composition of the reintroduced populations through recombination among genomes, which may result in the increased fitness of the progeny due to heterosis (Kephart, 2004; Vergeer et al., 2004). However, inter-population admixture may also have negative impacts on the demography of the populations. For example, outbreeding depression, which occurs when individuals from multiple-source populations interbreed, reduces individual vigor by disrupting co-adapted gene complexes (Kephart, 2004).

Clearly, maximizing genetic diversity in reintroduction plans must be balanced to avoid importing maladapted genes and disrupting local co-adapted gene complexes. Thus, the origin of introduced individuals is a key factor for successful re-establishments and restoration practitioners need to consider inbreeding depression, reproductive viability, local adaptation and the evolutionary potential of reintroduced populations (McKay et al., 2005; Broadhurst et al., 2008; Breed et al., 2013).

While many studies focus on demographic issues influencing the success of reintroductions, their genetic consequences have only recently received more attention (Ransler et al., 2011; Weeks et al., 2011). This is coupled with the technological advances that enable the use of molecular markers to assess the impact of genetic factors, such as genetic diversity and population structure, on the success of the reintroductions and translocations (Smulders et al., 2000; McGlaughlin et al., 2002; Cieslak et al., 2007; De Barba et al., 2010; Huff et al., 2010; Ransler et al., 2011).

Although the majority of the reintroduction studies monitor the populations for a relatively short time (<4 years) after reintroduction/transplantation (Sutherland et al., 2010; Godefroid et al., 2011), long-term monitoring is particularly important to ensure the persistence of the populations (Breed et al., 2013). This is especially true because initially high survival rates are often followed by population decline and restoration failure (Godefroid et al., 2011 and references within, but see also Albrecht et al., 2011). Only a few studies have documented long-term (>4 years) monitoring of populations after reintroductions. These are mainly demographic studies (e.g. Maschinski and Duquesnel, 2006; Guerrant and Kaye, 2007) and a handful of genetic studies (e.g. Cieslak et al., 2007; De Barba et al., 2010).

In France, a number of restoration plans for plant and animal species have been conducted, but only a few have documented long-term monitoring. One of them, the reintroduction experiment of *Arenaria grandiflora*, was conducted in the Fontainebleau forest, in the Parisian region, where the populations have rapidly declined in the last three decades (Bottin et al., 2007). Apart from the impact of changes in the forest management, it was suggested that these populations might have also suffered from fixation of deleterious alleles and/or inbreeding (Bottin et al., 2007). To restore *A. grandiflora* in the Fontainebleau forest, a reintroduction experiment was conducted in 1999. To counteract possible inbreeding depression, transplants from local (Fontainebleau forest) and non-local (Loire valley) populations were used. Since 1999, the reintroduced populations have been left to persist without human intervention, but they are monitored annually for the survival and fitness of individuals. Moreover, species-specific microsatellite markers (Zavodna et al., 2009) allowed a complete genetic assessment of this reintroduction experiment by genotyping preserved cuttings of the founding individuals and all flowering individuals sampled in the populations eight and twelve years after reintroduction. This genetic study was conducted to (1) assess the temporal dynamics of the genetic composition of the persisting reintroduced populations, (2) characterize the level of admixture within individual genomes and (3) evaluate the relationship between individual flowering and admixture rates as an assessment of the heterosis, outbreeding depression and local adaptation phenomena in the reintroduced populations. Our long-term genetic monitoring allows for a better understanding of the complex trade-off between the risks and benefits associated with mixing multiple-source populations for species restorations.

2. Material and methods

2.1. Study species and native sites

A. grandiflora is a perennial Caryophyllaceae that is believed to be insect-pollinated; it predominantly outcrosses, but selfing and vegetative reproduction are also possible (Bottin et al., 2007). It occurs on the calcareous rocks and screes of southern and central European mountains (the Alps, the Jura Mountains and the Pyrenees) at high elevation of 1500 to 2500 m. These high-elevation populations typically consist of tens to hundreds of individuals. In France, it can also be found, albeit rarely, in lowlands. To date, two lowland locations are still extant. One is approximately 200 km southwest of Paris (Chinon in Loire valley; 47°09' N, 0°14' E) and consists of a few hundred individuals. The second is located approximately 50 km south of Paris (Fontainebleau forest; 48°24' N, 2°42' E) and, while it was still abundant in the 1950s, there were less than 10 individuals in early 2000, and only one persisting individual was observed in 2009. Since 1991, *A. grandiflora* has been legally protected in both lowland locations.

Previous demographic and genetic studies suggested that populations of *A. grandiflora* in the Fontainebleau forest might have declined rapidly not only due to changes in the forest management and excessive harvest by collectors of rare plants but also because populations might have suffered from the fixation of deleterious alleles by genetic drift and/or inbreeding (Bottin et al., 2007). Further details on the description of natural sites and previous studies on *A. grandiflora* can be found in Bottin et al. (2007).

2.2. Reintroduction project – material and sites

Given that (1) local (Fontainebleau) populations likely suffered from inbreeding depression and (2) presumably genetically differentiated (based on presence of private isozyme alleles, Bottin et al., 2007) individuals from non-local (Chinon) populations of very similar habitat were available, a reintroduction experiment was conducted using individuals from both origins – local (Fontainebleau forest) and non-local (Chinon). The experiment is detailed in Bottin et al. (2007). Briefly, due to poor seed production and a very low number of total *A. grandiflora* individuals in the native Fontainebleau populations, cuttings from nine individuals of local populations and 11 individuals of non-local populations were taken in 1997 and propagated in vitro culture for two years to obtain a sufficient number of individuals. Although this relatively low number of founding genotypes might appear limiting, the use of additional founders from high-elevation populations was considered to be a higher risk due to possible introduction of maladapted genotypes and outbreeding depression. Thus, in 1999, approximately 1320 individuals were produced in vitro and after acclimatization were planted out at three reintroduction sites (Bois Rond – BR, Cuvier Châtillon – CC, Queue de Vache – QV), located in the Fontainebleau forest, approximately 10 km away from the native *A. grandiflora* populations. These sites were selected because they exhibited ecological characteristics that were similar to those of native populations. At each site, two fenced enclosures (BR1 and BR2, CC1 and CC2, QV1 and QV2) were established, and, in each enclosure (100 m²), a total of 220 individuals were randomly planted out. These individuals were approximately 2/3 of local (Fontainebleau) origin and 1/3 of non-local (Chinon) origin. The planted individuals were numbered and labeled. Thus, six genetically identical populations were reintroduced and left to grow without human intervention. In addition, a few individuals of each of the 20 initial clones have been maintained in vitro culture.

2.3. Demographic data sampling

Since 1999, the reintroduced populations have been monitored annually for individual survival, recruitment and fitness. The two populations at the BR site became extinct in 2004 most likely due to

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