



To mix or not to mix the sources of relocated plants? The case of the endangered *Iris lortetii*

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ABSTRACT

Active management of endangered species is required for the persistence of many rare species. Species translocation, a common practice used to mitigate the negative effects of small population sizes, entails risks of outbreeding depression due to dilution of local adaptations, and therefore must be weighed against the costs of a hands-off conservation approach. *Iris lortetii* is an endangered rhizomatous plant, growing in a small number of isolated populations in northern Israel. We implemented a quasi-in-situ reintroduction program by planting 234 rhizomes from diverse origins in five new sites. All new sites were selected to be as similar as possible to those of the largest natural population. We recorded plant survival and flowering in the field after four years. Flowering plants were artificially crossed either with plants from the same population of origin (within population) or with plants from different origin (between populations). We found no differences in survival between populations of origin and only some indication of local adaptations in the form of increased flowering of the local population. Nonetheless, seed set was significantly higher (a 73% increase) in crosses between populations of origin, compared to within-population crosses, suggesting low genetic diversity within the natural populations. The ability to combine active conservation with rigid testing of theoretical hypothesis, while avoiding all risk to natural populations, highlights the value of the quasi-in-situ approach for restoration. Our results indicate that, in the case of *Iris lortetii*, active relocation of genotypes, seeds or pollen can enhance the survival of natural populations over time.

1. Introduction

The preservation of species diversity is one of the main goals of modern conservation (Dawson, Jackson, House, Prentice, & Mace, 2011; Pimm et al., 2014). Rare species often receive much conservation attention and resources (Early & Thomas, 2007; Sapir, Shmida, & Fragman, 2003), where the conservation strategy is frequently derived from knowledge of the species' biology, level of threat and spatial distribution (Bacchetta, Farris, & Pontecorvo, 2012; Sapir et al., 2003). In many cases, habitat destruction and fragmentation limit the spatial distribution of rare species to a few isolated patches, increasing their probability of extinction, thus prioritizing them for conservation (Sapir et al., 2003).

Small and isolated populations are known to be exposed to a variety of processes that might lead to population decline and local extinction. Among these are genetic drift and fixation of deleterious mutations and

inbreeding depression (Elam, Ridley, Goodell, & Ellstrand, 2007; Ellstrand & Elam, 1993), demographic stochasticity (Volis, Bohrer, Oostermeijer, & Van Tienderen, 2005) and habitat loss (González-Varo, Albaladejo, Aizen, Arroyo, & Aparicio, 2015). Mitigating these risks requires the increase of their population sizes, as well as their genetic diversity. Such goals may be achieved by various conservation actions that facilitate gene flow and immigration among populations. The nature of these actions depends on the levels of isolation, species biology and resource availability. For example, in organisms with limited movement or dispersal, such as plants, establishment of protected areas and corridors may prove insufficient, and additional strategies, such as genetic rescue, might be required. This is especially true in fragmented habitats where the distance between patches is large or when the fragmentation is caused by irreversible factors, such as urban development.

Genetic rescue is a strategy to alleviate reduced genetic diversity in

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small and fragmented populations (Frankham, 2015; Richards, 2000). Genetic rescue involves enrichment of genetically poor populations by transferring pollen (Christmas, Breed, & Lowe, 2015; Xiao, Jiang, Tong, Hu, & Chen, 2015), seeds or propagules from another population, a method called 'species translocation' or 'assisted migration' (Kramer & Havens, 2009; Richards, 2000). Seeds or pollen used for genetic rescue may come from different geographical or ecological regions, in order to increase the genetic variation in the fragmented population (Ingvarsson, 2001; Richards, 2000; Vandepitte, Honnay, Jacquemyn, & Roldán-Ruiz, 2010). However, in some cases, crosses may result in negative outcomes, due to outbreeding depression in cases of strong divergence following local adaptation (Edmands, 2007).

Outbreeding depression is expressed as reduced cross success with increasing ecological differentiation, due to divergent selection (Ruane, Dickens, & Wall, 2015; Sapir & Mazzucco, 2012; Schierup & Christiansen, 1996). Thus, genetic rescue with source population of intermediate ecological distances is likely to maximize success (Grindeland, 2008; Hufford, Krauss, & Veneklaas, 2012; Pélabon, Carlson, Hansen, & Armbruster, 2005; Price & Waser, 1979; Sapir & Mazzucco, 2012; Waddington, 1983). However, when populations have been separated for longer time periods, possible local adaptations may result in an advantage to local gene pools (Anderson, Willis, & Mitchell-Olds, 2011; Griswold, 2006). Conceivably, in some cases, the benefit of increased genetic diversity due to genetic rescue might be outweighed by the dilution of local adaptations. This trade-off confronts conservationists with a dilemma – whether to mix or not to mix plants from different sources in relocation practice (Edmands, 2007; Frankham, 2015; Ouborg, Vergeer, & Mix, 2006).

Quasi in-situ conservation offers a way to partially circumvent this dilemma: new populations are established in habitats similar to natural sites, but not within the natural populations, in order to prevent genetic contamination and consequent outbreeding depression (Volis & Blecher, 2010; Volis, Blecher, & Sapir, 2010). Use of a comparison of plants from multiple populations, grown under the same ecological conditions could help quantify the relative effects of local adaptations and lack of genetic diversity, without jeopardizing the natural populations. To the best of our knowledge, while numerous studies tested for local adaptation per se, only a few empirical studies explicitly tested the relative roles of diluting local adaptations and increasing genetic diversity (Volis et al., 2010).

Adding to the “mixing or not mixing” dilemma are the long-term effects. While the first generation after assisted gene flow may be viable, the second generation may experience introgression of deleterious (or beneficial) mutations among the mixed populations (Campbell, Snow, & Ridley, 2006; Oakley, Agren, & Schemske, 2015). As a first proxy for long-term effect, it is hence important to elaborate on the outcome of crossing among plants from different populations when testing for the advantages and disadvantages of mixing sources in re-locating endangered plants.

Iris lortetii Barbey (*Iris* section *Oncocyclus*; Fig. 1a) is a Mediterranean rhizomatous endangered species, endemic to the Upper Galilee in northern Israel and southern Lebanon (var. *lortetii*), with a disjunctive population in central Palestine (var. *Samaria*; (Feinbrun-Dothan, 1986; Sapir, 2016). Different populations are found in sites with notably diverse environmental conditions, in terms of bedrock (either chalk or limestone with brown rendzina or shallow terra-rossa soils), slope (12–30 degrees), aspect, elevation (525–718 m a.s.l) and surrounding woody vegetation cover (4–53%). Most populations are found on stony steep slopes, perhaps because other microhabitats were target for either collection by 19th century commercials or porcupine herbivory (Sapir, 2016). Due to its limited distribution (about 220 km² area of occupancy), accompanied by a severe decline in population size and number of sites, it is considered “endangered”, according to the International Union for Conservation of Nature categories (Sapir, 2016), and is listed in the Red Data Book of the Israeli Endangered Plants (Shmida & Pollak, 2008). Major threats to *I. lortetii* include collection of rhizomes for

commercial use and habitat transformation and fragmentation due to agriculture and afforestation (Shmida & Pollak, 2008). The species has experienced significant population decline and fragmentation in northern Israel, and has probably become extinct in southern Lebanon (Sapir, 2016; M. Semaan, per. comm.). In the Upper Galilee the species is currently limited to three populations (a few hundred individuals each) and a handful of satellite sites (a few dozen individuals in each). The total number of individual plants in all populations is estimated at between 2000–2500 (Sapir, 2016). Like all other species in the section *Oncocyclus*, *I. lortetii* is self-incompatible and is obligatorily pollinated by males of a solitary bee (*Eucera* spp.; Sapir, Shmida, & Ne'eman, 2005). Some evidence for inbreeding depression in crosses within populations was shown in two other related species, *Iris bismarckiana* Regel (Segal, Sapir, & Carmel, 2007) and *I. atropurpurea* Dinsm. (Sapir & Mazzucco, 2012), suggesting low within-population genetic diversity resulting in reduced seed production. Evidences from other species suggest that seed dispersal is limited to a few tens of meters, and pollen flow is restricted to a few hundreds of meters (Sapir, un-published). The low dispersal and pollination distances of *I. lortetii* and the isolation among subpopulations are likely to minimize the effectiveness of ecological corridors and highlight the need for an active conservation strategy.

In this study we estimated the relative importance of local ecological adaptations and genetic diversity, in order to answer the question – should we use mixed or non-mixed seed sources for establishing new populations of *I. lortetii*. This question is an extension of the quasi in-situ conservation framework, proposed by Volis et al. (2010, 2015). In light of the small population sizes and the results of previous studies (Segal, Sapir, & Carmel, 2006), we hypothesized that cross-pollination between plants that differ in their population of origin will increase seed production due to increased genetic diversity. Due to the large environmental variability between the sites of the natural populations, as well as the short dispersal and pollination distances of iris species, we further hypothesized that plants growing in their habitat of origin would show higher survival and flowering rates due to a possible home advantage. Briefly, we created new populations of *I. lortetii* and tested whether local adaptations have developed in plants from one of the three major populations, and whether mixing genotypes (by crosses) between populations is beneficial or maladapted, by measuring the reproductive success of crosses.

2. Materials and methods

2.1. Seed collection and germination

We collected the seeds in April 2011 at five sites throughout the distribution of the species in the Upper Galilee. Fruits (pods) were collected haphazardly at each site in order to represent the entire population. Largely, in cases where genets were clearly defined one pod was collected per genet (see below). The sites (and their codes) were as follows: Avivim (AVI; 37 pods, 943 seeds); Malkiya (MLK; 50 pods, 1236 seeds); Mt. Pua (PUA; 37 pods, 934 seeds); Ayelet Hashachar (ALT; 11 pods, 253 seeds); and, Dishon (DSH; 3 pods, 47 seeds). Fig. 1b shows the location of these sites. Altogether, 138 pods containing 3413 seeds were collected. Of these five sites, the populations of Pua, Avivim and Malkiya were substantially larger (more than 50 clearly distinguishable individuals). In Malkiya the population is relatively dense and defining the exact population size was practically impossible because genets were growing continuously. Hence, pods in the MLK population were collected without defining the genets. The small number of fruit collected in DSH was the result of lack of fruit production.

In November 2011 the seeds were planted into small pots (~1 L), in a mixture of commercial potting soil mixed with ~5% natural soil inoculum collected from Pua site, in order to provide possible mycorrhizal symbiosis, if exists. The seeds were planted in the nursery of Tel Aviv University Botanical Garden and watered twice daily by misters

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