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Low population viability in small endangered orchid populations: Genetic variation, seedling recruitment and stochasticity



Hilde Hens^{a,b,*}, Veli-Matti Pakanen^a, Anne Jäkäläniemi^c, Juha Tuomi^{a,d}, Laura Kvist^a

^a Department of Ecology and Genetics, University of Oulu, P.O. Box 3000, 90014 Oulu, Finland

^b Thule Institute, University of Oulu, P.O. Box 7300, 90014 Oulu, Finland

^c Thule Institute, Oulanka Research Station, Liikasenvaarantie 134, 93999 Kuusamo, Finland

^d Section of Ecology, Department of Biology, University Turku, 20014 Turku, Finland

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ABSTRACT

There are only few studies that use both demographic and genetic data to assess population viability of plant species. We combined genetic and demographic data from 11 endangered perennial orchid populations of varying size in order to reveal determinants of viability. Small populations had substantially lower viability compared to large populations. Seedling recruitment rates were remarkably lower in small populations; this was not due to pollination limitation or inbreeding depression because the fruit set and heterozygosity were not correlated with population size, suggesting that there may be differences in successful germination. Low recruitment resulted in significantly lower predicted populations growth rates in small populations. The impact of stochasticity on viability varied among populations and stochastic simulations indicated that only one large population was viable, whereas all the other large populations were predicted to go extinct within decades. While there was a positive correlation between the deterministic population growth rate and allelic richness, we did not find any other correlations between genetic variation and fitness or population size. The study populations are likely remnant populations. Management should focus on the maintenance of large population size, which is needed to avoid negative consequences of stochasticity and to enhance seedling recruitment rates.

1. Introduction

Endangered species often consist of small and fragmented populations, which are vulnerable to extinction due to environmental and demographic stochasticity (Lande, 1988; Shaffer, 1981). In addition, small populations suffer from genetic stochasticity caused by genetic drift and inbreeding (Young et al., 1996). A higher probability to mate with related individuals or elevated selfing rates lead to increased levels of homozygosity, which may result in the expression of harmful and deleterious recessive alleles, and consequently reduced fecundity and survival of individuals in small populations (Ellstrand and Elam, 1993; Reed and Frankham, 2003; Young et al., 1996). Additionally, random genetic drift is expected to lead to a reduced genetic diversity in small populations. Reduced genetic variation can constrain the evolutionary potential, and thus lower long-term viability of plant populations especially in rapidly changing environments (Ellstrand and Elam, 1993; Young et al., 1996). While it is recognised that genetic variation is important for long-term evolutionary processes, its short-term influence on the extinction risk has been questioned (Caro and

Laurenson, 1994; Caughley, 1994; Lande, 1988). It has been suggested that genetic factors only act after populations have already undergone significant declines in population size. However, there is extensive evidence for the influence of genetic factors on the extinction risk (Angeloni et al., 2011; Hedrick and Kalinowski, 2000; Reed and Frankham, 2003). For example, genetic erosion has been observed in small fragmented populations (Aguilar et al., 2008; Honnay and Jacquemyn, 2007; Leimu et al., 2006), and inbreeding has been shown to decrease fitness in small populations (Oostermeijer et al., 1994). Levels of populations' genetic diversity are thus expected to correlate with both the population size and the long-term population viability.

In addition, ecological processes may reduce the population size further, after the population sizes are reduced due to deterministic processes. Such ecological processes include a reduced pollination due to the lack of conspecifics or low density (Allee effect; Courchamp et al., 1999; Groom, 1998; Lamont et al., 1993) or due to the failure of small populations to attract pollinators (pollination limitation; Sih and Baltus, 1987; Ågren, 1996).

A key for undertaking effective conservation actions is to under-

* Corresponding author at: Department of Ecology and Genetics, University of Oulu, P.O. Box 3000, 90014 Oulu, Finland.

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E-mail addresses: hilde.hens@oulu.fi (H. Hens), veli-matti.pakanen@oulu.fi (V.-M. Pakanen), juhatuomi53@gmail.com (J. Tuomi), laura.kvist@oulu.fi (L. Kvist).

stand the importance of genetic variation, stochasticity, demographic parameters and deterministic population dynamics on the performance of populations. To date, mostly demographic parameters have been used to gain knowledge on the population viability (Reed et al., 2002) and only few studies have incorporated both demographic and genetic parameters (e.g. Menges and Dolan, 1998; Oostermeijer et al., 2003; Reed et al., 2002; Schmidt and Jensen, 2000). Furthermore, studies often ignore important life history factors, such as dormancy, seed banks or clonal reproduction (Zeigler et al., 2013).

The family of Orchidaceae has the highest proportion of endangered species of all plant families (Swarts and Dixon, 2009). Orchids typically depend on biotic interactions for reproduction and germination, and are specialised in specific mycorrhizal fungi (Rasmussen, 1995) and pollinators (Micheneau et al., 2009). In addition, orchids tend to be specialised in particular abiotic habitat conditions. High specialisation makes orchids vulnerable to the negative consequences of changing environmental conditions, as these inter-specific interactions can be altered, leading to decreased population sizes and, eventually local extinctions (Fay et al., 2015; Micheneau et al., 2009). Conservation of orchid species is challenging, because these interactions can be altered in many different ways by environmental factors, such as climate change and habitat fragmentation (Fay et al., 2015). Understanding the consequences of declining population sizes and environmental changes on the demography of orchids is thus important for the conservation of these species (Swarts and Dixon, 2009).

In this study, we combined genetic and demographic data to examine population viability of an endangered perennial orchid, the dark red helleborine (Epipactis atrorubens (Hoffm. Ex Bernh.) Besser). We used data collected from eleven populations of varying size to examine whether there was variation in the performance of different populations. The data enabled the examination of the effect of population size, and associated processes (demography, stochasticity and genetics) affecting population viability. We first estimated demographic parameters from long-term data (three to sixteen years). We then used matrix population models to estimate population growth rates, identified the most important life stages for population growth rates, and used them in population viability analysis to estimate extinction risks and the effect of stochasticity. Second, we genotyped individuals based on six nuclear microsatellite markers, and quantified different measures of genetic variation. We then assessed the effect of genetic diversity on population viability by testing for correlations between genetic variation and viability measures, which included application of capturerecapture methods for modelling the effect of individual heterozygosity on survival.

2. Material and methods

2.1. Study species

E. atrorubens is a perennial orchid, with a distribution extending from Europe until the Ural Mountains in Asia and western Siberia (Efimov, 2004; Tuulik, 1998). In Finland, its distribution is patchy, with populations occurring in only three regions, separated by at least 350 km. The species is currently categorized as vulnerable in Finland according to the IUCN red list criteria (Rassi et al., 2010). Their habitat consists mainly of rocky slopes and shorelines, and it is characterized by limestone or dolomite. It has a predominantly allogamous reproduction, where pollination occurs by both wasps and bumblebees (Brzosko et al., 2006; Jakubska-Busse and Kadej, 2011; Talalaj and Brzosko, 2008). E. atrorubens has been shown to be predominantly allogamous, but no self-incompatibility has been observed (Talalaj and Brzosko, 2008). Individuals live in close association with mycorrhiza and the life-cycle is characterized by a protocorm life stage, overwintering as an underground rhizome and the ability to go into vegetative dormancy for several years (Jäkäläniemi et al., 2011). Its nectar producing flowers bloom at the end of July and capsules ripen in August. Individual plants

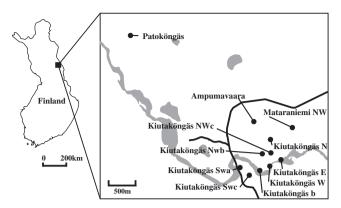


Fig. 1. Map of the studied populations. Black lines represent roads. Grey areas represent rivers or lakes.

can ramify from the single root neck just above the ground surface and consequently big plants can have several shoots (1–28 shoots). No indications of vegetative reproduction have been found for this species in the studied populations based on herbarium and field collections (own observations).

2.2. Study area and sampling

This study was carried out in the Oulanka National Park in Kuusamo, Northern Finland (66° 22' 27" N, 29°13" E). This region houses the northernmost populations (62 populations) of E. atrorubens in Finland. These populations are fragmented and genetically differentiated within the studied area (Hens et al., 2017). Three populations were monitored since 2000 or 2002 (for 16 and 14 years, respectively), as being part of a long-term monitoring project. As these populations were few and consisted of only large populations (> 170 individuals), additional and smaller populations were included and monitored since 2009 or 2013 (for six and three years, respectively; Fig. 1; Table 1). From each population, 1-32 leaf samples were collected during 2011-2012, depending on the population size. One leaf was taken from each individual and frozen at - 20 °C (Permits: LAPELY/348/ 07.01/2011, POPELY/568/07.01/2011). To ensure that the samples represent genetically distinct individuals, only one leaf was taken from groups of shoots and samples were taken from well separated individuals.

2.3. Monitoring

In the four large populations (Kiutaköngäs N and Ampumavaara, Patoköngäs, Mataraniemi), individuals were marked and monitored in subsequent years in permanent 10 m \times 10 m plots. The plots included different portions of the total population (Kiutaköngäs N 100%, Ampumavaara 80%, Patoköngäs 46%, Mataraniemi < 25%). In the seven small populations, all individuals were monitored. The individuals were tagged using numbered plastic tags in 2000 (Kiutaköngäs N and Ampumavaara), 2002 (Patoköngäs), 2010 (Kiutaköngäs SWa) and 2013 (Kiutaköngäs b, Kiutaköngäs E, Kiutaköngäs NWb, Kiutaköngäs NWc, Kiutaköngäs W, Kiutaköngäs SWc and Mataraniemi) and they were monitored yearly during the flowering time in early August. Each year, all newly found individuals were tagged. The recorded parameters included the number of shoots, number of flowers, number of capsules and the height of the plant for each individual.

2.4. Genetic analyses

2.4.1. Molecular methods

DNA was extracted using a modified $2 \times$ cetyltrimethylammonium bromide (CTAB) protocol (Doyle, 1987). Six nuclear microsatellite loci were amplified to assess genetic variation (Tranchida-Lombardo et al., Download English Version:

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