



Original article

Inferring population and metapopulation dynamics of *Liparis loeselii* from single-census and inventory data

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ABSTRACT

To conserve endangered species, information is needed on (meta)population responses to habitat quality and management. As possibilities for long-term studies are generally limited, it is important to obtain as much information as possible in a single field season.

We obtained such single-census data for the orchid *Liparis loeselii*, a European Habitat Directive species. Stage structures of 15 Dutch dune and fen populations were related to vegetation structure, environmental indicators, and management. Botanical inventory records from 1930 to 2003 were used to infer population life spans.

Cluster analysis did not reveal successional stage structure types. Dense populations with high recruitment mainly occurred in open, young-successional vegetation with high soil pH. High soil humidity and acidification negatively affected orchid densities. Early mowing was preferable over late mowing in dune slacks, because the latter reduced juvenile densities. The predominant population life span was three to eight years, and similar for dune slacks and fens. Longer life spans were occasionally observed at mown sites with influx of base-rich water.

Our results suggest high metapopulation dynamics. Long-term metapopulation viability requires the formation of new habitat by dune slack formation in dunes and peat removal in fens. Population persistence can be prolonged to some extent by mowing, extensive grazing, or sod removal if natural habitat formation is impossible. Our study demonstrates that useful information on (meta)population ecology and viability can be obtained in a single field season.

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1. Introduction

Decisions about the management and conservation of rare plant (or animal) species require insight in their ecology, demography, regional dynamics, and genetics (Harvey, 1985; Lande, 1988; Oostermeijer et al., 2003). Spatio-temporal dynamics, and their relation to life-history traits, form the basis for assessing and predicting the behaviour of plant species in communities and landscapes (Eriksson, 1996; Swab et al., 2012). These factors have implications concerning the effectiveness and timing of different management measures.

Demographic studies are very important to rare plant conservation because they allow calculation of population growth rates

and highlight critical stages in the life cycle (Harvey, 1985; Crone et al., 2011). Detailed demographic studies, censusing several populations for several years, require long-term commitment (Menges and Gordon, 1996; Crone et al., 2011). Because this is not always feasible, there is a strong demand for single-census methods to assess population viability, demographic status and responses to different management practices.

One approach to gain insight in the viability or successional stage of plant populations in a single census is to determine the population stage structure, i.e. the densities and relative proportions of individuals in the different ontogenetic stages of the life cycle (Oostermeijer et al., 1994; Rabotnov 1978), and compare this among different environments or management regimes. This method has been used successfully in several studies on herbaceous plants (Bühler and Schmid, 2001; Gatsuk et al., 1980; Harvey, 1985; Hegland et al., 2001; Hooftman and Diemer, 2002; Mehrhoff, 1989; Oostermeijer et al., 1994; Rabotnov 1978). Because this approach focuses on the static structure of populations, it provides no information on extinction and

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colonisation rates in a spatial context, which is needed to assess metapopulation viability (Hanski, 1999). Analysis of historical botanical inventory records to reconstruct the time period during which populations are present at a certain location can possibly provide this type of information, depending on the spatio-temporal resolution of the data. Herbarium or inventory records have been used to localize populations, which were subsequently (re)visited to establish local extinctions (Fischer and Stöcklin, 1997; Lienert et al., 2002; Matthies et al., 2004). In some inventories, population sizes or other abundance data have been recorded, enabling more detailed analyses of the causes of population extinction (e.g. Fischer and Stöcklin, 1997; Matthies et al., 2004).

In this study, we focus on *Liparis loeselii* (L.) Rich., which occurs in Europe and North America, but is declining in its overall distribution, including in the Netherlands (van der Slikke and van Dulmen, 2006). It is a small, perennial orchid that occurs in coastal dune slacks and inland fens (Kreutz and Dekker, 2000). In Europe, the species is listed as endangered in the Habitat Directive (92/43/EEC) and the Bern Convention, and has the highest conservation priority in all the countries it occurs in. In the United Kingdom, demographic monitoring of a population of *L. loeselii* in a dune slack complex (Jones, 1998) and a fen (Wheeler et al., 1998) indicated that populations are short-lived and rapidly expand or disappear as conditions change. Recruitment and survivorship in the dune slack populations in South Wales seemed to be correlated with hydrology and patch age (Jones, 1998).

Orchids are of course generally known for their complex life cycle and their relatively low recruitment, which is linked with a.o. dust seeds, high dispersal, specific edaphic factors and the availability of mycorrhizal fungi (McCormick and Jacquemyn, 2014). It therefore seems that very detailed studies are required to understand the behaviour of populations and metapopulations, studies for which there is often not enough funding. We hope to show that important data, highly relevant to a.o. conservation management, can also be obtained with relatively simple field work in a single growing season.

The purpose of our study is to understand the demographic responses of *L. loeselii* to variation in environmental conditions in its two main habitat types, and determine the life span of individual populations.

Specifically, we tested the following hypotheses:

- (a) The population structure is dominated by juveniles in open, early-successional vegetation, and is dominated by reproductive adults in late-successional, more closed vegetation;
- (b) Given the small size of the species, vegetation structure (cover, height, bare soil) is a more important driver of variation in its population structure than soil factors;
- (c) Because of (b), we expect that habitat management will strongly affect population structure, because it opens up vegetation structure and sets back succession;
- (d) Dune slacks and fens differ in vegetation composition and structure in that fens are more nutrient-rich, and have denser and taller vegetation. Therefore both habitat types are expected to differ with respect to *L. loeselii* plant size and population structure.
- (e) Because successional change in dune slacks and fens can progress rapidly, we expect that populations of *L. loeselii* have relatively short to intermediate life spans, meaning high metapopulation turnover rates. The more nutrient-rich fens may have higher succession rates, and thus shorter population life spans.

2. Materials and methods

2.1. Study species

Within *L. loeselii*, two varieties are sometimes distinguished: a narrow-leaved type variety (var. *loeselii*) occurring in fens, and a shorter, broader-leaved var. *ovata* Ridd. ex Godfrey of dune slacks. The genetic differentiation between dune slack and fen populations of *L. loeselii* in the United Kingdom and France is stronger than that among countries, supporting the distinction of the two varieties (Pillon et al., 2007). A recent study across Europe (Vanden Broeck et al., 2014) provided little evidence for ecotypic differentiation between habitat types, however. For clarity, we will simply refer to 'dune slack' and 'fen' populations in this paper.

The habitat of *L. loeselii* is formed by open vegetation on base-rich or calcareous, wet, and nutrient-poor soils (Kreutz and Dekker, 2000; Wheeler et al., 1998). It is a character species of the alliance Caricion davallianae, in which it occurs in the associations Junco baltici-Schoenetum nigricantis and Parnassio-Juncetum atricapilli in calcareous coastal dune slacks and the Scordio-Caricetum diandrae in base-rich inland fens (Westhoff et al., 1998). It formerly occurred in nutrient-poor brook valleys and wet heathlands as well, from which it has entirely disappeared because the influx of base-rich water ceased (Kreutz and Dekker, 2000).

Individual plants self-pollinate spontaneously, produce a large amount of dust-seeds, but also propagate by means of vegetative shoots (Mrkvicka, 1992). Plants flower after 4 years (Mrkvicka, 1992) and flowering takes place from the end of May until early July (Kreutz and Dekker, 2000). Genets with a single shoot can live for 8–10 years (Jones, 1998; Mrkvicka, 1992) but the life span of vegetatively reproducing genets can be much longer. Plants overwinter as a green pseudobulb, in which resources are stored during late summer and autumn.

Causes for the decline of *L. loeselii* are drainage, land reclamation, (atmospheric) eutrophication and acidification, shrub encroachment, restriction of natural ecosystem dynamics and unfavourable management of nature reserves (Bolier, 2001; Westhoff et al., 1998; Wheeler et al., 1998).

2.2. Vegetation analysis and determination of age-state structure

During a single growing season, we visited a total of 15 known populations in The Netherlands (Fig. 1): ten in coastal dune slacks, and five in inland fens. During this fieldwork period, between May and July, *Liparis* plants varied from the bud to the early fruiting stage. Most of the species present at a given location were already or still recognisable, so we assume that we were able to capture most of the species diversity.

The placement of quadrats within a site occurred randomly around at least a single *Liparis* plant. The number of quadrats per population ranged from 6 to 15, depending on population size, spatial distribution and variation in vegetation structure, leading to a total of 150 samples.

Quadrat size was $25 \times 25 \text{ cm}^2$, to ensure that we measured the vegetation and environmental conditions at the small spatial scale appropriate for the species. We reasoned that *Liparis* plants, in particular juveniles (<3 cm) but also adults (<15 cm), are so small that using larger plots would average out the microscale variation in its environment. It could be argued that using multiple small quadrats per population produces problems with pseudoreplication and spatial autocorrelation. The structure of plant populations will indeed show spatial structure due to autocorrelation in a uniform habitat. In most field situations, however, the structure will also be heterogeneous because of the heterogeneity in

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