

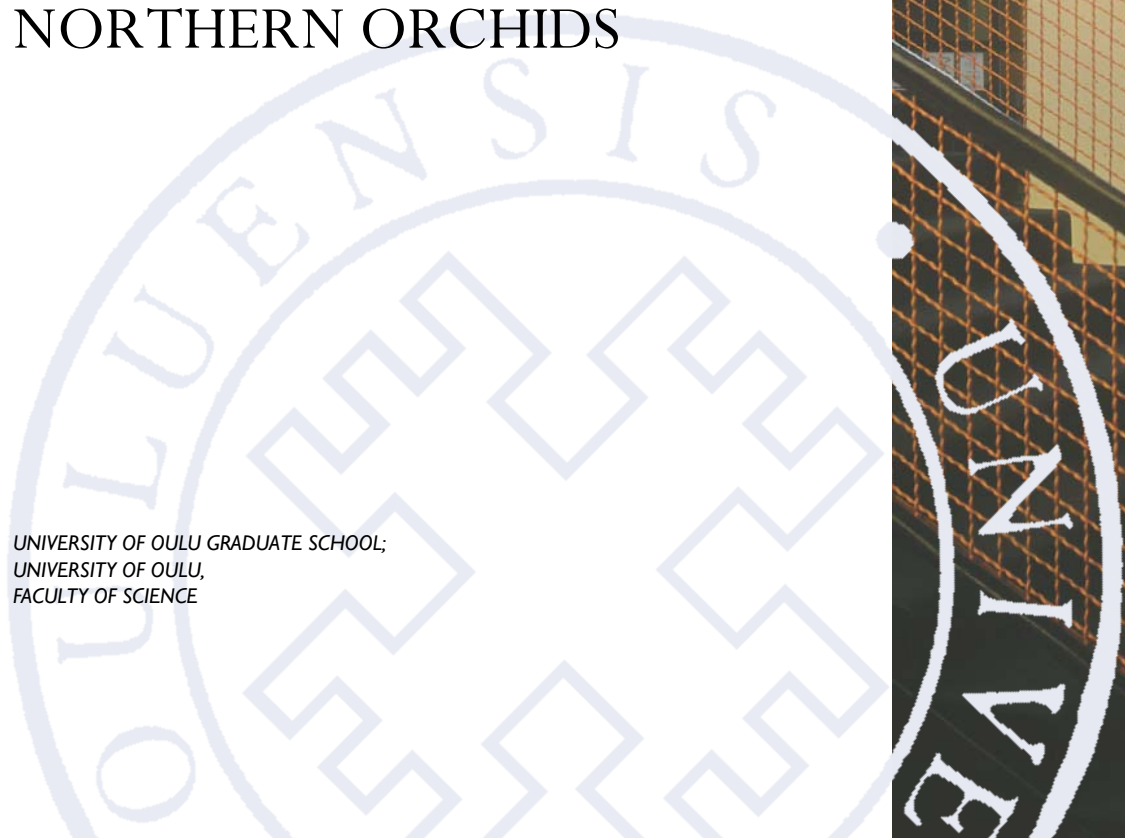
Sonja Hurskainen

THE ROLES OF INDIVIDUAL
DEMOGRAPHIC HISTORY AND
ENVIRONMENTAL CONDITIONS
IN THE PERFORMANCE AND
CONSERVATION OF
NORTHERN ORCHIDS

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE

A

SCIENTIAE RERUM
NATURALIUM



ACTA UNIVERSITATIS OULUENSIS
A Scientiae Rerum Naturalium 727

SONJA HURSKAINEN

**THE ROLES OF INDIVIDUAL
DEMOGRAPHIC HISTORY AND
ENVIRONMENTAL CONDITIONS
IN THE PERFORMANCE AND
CONSERVATION OF NORTHERN
ORCHIDS**

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Keckmaninsali (HUI06), Linnanmaa, on 30 November 2018, at 12 noon

UNIVERSITY OF OULU, OULU 2018

Copyright © 2018
Acta Univ. Oul. A 727, 2018

Supervised by
Docent Laura Kvist
Professor Juha Tuomi
Docent Anne Jäkäläniemi
Doctor Satu Ramula

Reviewed by
Professor Jon Ågren
Doctor María Begoña García

Opponent
Professor Kari Lehtilä

ISBN 978-952-62-2087-1 (Paperback)
ISBN 978-952-62-2088-8 (PDF)

ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)

Cover Design
Raimo Ahonen

JUVENES PRINT
TAMPERE 2018

Hurskainen, Sonja, The roles of individual demographic history and environmental conditions in the performance and conservation of northern orchids.

University of Oulu Graduate School; University of Oulu, Faculty of Science

Acta Univ. Oul. A 727, 2018

University of Oulu, P.O. Box 8000, FI-90014 University of Oulu, Finland

Abstract

A population growth rate is the sum of all individuals' reproduction and survival, which in turn depend on many external and internal factors, e.g. weather and individual reproductive history. In plants, for example, previous reproduction can deplete an individual's resources, resulting in trade-offs between demographic functions.

To understand these demographic processes, it is necessary to follow populations for many years. Such long-term studies are especially crucial for endangered species, as they can reveal the causes of population declines and provide information that is directly applicable for the management. In my thesis, I applied this approach to the study of rare orchids. Specifically, I analyzed long-term orchid monitoring data from two countries, Finland and Estonia, to assess the external and internal factors that affect the performance of these long-lived plants, which reproduce both sexually (via seeds) and vegetatively (via new ramets).

My research reveals that plant performance depends on both the demographic history and the environment of a plant. For example, although Finnish and Estonian populations of the lady's slipper orchid, *Cypripedium calceolus*, differed in direction and statistical significance of their responses to environmental factors, the two most-influential weather variables in both cases were spring snow depth and the temperature of the previous summer. However, the influence of weather on both flowering and vegetative growth was dwarfed by the effect of plants' own demographic histories: there was a trade-off between current and future reproduction which created asynchronous two-year cycles in reproduction and growth. Furthermore, in all three studied orchid species – the lady's slipper orchid (*C. calceolus*), the fairy's slipper orchid (*Calypso bulbosa*), and the dark-red helleborine (*Epipactis atrorubens*) – the probability of dormancy (a state in which the plant spends a year or more underground) and the demographic costs this state incurred with respect to size or future reproduction depended on a plant's size and whether it flowered prior to dormancy. In other words, dormancy had both absolute and relative costs in large, but not in small, individuals. Finally, I show here that environmental alteration via selective tree removal can be used as a management method to increase orchid reproduction via both seeds and ramets.

Keywords: canopy cover, dormancy, growth, individual history, life-history costs, Orchidaceae, reproduction, weather

Hurskainen, Sonja, Yksilöhistorian ja ympäristötekijöiden merkitys pohjoisten kämmekköiden menestykselle ja suojelulle.

Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta

Acta Univ. Oul. A 727, 2018

Oulun yliopisto, PL 8000, 90014 Oulun yliopisto

Tiivistelmä

Populaation kasvunopeus riippuu siitä, kuinka monta yksilöä populaatioon syntyy ja kuinka monta yksilöä kuolee. Yksilöiden lisääntyvyyteen ja elossa säilyvyyteen puolestaan vaikuttavat monet ulkoiset ja sisäiset tekijät, kuten sää ja yksilön oma lisääntymishistoria. Kasvilla on rajallinen määrä resursseja, joten sen pitää tehdä kompromisseja eri elintoimintojen, esimerkiksi kasvun ja lisääntymisen, välillä. Klonaaliset kasvit voivat myös lisääntyä usealla tavalla: joko suvullisesti siemenistä tai kasvullisesti tuottamalla uusia versoja.

Demografisten prosessien tutkimisessa pitkäaikaiset seuranta-aineistot ovat välttämättömiä. Pitkäaikaisseurannat voivat myös paljastaa uhanalaisen lajin populaation taantumisen syyt ja näistä seurannoista saatua tietoa voidaan soveltaa harvinaisten lajien, esimerkiksi kämmekköiden, suojelutoimien suunnittelussa. Tässä väitöskirjassa analysoin aineistoa kämmekköiden pitkäaikaisseurannoista Suomesta ja Virosta. Tavoitteenani oli arvioida ulkoisten ja sisäisten tekijöiden merkitystä pitkäikäisten kasvien menestykselle.

Tulokset osoittavat, että kasvin menestys riippuu sekä yksilön omasta demografisesta historiasta että sen ympäristöstä. Eri säätekijöiden vaikutus tikankontin (*Cypripedium calceolus*) kasvuun ja kukkimiseen vaihteli Suomen ja Viron välillä, mutta lumen syvyys ja edellisen kasvukauden lämpötila nousivat merkittävimiksi tekijöiksi molemmissa maissa. Tikankontin kasvu ja kukinta riippuivat kuitenkin säästä enemmän kasvin omasta demografisesta historiasta. Runsas lisääntyminen edeltävällä kasvukaudella vähensi lisääntymistä tulevalla kasvukaudella, mikä johti kaksivuotiseen jaksottaisuuteen tikankontin lisääntymisessä ja kasvussa. Tutkiessani dormanssia (lepotila, jossa kasvi ei tuota maanpäällistä versoja) kolmella kämmekkälajilla, tikankontilla, neidonkengällä (*Calypso bulbosa*) ja tummaneidonvaipalla (*Epipactis atrorubens*), havaitsin lisäksi, että todennäköisyys siirtyä dormanssiin riippui kasvin koosta. Myöskin tämän lepotilan aiheuttamat kustannukset olivat riippuvaisia kasvin aikaisemmasta tilasta. Isoilla kasveilla dormanssilla oli sekä suoria kustannuksia että kustannuksia suhteessa versomiseen. Pienillä kasveilla näitä kustannuksia ei ollut. Osoitan väitöskirjassani myös, että maltillisella puunpoistolla voidaan lisätä tikankonttipopulaatioiden siementuottoa ja versotiheyttä.

Asiasanat: demografiset kustannukset, dormanssi, kasvu, latvuspeittävyys, lisääntyminen, Orchidaceae, säätekijät, yksilöhistoria

To my family and friends

Acknowledgements

I would like to thank all the people who have supported me during this PhD project. First of all, I need to thank my supervisors for all their advice, and for shaping of this thesis. When I first walked into Juha's office to ask if he had any open positions for a PhD student, I had no idea what I was in for. Still, thank you Juha for taking me on, becoming my supervisor and supporting me throughout this crazy journey. Thank you Anne for all the long hours you have spent in the field observing the orchid populations. This study really would not have been possible without the enormous amount of work you have done. Thank you Satu for all your invaluable help and advice with statistics and writing. Your careful, detailed and critical feedback really helped me to hone this thesis to its best. And thank you Laura for hopping in to take care of the official arrangements after Juha's retirement, and for ushering me along the final steps to get my thesis published.

I also wish to thank my follow-up group, Annamari Markkola, Kari Koivula and Arja Kaitala for support and guidance. I express my thanks to Prof. Jon Ågren and Dr. Maria Begoña García for pre-examing my thesis. I thank the University of Oulu Graduate School, the Department of Ecology and Genetics and my colleagues for providing me this pleasant and calm setting to study and conduct my research.

I owe my deep gratitude to Metsähallitus, as well as my co-authors Tiiu Kull, Marilyn Mõtlet, Kirsi Alahuhta and Hilde Hens for sharing their orchid data with me. Veijo Kaitala and Richard Shefferson also gave the idea and first push for the two first papers. I wish to impress my thanks to the Oulanka research station for providing facilities and help for the field-work. Thanks also to my field assistants Elisabet Rams, Anna-Maria Borshagovski, Timo Hyttinen and Sakari Hautala!

Above all, I need to thank my parents for their love and support, and my friends for all the fun times we have had. I could not have done this without you.

This work was financially supported by the Jenny and Antti Wihuri Foundation, Societas pro Fauna et Flora Fennica, Oulun luonnonystävään yhdistys and the Oulangan rahasto Fund.

25.09.2018

Sonja Hurskainen

List of original publications

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

- I Hurskainen, S., Jäkäläniemi, A., Kaitala, V., Kull, T., Mötler, M., Ramula, S., & Tuomi, J. (2017). Temporal cycles and spatial asynchrony in the reproduction and growth of a rare nectarless orchid, *Cypripedium calceolus*. *Botanical Journal of the Linnean Society*, 183(2), 316-326.
- II Hurskainen, S., Alahuhta, A., Hens, H., Jäkäläniemi, A., Kull, T., Shefferson R.P., & Tuomi, J. (in press). Prolonged dormancy in orchids incurs absolute and relative costs in large, but not in small plants. *Botanical Journal of the Linnean Society*.
- III Hurskainen, S., Jäkäläniemi, A., Ramula, S., & Tuomi, J. (2017). Tree removal as a management strategy for the lady's slipper orchid, a flagship species for herb-rich forest conservation. *Forest Ecology and Management*, 406, 12-18.

Author's contributions:

The original idea for paper I came from Veijo Kaitala and Juha Tuomi, the idea for paper III from Anne Jäkäläniemi and Juha Tuomi, and the original idea for paper II was proposed by Richard Shefferson and Tiiu Kull. Ideas for all the papers were further developed by the co-authors and me. The Finnish *Cypripedium calceolus* data is collected by Anne Jäkäläniemi and me. Kirsi Alahuhta and Hilde Hens provided data for the other two Finnish orchids, and the Estonian data is provided by Tiiu Kull and Marilin Mötler. All the statistical analyses are conducted by me (partly by Kirsi Alahuhta for paper II) under guidance by Satu Ramula. I wrote the first drafts of all the manuscripts, which were then commented by co-authors.

Contents

Abstract	
Tiivistelmä	
Acknowledgements	9
List of original publications	11
Contents	13
1 Introduction	15
1.1 Clonal growth strategy	15
1.2 Carryover effect of individual demographic history	17
1.3 Dormancy	18
1.4 External factors	21
1.5 Conservation aspects	23
1.6 Aims	25
2 Materials and methods	27
2.1 Study species.....	27
2.1.1 <i>Cypripedium calceolus</i>	29
2.1.2 <i>Calypso bulbosa</i>	31
2.1.3 <i>Epipactis atrorubens</i>	31
2.2 Field methods.....	33
2.2.1 Long-term demographic surveys	33
2.2.2 Tree removal experiment.....	35
2.3 Statistical analyses.....	36
3 Results & discussion	39
3.1 Effect of individual history	40
3.1.1 Cycles and asynchrony	40
3.1.2 Dormancy	42
3.2 Effect of environment	43
3.2.1 Weather factors	43
3.2.2 Tree removal.....	44
4 Conclusions and future directions	47
References	51
List of original publications	67

1 Introduction

The study of demography seeks answers to basic ecological questions about the viability, evolution, and adaptation of populations by exploring temporal and spatial changes in population size due to birth, death, and migration. Overall, the numbers of births and deaths in a population are the sum of all individuals' survival and reproductive success. In turn, these individual parameters often depend on an individual's age and/or size (Geber, Kroon, & Watson, 2016; Hutchings, 1987; Miller, Williams, Jongejans, Brys, & Jacquemyn, 2012; Worley & Harder, 1996). In addition to age and size, the reproduction and survival of a plant can also depend on its current and past demographic state, but how such states are defined varies among species. For example, the life cycle of a terrestrial orchid can be divided into four states: young, vegetative, flowering, and dormant. As Ehrlén (2000) demonstrated, if we do not take into account plants' demographic histories, this can affect our estimates of how the growth rate responds to changes in vital rates, as well as estimates of the population growth rate itself.

In nature, populations (and individuals within populations) do not exist in isolation, but interact with their biotic and abiotic environments in myriad ways. Environmental factors such as temperature, precipitation, and light availability can have profound implications for both individual survival and reproduction. In this thesis, I assess how individual demographic history and environmental factors affect measures of individual and population performance (see Fig. 1).

1.1 Clonal growth strategy

Any demographic study must first begin by identifying the individuals in question. In plants, there are multiple definitions for what constitutes an individual (Clarke, 2012). One definition for an individual is a genet, also called a clone, which is the genetic individual and a product of a single zygote (Harper, 1987). Most plants are modular in structure, meaning that they consist of repeated self-reproducing and semi-autonomous units called modules (e.g., shoots of a birch tree). In clonal plants, these sub-units form physically coherent structural entities in themselves (e.g., runners of strawberry or trees in an aspen stand) and are called ramets (Clarke, 2012; Harper, 1987). For these plants, the rate of individual turnover varies depending on whether it is measured at the level of the genet or the ramet. For example, in the orchid *Cypripedium calceolus*, ramets live for only one growing season and therefore have rapid turnover rates, while genets can live for a hundred

produced either by clonal growth or by sexual reproduction (Clarke, 2012; Sackville Hamilton, Schmid, & Harper, 1987). The length of time that ramets remain physically connected to their mother plant varies from species to species. In some clonal plants, new ramets depend on their parents for resources (Hartnett & Bazzaz, 1983; Isogimi, Matsushita, Watanabe, & Nakagawa, 2011). The integration and sharing of resources among ramets can increase the performance of daughter ramets and allow plants to spread to otherwise unattainable, unfavorable patches (Alpert, 1991, 1996; Roiloa & Retuerto, 2005; Saitoh, Seiwa, & Nishiwaki, 2002). Consequently, by sharing resources among clones, the plant can better exploit a heterogeneous environment (Stuefer, During, & de Kroon, 1994). Furthermore, the higher number and wider spatial spread of ramets reduces the probability of genet-level mortality (Clarke, 2012). However, the parent ramet incurs costs for supporting daughter ramets that are growing in unfavorable patches, and sometimes these costs outweigh the benefits at the whole-clone level (Alpert, 1991, 1996; Chesson & Peterson, 2002; Hutchings & Mogie, 1990). The costs of resource sharing can be mitigated if integration increases the photosynthetic efficiency of parent ramets via strong sink effects (Roiloa & Retuerto, 2005).

1.2 Carryover effect of individual demographic history

The demographic history of a plant can affect its current and future performance (Bullock, Mortimer, & Begon, 1993; Ehrlén, 2000), for example via organ preformation or storage effects (Geber et al., 2016). In the former case, organs (such as leaf and floral primordia) are formed during the previous growing season and are thus affected by the conditions at that time (Worley & Harder, 1999). In the latter situation, the levels of stored resources, on which current vital traits depend, can be depleted by past events (Cunningham, 1997; Sala, Hopping, McIntire, Delzon, & Crone, 2012; Worley & Harder, 1996). Plants usually have limited resources which must be allocated among growth, survival, and reproduction, and this constraint leads to trade-offs between these functions (Fig. 1; Obeso, 2002; Stearns, 1989; Worley & Harder, 1996). Reproduction in particular is widely assumed costly: current reproduction can decrease survival, future reproduction, and/or future growth (Meléndez-Ackerman, Ackerman, & Rodríguez-Robles, 2000; Miller et al., 2012; Obeso, 2002; Primack & Stacy, 1998). Such reproductive costs can lead to intermittent reproduction, the most extreme examples of which occur in masting or mast-seeding species, in which the differences in reproductive intensity between high and low years are great and reproduction is synchronous among

individuals (Crone, Miller, & Sala, 2009; Crone & Rapp, 2014; Satake & Iwasa, 2002). Similarly, in clonal plants, extensive vegetative growth can be expected to also deplete resources, and therefore contribute to a trade-off between reproduction, survival, and future growth.

1.3 Dormancy

Prolonged vegetative dormancy, hereafter ‘dormancy’, is a state in which a plant does not sprout for one or more years, instead spending the growing season(s) below ground before eventually re-sprouting (Lesica & Steele, 1994; Shefferson, 2009). Dormancy is widely distributed in the plant kingdom, as it has been observed in at least 112 species from 23 families (Shefferson et al., 2018). In some species, a large proportion of a population may be dormant every year (Kéry & Gregg, 2004; Shefferson, Sandercock, Proper, & Beissinger, 2001). In traditional life-cycle graphs, it is assumed that dormancy resets all plants to the same state, i.e. that the vital rates of all dormant plants are equal irrespective of their age or demographic state before dormancy. However, Jäkäläniemi et al. (2011) showed that the state in which an individual emerges from dormancy depends on the state it was in before going dormant, and, likewise, Gremer et al. (2012) revealed that dormant plants do not necessarily constitute one uniform class.

The obvious costs of dormancy include losing opportunities for photosynthesis and reproduction for that year. The life-history costs and benefits of dormancy (possible scenarios in Fig. 2) have been widely studied, but with somewhat contradictory results. Dormancy is often considered an adaptive response that allows the plant to enter a state that has lower mortality during stressful periods (Shefferson et al., 2001). Indeed, several studies have observed that during stressful events the probability of going dormant is higher, and dormant plants have higher survival than those sprouting aboveground (Davison, Nicole, Jacquemyn, & Tuljapurkar, 2013; Gremer et al., 2012). Moreover, when the proportion of dormant plants is high, the non-dormant plants show reduced growth or survival (Davison et al., 2013; Gremer & Sala, 2013). Therefore, dormancy can have benefits relative to sprouting in the form of avoidance of some costs incurred by aboveground plants (Fig. 2g-i). Dormancy can also have absolute benefits, i.e. a net gain in resources, via mycoheterotrophy or the remobilization of structural carbon (Gremer 2010; Fig. 2c, f, i). Whether this resource gain is beneficial also in the relative sense (situation in Fig. 2c, f, or i) depends on the costs that dormancy has relative to sprouting (e.g., missing the opportunity for photosynthetic gain). Furthermore, it is

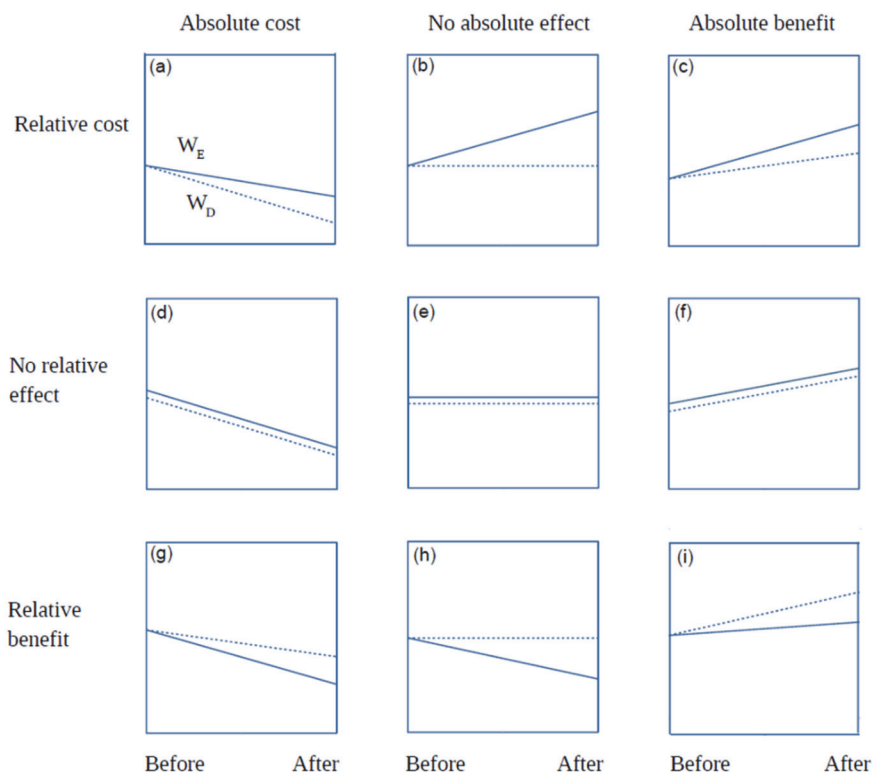


Fig. 2. Schematic presentation of the performance (W) of a plant before and after a given period of time, depending on whether the plant stayed emergent (E, solid line) or went dormant (D, dashed line). An absolute effect of dormancy refers to a change in plant performance after dormancy compared to the pre-dormancy state. A relative effect refers to improved or decreased performance of a post-dormancy plant as compared to a scenario in which it stays emergent.

possible that the benefits of dormancy are not necessarily realized after a single stressful event, but only after longer, cumulative stress (Gremer & Sala, 2013).

In contrast, other studies have found dormancy to have no benefits and only costs for survival and reproduction compared to the sprouting state (Gregg & Kéry, 2005; Hutchings, 1987; Shefferson & Tali, 2007; Shefferson, Proper, & Beissinger, 2003). The benefits of dormancy may also depend on the age and size of an individual plant. Even in species in which dormancy appears to be a means for mature orchids to survive difficult times, it has clear survival or size costs for young individuals, presumably due to their lack of sufficiently developed rhizomes

(Davison et al., 2013; Kéry & Gregg, 2004). In other species, there are even reports that dormancy may not necessarily have any notable effect at all on demographic rates. For example, in Spalding's catchfly (*Silene spaldingii*), survival did not differ between sprouting and dormant states (Lesica & Crone, 2017). Furthermore, both in Spalding's catchfly and in the dark-red helleborine (*Epipactis atrorubens*), individuals tended to emerge from dormancy in the same demographic state in which they had previously been seen aboveground (Jäkäläniemi et al., 2011; Lesica & Crone, 2007).

The probability of going dormant has been observed to depend on the demographic state and age of a plant, such that young plants and already-dormant plants typically have the highest probabilities of going or remaining dormant, presumably due to low resource levels (Gremer, Sala, & Crone, 2010; Hutchings, 1987; Jäkäläniemi et al., 2011; Primack & Stacy, 1998; but see Shefferson, Kull, Tali, & Kellett, 2012). On the other hand, in the lady orchid (*Orchis purpurea*), large plants had higher probabilities of dormancy than smaller ones (Miller et al., 2012), and in *Cypripedium parviflorum*, vegetative genets had higher probabilities of going dormant than flowering or young genets (Shefferson et al., 2003). Gremer et al. (2010) noted that in the legume *Astragalus scaphoides*, dormancy seems to be a response to a lack of resources, as the plants that entered dormancy had less carbon stored than those that remained sprouting. However, by the end of the growing season, the dormant legumes had acquired enough carbon so that their levels were comparable with those of the sprouting, photosynthesizing plants. This indicates that dormancy can have absolute benefits in terms of resource levels. Gremer et al. (2010) speculated that an increase in carbon levels during dormancy was due to the mobilization of structural carbon (e.g., hemicellulose of cell walls) or the acquisition of carbon from symbionts

In addition to individual-level benefits and costs, dormancy has implications for population genetics. For example, dormancy can facilitate outbreeding: if only a part of the population emerges yearly, there is more potential variation in plant crosses, and genetic diversity is increased (Jäkäläniemi et al., 2011). Dormancy has also been suggested to act as a conservative bet-hedging trait (Gremer et al., 2012; Shefferson, 2009). The implicit assumption is that there are some “dormancy genes” and that different genotypes give rise to phenotypes that differ in how they react to certain cues in the environment and plant resource status (i.e., how sensitive their “dormancy trigger” is). Dempster (1955) showed that heterogeneity could be maintained in a population if the success of different alleles varies from year to year, even if this strategy briefly reduces performance during good years.

Furthermore, bet-hedging models offer a parallel explanation of how dormancy can arise and prevail under variable environments: it increases the geometric mean fitness of a genotype by buffering fitness against environmental stochasticity and thus decreasing the variance of the fitness (Cohen, 1966; Seger & Brockman, 1987; Slatkin, 1974).

1.4 External factors

In addition to the demographic history of an individual, a plant's performance also depends on several external factors, both abiotic and biotic. Abiotic factors include, for example, carbon dioxide concentration (Bazzaz, 1990; Reddy, Reddy, & Hodges, 1995), soil chemical and physicochemical properties (Gough, Shaver, Carroll, Royer, & Laundre, 2000; Parviainen, Luoto, Rytteri, & Heikkinen, 2008), topography (Nicolè, Dahlgren, Vivat, Till-Bottraud, & Ehrlén, 2011; Parviainen et al., 2008), and climate (Parviainen et al., 2008), all of which contribute to determining plant species' abundance and distribution. In particular, weather often correlates with plant vital rates, such as survival, reproduction, and sprouting (Fig. 1, orchid examples in Kéry et al. 2005; Nicolè et al. 2011; Shefferson et al. 2017; Sletvold et al. 2013; Williams et al. 2015). Due to the effects of anthropogenic emissions, Earth's climate is changing: atmospheric and ocean temperatures are increasing and extreme precipitation events are becoming more intense and frequent (IPCC, 2014). At medium-to-high latitudes, increases in temperature are predicted to have a positive effect on plants, birds, and invertebrates, leading to increases in abundance (Pearce-Higgins et al., 2015). Moreover, distribution ranges are expected to expand and shift polewards (Berry, Dawson, Harrison, Pearson, & Butt, 2003; Parmesan & Yohe, 2002), and growing seasons are expected to lengthen as springs advance and autumns are delayed (Fitter & Fitter, 2002; Marchand et al., 2004; McEwan, Brecha, Geiger, & John, 2011). However, the effect of weather on plants can differ between habitats, times of the year, and the vital rates under consideration (Jäkäläniemi, 2011; Nicolè et al., 2011; Sletvold et al., 2013; Williams et al., 2015). As an example, in tundra plants, the poleward shift of the southern distributional border can lead to range compression (Lesica & McCune, 2004; Parmesan & Yohe, 2002) and advancing spring phenology can also lead to phenological mismatches in pollination (Bartomeus et al., 2011; Hegland, Nielsen, Lázaro, Bjercknes, & Totland, 2009). To be able to predict how plants respond to future changes in climate, there is a need to first understand the present relationship between plant performance and weather.

Plant performance depends on physiological factors such as photosynthesis and respiration rates, which are temperature dependent (Atkin & Tjoelker, 2003; Ryan, 1991). This means that temperature has a direct effect on plant resource status via both current and past resource gains. In addition, dormancy rates in orchids have also been reported to be dependent on weather conditions (Gremer, 2010; Lesica & Crone, 2007; Shefferson et al., 2001, but see Hutchings, 1987). Weather factors can also have indirect effects on plant resource status via physiological damage (e.g., frost, Inouye 2000)

Biotic factors affect plants through their interactions with other organisms. For example, some plants synchronize their reproduction with others, mostly in the context of masting. There are several hypotheses for this, one of which is that this phenomenon represents a unified response to a shared environment (Crone & Rapp, 2014; Pesendorfer, Koenig, Pearse, Knops, & Funk, 2016; Rees, Kelly, & Bjørnstad, 2002; Satake & Iwasa, 2002). This behavior has been noted to respond to both abiotic factors, e.g., precipitation and temperature (Kon, Noda, Terazawa, Koyama, & Yasaka, 2005; Maria, Cortés, Molowny-Horas, Sánchez-Humanes, & Retana, 2011), as well as biotic factors, such as pollen limitation during the years that flower density is low (pollen coupling hypothesis, Crone, 2013; Satake & Iwasa, 2002). Masting has benefits for pollination efficiency, which increases with increasing flower density, especially in wind-pollinated plants (Moreira, Abdala-Roberts, Linhart, & Mooney, 2014; Shibata, Tanaka, & Nakashizuka, 1998). However, synchronous reproduction can also have disadvantages, including increased competition for pollinators (Parra-Tabla & Vargas, 2007; Ward, Johnson, & Zalucki, 2013) and, in the case of plants with deceptive pollination, faster pollinator learning (Internicola, Juillet, Smithson, & Gigord, 2006; Smithson & MacNair, 1996; Sun, Cheng, Zhang, Luo, & Ge, 2009).

Another example of biotic interaction is the effect of a surrounding tree stand and canopy cover on a forest understory. Canopy cover and light availability, as well as associated changes in, e.g., temperature and moisture, are the main factors that define understory cover and species richness in temperate and boreal forests (Barbier, Gosselin, & Balandier, 2008; Brosnokske, Chen, & Crow, 2001; Galhidy, Mihok, Hagyo, Rajkai, & Standovar, 2006; Hart & Chen, 2006). Canopy gaps not only have a higher amount of light, but also different light quality compared to under a closed canopy, where the light is “greener” and the ratio of red to far-red wavelengths is lower (Lieffers, Messier, Stadt, Gendron, & Comeau, 1999). Increased insolation also increases air and soil temperature (Abd Latif & Blackburn, 2010), and leads to higher decomposition rates (Binkley, 1984). In addition to light,

a forest canopy also intercepts rain, so that a decrease in canopy cover results in an increase in precipitation reaching the ground (Geiger, Aron, & Todhunter, 1995). However, the warmer temperatures found in gaps also increase evaporation (Geiger et al., 1995), meaning that the overall effect of the canopy on humidity and soil water content can be hard to predict. In temperate forests, most studies have observed increased soil moisture in gaps or with decreasing canopy closure (Abd Latif & Blackburn, 2010; Galhidy et al., 2006; Ma, Concilio, Oakley, North, & Chen, 2010; Rydgren, 1996), though the opposite effect has been reported from arid areas (D'Odorico, Caylor, Okin, & Scanlon, 2007; De Boever, Gabriels, Ouessar, & Cornelis, 2016). These results take on increased significance when viewed in the context of logging, which depending on its intensity may have profound effects on the microclimate and nutrient availability in the forest understory.

Gaps can have both positive and negative effects on plant species growing in the forest understory. The intermediate disturbance hypothesis (Connell, 1978) predicts that, for some plant species, gaps provide a window of opportunity to reproduce (Brumback, Cairns, Sperduto, & Fyler, 2011; Kirchner, Kammermeier, & Bruelheide, 2009; Valverde & Silvertown, 1998), increasing microhabitat diversity and, consequently, species richness (Peterson & Pickett, 1995). Negative effects of forest gaps include the increased risk of frost (Geiger et al., 1995) or intensified competition from grasses or other species that spread aggressively, especially in large gaps (Sjöberg & Ericson, 1992). Overall, the effects of canopy gaps on forest plants and microhabitat may depend on the intensity and frequency of logging or the size of the gap (Galhidy et al., 2006; Romme, Everham, Frelich, Moritz, & Sparks, 1998), with effects often being the strongest in young gaps, then returning to pre-harvest conditions as the canopy gap closes (Brokaw, 1987; Dirzo, Horvitz, Peterson & Pickett, 1995; Quevedo, & Lopez, 1992; but see Kirchner et al., 2009)

1.5 Conservation aspects

Probably no other single species has transformed our planet as thoroughly as humans have, which has led to several kinds of conservation concerns. For example, in Finland, changes in the forest environment and overgrowth of meadows and other open habitats are the two most common threats to endangered plant species (Ryttäri, Kalliovirta, & Lampinen, 2012). Similarly, both the intensification of livestock farming (especially grazing) as well as the total abandonment of agricultural activities (leading to succession of woody plants) are listed among the

main threats in the European Red List of Vascular Plants (Bilz, Kell, Maxted, & Lansdown, 2011).

Approaches to conservation questions can be roughly divided into two categories: single-species approaches and ecosystem approaches, both of which have their benefits and drawbacks (Lindenmayer et al., 2007). Although single-species studies are often criticized for concentrating on few charismatic species and having limited generalizability (Lindenmayer et al., 2007; Simberloff, 1998), they can pinpoint causal processes that lead to population declines, which increases our understanding of the relationships between a species and its environment. Moreover, single-species studies can offer specific and directly applicable information for policymaking and management for threatened species, problematic invaders, flagship species, or other surrogate species (Lindenmayer et al., 2007; Simberloff, 1998).

The idea of the surrogate species approach is that it is possible to identify one or a few species that are in one way or another especially important for or indicative of the health of the ecosystem. There are several types of surrogate species (Caro & O'Doherty 1999; Simberloff 1998). For example, umbrella species, such as the capercaillie (*Tetrao urogallus*, Suter et al. 2002), white-backed woodpecker (*Dendrocopos leucotos*, Martikainen et al. 1998), or various birds of prey (Sergio, Newton, Marchesi, & Pedrini, 2006), are species that require such a large area of a specific habitat type that providing this surely meets the habitat requirements of several other species as well (Caro & O'Doherty 1999). Flagship species, such as orchids (Gale, Fischer, Cribb, & Fay, 2018), on the other hand, are not necessarily of any particular direct importance to the ecological community, but are charismatic and attractive; they can be used in marketing conservation to the public and in doing so generate resources, goodwill, and the funds necessary for successful management (Bowen-Jones & Entwistle, 2002; Caro & Girling, 2010; Simberloff, 1998; Verissimo, Fraser, Groombridge, Bristol, & MacMillan, 2009). In order to evaluate how long-lived species, surrogate or otherwise, respond to changes in their environment, long-term studies are necessary

As Finland's largest orchid, the lady's slipper orchid (*Cypripedium calceolus*) is one example of a charismatic plant that could serve as a flagship species for conservation efforts. It has also been suggested to be an umbrella species (Nicolè et al., 2011). In a 2014 IUCN report, this orchid was described as threatened due to increased shading and soil degradation arising from the abandonment of traditional grazing activities and the replacement of natural forests with spruce plantations (Rankou & Bilz, 2014). The report further stressed the importance of

ensuring sufficient light conditions on the forest floor for the maintenance of these orchid populations (Rankou & Bilz, 2014). In Finnish boreal herb-rich forests, Norway spruce (*Picea abies*) is often the dominant species during later successional stages (Kujala, 1979; Similä & Juninen, 2011). While Norway spruce is important for forest biodiversity, e.g., as a substrate for Aphyllophorales fungi (Tikkanen, Martikainen, Hyvärinen, Junninen, & Kouki, 2006), overgrowth of spruce can have negative impacts on the understory vascular plant community via, e.g., shading and the acidic litter it produces (Similä & Juninen, 2011). In a 60-year study of an old-growth boreal forest in Norway (Nygaard & Odegaard, 1999), an increase in the tree basal area of Norway spruce was observed to reduce understory species richness. Similarly, in North American boreal forests, understory biomass and species richness peaks during the first decades of succession, and tree harvesting was observed to increase the number of vascular plant species (Hart & Chen, 2006). Multiple studies have reported that the growth and reproduction of herbaceous species in the forest or shrub understory are increased in lighter patches (e.g., Kelly, 1994; Miller et al., 2012; Valverde & Silvertown, 1998). In addition to shade, conifers are often assumed to produce more acidic and nutrient-poor soil compared to deciduous trees (Barbier et al., 2008; Hart & Chen, 2006; Oostra, Majdi, & Olsson, 2006). Nutrient availability in boreal forests further decreases as a forest matures due to two factors: more and more nutrients are fixed in woody biomass and the nutrient turnover rate decreases (Hart & Chen, 2006).

1.6 Aims

My major aim in this thesis was to study the ways in which plants' current and future performance are affected by environmental factors and/or plants' individual demographic histories. Using long-term demographic data of northern orchids, I asked: 1) How do different vital rates vary spatially and temporally (I), and how are these rates affected by environmental factors (such as weather (I) or tree removal (III))? 2) How does the individual history of a plant affect dormancy, and how does dormancy affect the future performance of the plant (II)? and 3) What are the management implications of environmental alteration (such as selective removal of trees, III) for understory orchid populations?

Firstly, I studied spatial and temporal variation in reproduction (measured as flowering intensity) and plant size (measured as the number of ramets in a clump) of the lady's slipper orchid, *Cypripedium calceolus* (I). Specifically, I tested for the existence of temporal trends, cycles, and synchrony in flowering and plant size

within and between populations. I also assessed how weather regulates reproduction and growth by evaluating the correlation of these traits with several temperature, precipitation, and snow-cover variables. Secondly, I studied the two-way interaction between dormancy and plant performance in three Finnish orchids: *C. calceolus*, the fairy's slipper orchid (*Calypso bulbosa*), and the dark-red helleborine (*Epipactis atrorubens*) (II). I was especially interested in the absolute and relative costs and/or benefits dormancy may have, and whether the size of a plant in a certain year affected its probability of being dormant the following year. Lastly, I evaluated selective tree removal as a management method for *C. calceolus* at over-grown herb-rich forest sites, and assessed how harvesting different amounts of tree basal area affected the survival, dormancy, ramet density, flowering, and fruiting of this orchid (III).

2 Materials and methods

2.1 Study species

My study species were the lady's slipper orchid, *Cypripedium calceolus* L.; the fairy's slipper orchid, *Calypso bulbosa* L.; and the dark-red helleborine, *Epiactis atrorubens* (Hoffm. Ex Bernh.) Besser (Fig. 3). All three species are long-lived perennial orchids in the family Orchidaceae of the monocot order Asparagales. Family Orchidaceae is estimated to be the largest vascular plant family, comprising 736 genera and 28 000 species (Christenhusz & Byng, 2016), many of which are endangered (518 species out of the 808 that have been assessed, IUCN 2017). This cosmopolitan family includes large-flowered epiphytes, many of which are popular among horticulturalists, as well as lithophytes and terrestrial species that typically have more humble-sized flowers. Orchids exhibit a plethora of unique flower shapes and pollination mechanisms that were already the focus of studies by Darwin's time (Darwin, 1862). Many orchids use deception in pollination: they attract pollinators via colors and odors that mimic, for example, specific flowers, flowers in general, or even females of the pollinator species, but offer no nectar as a reward (Ackerman, 1986; Dafni, 1984; Jersáková, Johnson, & Kindlmann, 2006). Nectarless orchids typically have low fruit set (Brzosko, 2002; Neiland & Wilcock, 1998; Suetsugu & Fukushima, 2014; Sun et al., 2009; Tremblay, Ackerman, Zimmerman, & Calvo, 2005). It has been hypothesized that the specialization of orchids to their pollinators is an adaptation to increase reproductive success by decreasing the loss of pollen to flowers of the wrong species. Indeed, the correct transfer of pollen is especially important in orchids, because all pollen is packed in few pollinia that are removed together as a single pollinarium, and deposited as individual pollinia or in few separate massulae (Johnson & Edwards, 2000; Micheneau, Johnson, & Fay, 2009). Despite the large range of flower shapes and pollination mechanisms, all orchids share some common traits. For example, they produce masses of tiny dust-like seeds that contain very few nutrients, which makes seedlings dependent on mycorrhizal fungi, especially in early life stages (Leake, 1994; Phillips et al., 2014; Rasmussen & Rasmussen, 2009). In general, arbuscular and ectomycorrhizal fungi provide their host plants minerals and water in exchange for carbon (Allen, 1991), but in the case of orchid mycorrhiza, it is the plants that exploit their fungal partners for carbon. Indeed, there are achlorophyllous orchids that remain dependent on their mycorrhiza for carbon for their entire lives

(mycoheterotrophy, Leake, 1994; Motomura, Selosse, Martos, Kagawa, & Yukawa, 2010); less extreme are the many photosynthesizing orchids that obtain additional



Fig. 3. The three study orchids. A) The lady's slipper orchid, *Cypripedium calceolus*. Photo by Juha Tuomi. B) The fairy's slipper orchid, *Calypso bulbosa*. Photo by Sonja Hurskainen. C) The dark-red helleborine, *Epipactis atrorubens*. Photo by Hilde Hens.

carbon via their fungal networks (mixotrophy, Bidartondo et al. 2004; Gebauer & Meyer 2003; Julou et al. 2005; Motomura et al. 2010). The ultimate source of this carbon is dead organic material (if the fungal partner is saprotrophic) or a nearby tree (if the fungal partner is ectomycorrhizal) (Bidartondo et al., 2004; Lee, Yang, & Gebauer, 2015; McKendrick, Leake, & Read, 2000; Rasmussen, 2002; Taylor & Bruns, 1997). In general, mycorrhizae do not appear to restrict the distribution of orchids (Phillips et al. 2014; Shefferson et al. 2005; but see McCormick et al. 2012; Swarts et al. 2010), but the often highly specialized pollination system does (Pauw & Bond, 2011; Phillips et al., 2014); this high degree of specialization partly explains the great number of species in the orchid family (Cozzolino & Widmer, 2005; Givnish et al., 2015). However, due to their dependency on a few very specific fungal species and pollinators, all of whom have their own specific habitat requirements, orchids can be expected to be especially sensitive to environmental changes (Rasmussen, Dixon, Jersáková, & Těšitelová, 2015; Swarts & Dixon, 2009) and prone to extinction (Dunn, Harris, Colwell, Koh, & Sodhi, 2009), making them excellent indicators of ecosystem health. All orchids are included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

2.1.1 *Cypripedium calceolus*

My main study species was the lady's slipper orchid, *Cypripedium calceolus* (Fig. 3a). Pollination of *C. calceolus* occurs by food deception: the orchid uses odors and a bright yellow color to attract pollinators – mostly solitary bees of the genus *Andrena*, but also of *Lasioglossum* and *Halictus* (Antonelli, Dahlberg, Carlgren, & Appelqvist, 2009; Erneberg & Holm, 1999; Kull, 1999) – but offers no nectar as reward. The insects coming to inspect the flowers fall into the yellow “slipper” formed by the labellum, and are guided out by the base of the labellum, so that they get pollinia stuck to them on the way (Kull, 1999).

The roots of *C. calceolus* are colonized by mycorrhizal fungi belonging to the families Tulasnellaceae and Thelephoraceae (Shefferson et al., 2005), but the long horizontal rhizome remains uncolonized (Kull, 1999). Each tip of the rhizome produces two apical buds annually; the larger one forms the next year's shoot, while the smaller one often stays dormant (Blinova, 2004; Kull & Kull, 1991). The whole genet is considered dormant when all buds are dormant. *C. calceolus* can grow as a single ramet, but typically ramets form dense clumps, in which there can be several genets intermingled (Nicolè et al., 2005). Flowering occurs in late June to early July in Finland and in May to early June in Estonia. (Kuusk, 1984). One stalk (20-60 cm) supports three to five leaves and one to two, rarely three, yellow slipper-shaped flowers (Kull, 1999). The aboveground parts of the plant wilt in August, meaning that the lifespan of a ramet is only one growing season. The genet, however, can be over 100 years old (Kull, 1999).

Despite its wide distribution in Europe and Asia, *C. calceolus* is rare everywhere it occurs (Rankou & Bilz, 2014). This can be at least partly explained by its preference for partial shade and lime-rich soils (Rankou & Bilz, 2014). The species is becoming even rarer because of habitat destruction (Rankou & Bilz, 2014). When undisturbed, *C. calceolus* has slow population dynamics that are typical to long-lived species, and a long-term population growth rate close to unity (Nicolè et al., 2005). This suggests that the severe declines observed in the past in many European countries (Rankou & Bilz, 2014) were caused by external factors. The main threats to *C. calceolus* include agricultural intensification, collection, and forest management, such as clear cutting and the replacement of natural forests with spruce plantations. The abandonment of traditional grazing activities has led to increased competition through plant succession (Rankou & Bilz, 2014; Rassi et al., 2010), and in addition, previous studies have shown that shading has detrimental effects on the flowering and seedling establishment of this orchid (Brzosko, 2002;

Laitinen, 2006). Herbivory is likely not a serious threat to this species. Herbivory is documented as the reason for disappearance for only one population in Finland. However, one location in Southern Finland is reported to fail at fruit production due to moose herbivory (Laitinen, 2006). In Poland, on average 5% ramets were eaten (Brzosko, 2002).

Fortunately, conservation measures have been largely successful, and the species is not currently listed as endangered (IUCN Red List status in European regional assessment is “Near Threatened”, globally “Least Concern”, Rankou & Bilz 2014). Similarly, in Finland the species has been reclassified from vulnerable to near-threatened in the most recent Red List of Finnish Species (Rassi, Hyvärinen, Juslén, & Mannerkoski, 2010). However, the species is still declining and listed as endangered in several countries, including Luxembourg, where it is regionally extinct, and in Britain, where only a single population remains (Rankou & Bilz, 2014).

C. calceolus is listed on Annex II of the Habitats Directive and under Appendix I of the Convention on the Conservation of European Wildlife and Natural Habitats (Rankou & Bilz, 2014).

C. calceolus occurs in whole Finland, except the northernmost Lapland, although it is more common in the calcium-rich regions in the north. The total number of ramets in Finland is estimated to be 240 000 (Laitinen, Eeronheimo, & Ilmonen, 2009). In 2006, there were records of 1249 localities, of which 80% were known to still exist (Laitinen, 2006). Of these localities, only 4% were known to be extinct by 2006; the status of the rest of the localities was unknown. However, there are regional differences in the extinction probabilities: while the population size in Northern Finland seem to be increasing, 25-35% of the recorded southern Finland localities are estimated to be now extinct (Laitinen, 2006). Most (85%) of these extinct populations disappeared before the 1980's, and were on privately owned land. Furthermore, the first recorded *C. calceolus* sightings from southern Finland are from 1800s, and it is highly likely that agriculture has destroyed several populations before this. Fortunately, most (65%) of the recorded localities are on state owned land in Natura 2000 sites or other protected sites (Laitinen, 2006).

In Estonia there are about 200 documented localities with *C. calceolus*, most of which contain less than 100 ramets. However, the largest populations, located on the western islands and in the central part of the mainland, support thousands of ramets (Kull, 2003). The population trend is reported to be increasing (Kull 1997, Kull, 2003).

2.1.2 *Calypso bulbosa*

The fairy's slipper orchid, *Calypso bulbosa* (Fig. 3b), is short in stature (8-16 cm) and has only one leaf which wilts by midsummer. In August, the plant produces a new, over-wintering leaf which is ridged above and purple underneath. *C. bulbosa* is non-clonal and has a bulb-like corm. The single flower is pink and shaped like a fanciful slipper, giving rise to the common name of the species. *C. bulbosa* flowers in May-June, and pollination occurs by food deception as in *C. calceolus*. The main pollinators are naïve bumblebee queens (Jäkäläniemi, Illarionova, & Rankou, 2011), who emerge early in spring when not many other plant species are in flower; this possibly explains why this orchid has a surprisingly high pollination rate for a deceptive species (Abeli, Jäkäläniemi, Wannas, Mutikainen, & Tuomi, 2013). The success of pollination can depend on the local density of flowering willows, which function as a magnet species that attract pollinators to the site (Alexandersson & Ågren, 1996).

C. bulbosa has a circumpolar distribution (Hultén & Fries, 1986). In Finland, the species prefers old-growth forests, and its habitats range from dry and mesic herb-rich forests to rich spruce-birch fens (Rassi et al., 2010). There are 918 known localities in Finland, and the total number of flowering ramets is estimated to be 27 000 – 37 000 (Paalamo, Eeronheimo, & Ilmonen, 2009). The population size is expected to decrease, and 4% of all known sites disappearing during 1980-2006 (Alahuhta, 2003; Paalamo et al., 2009; Rassi et al., 2010). However, most of these sites were in the core region of the distribution area. The extent of the distribution area is therefore stable or even expected to increase slightly (Paalamo et al., 2009). The species is classified as vulnerable and under strict protection in Finland (Rassi et al., 2010), and near-threatened in Europe (Jäkäläniemi et al., 2011). It is threatened by human activities such as forest management, mining, and construction, as well as climate change and vole herbivory (Jäkäläniemi et al., 2011; Rassi et al., 2010). In Oulanka, the observed percentage of eaten flowers and capsules was 0-70% (Alahuhta, 2013). *C. bulbosa* is listed on Annex II of the Habitats Directive (Jäkäläniemi et al., 2011).

2.1.3 *Epipactis atrorubens*

The dark-red helleborine, *Epipactis atrorubens* (Fig. 3c), is a non-clonal, rhizomatous orchid. It is perennial, but the aboveground parts wilt in winter. In Finland, it grows up to 40 cm tall and the stems arising from the short vertical

rhizome have 1-13 spirally arranged leaves. The inflorescence is a raceme with 1-12 dark-purple flowers with five petals (Jäkäläniemi, 2003). Four of the petals are identical, and one has developed into a lip that functions as a landing place for pollinators. Flowering takes place in July (Jäkäläniemi, 2003). Pollination is by wasps, bees, and hoverflies (Jakubská-Busse & Kadej, 2011). Unlike the other two study species, *E. atrorubens* rewards its pollinators with nectar, the key attractants being vanillin derivatives (Jakubská-Busse & Kadej, 2011).

The distribution of *E. atrorubens* stretches from Europe to the Ural Mountains and Siberia, with the species preferring lime-rich sites (Jäkäläniemi, 2003). In Finland, *E. atrorubens* has been found in only a few areas, most important of which are Hanko, Juuka-Juankoski, and Kuusamo-Salla (Jäkäläniemi, 2003; Laitinen & Ilmonen, 2009). There are 60 known localities, and the total number of individuals in Finland is estimated to be 1578 (Laitinen & Ilmonen, 2009). The preferred habitats of *E. atrorubens* include dry and mesic herb-rich forests, but also calcareous rock outcrops and roadsides, and it has a fragmented distribution (Rassi et al., 2010). There are likely to be some yet unknown small locations in the calcium-rich sites and lime quarries in the Western Finland that have not yet been found, as well as some short-lived occurrences along the coast. These ephemeral coast sites are likely founded by long-distance seed dispersal from Baltic Sea islands and Estonia, where the species is common. Therefore, it is estimated that the known distribution could slightly increase in the future (Laitinen & Ilmonen, 2009). *E. atrorubens* is classified as vulnerable and is under strict protection in Finland, Belarus, Denmark, Lithuania, Luxembourg, and the Czech Republic, while in Europe as a whole its conservation status is least concern (Bilz et al., 2011). In Finland, the main threats to the species are the wearing away and overgrowth of habitats (Laitinen & Ilmonen, 2009; Rassi et al., 2010). Previously also construction and the intensification of land use has likely destroyed sites in Southern Finland (Laitinen & Ilmonen, 2009). Herbivory is rare and restricted to few eaten flowers and capsules (A. Jäkäläniemi, personal observations). The genetic variation in the northern populations is low, but does not seem to correlate with population size or lead to inbreeding depression (Hens, Pakanen, Jäkäläniemi, Tuomi, & Kvist, 2017). Seedling production is very low, and some of the northern populations may become soon extinct (Jäkäläniemi, 2003; Hens et al., 2017). The lack of seedling production seems to be caused by failure in germination rather than in pollination, as the capsules are maturing normally also in small populations (Jäkäläniemi, 2003; Hens et al., 2017). However, there is great variation between populations in the growth rate, and some populations seem to be increasing in the

total number of ramets, although the number of emergent ramets per year has decreased (Jäkäläniemi, 2003). The overall population trend in Finland is estimated to be increasing, and the species has been known to disappear only from few localities (Laitinen & Ilmonen, 2009).

2.2 Field methods

2.2.1 Long-term demographic surveys

Long-term demographic survey data of *Cypripedium calceolus* were collected at three sites in Oulanka National Park, municipality of Kuusamo, northern Finland (I and II, Fig. 2). A 10 x 10 m permanent plot was established at each site during the summer of 2000 by Metsähallitus as a part of their own monitoring program. In these plots, each clump of ramets (either a single ramet that was clearly separate from others or a group of ramets growing densely together) was marked with an individually numbered plastic tag. Each individually marked clump was used as a demographic unit, because ramets in the clumps grew so densely together that we could not reliably differentiate between individual ramets, and differentiation between clones was impossible without genetic analysis or digging up the plants. Each July from 2000 to 2016, the following variables were recorded for each clump: the numbers of ramets, flowers, and capsules; the demographic state of the clump (seedling, young, mature vegetative, flowering, dormant); and the height of the tallest ramet of each state.

To assess spatial and temporal variation in vital rates and the influence of weather, I obtained data from a similar demographic survey of two *C. calceolus* populations in Estonia (Fig. 4). These populations were visited and counted once a year in June by professor Tiiu Kull (Estonian University of Life Sciences, Tartu) and her research group from 1987 to 2012.

To reliably determine if *C. calceolus* ramets were dormant or not, only clumps consisting of single ramets were included in the dormancy models. To compare



Fig. 4. A map showing the locations of the tree removal sites (Oulanka National Park and surroundings in Kuusamo, and municipalities of Tervola and Ylitornio in SW Lapland) and the long-term demographic survey sites in Finland (Kuusamo) and in Estonia (Muhu and Ussisoo). The map was created with Adobe Photoshop. Map templates are from d-maps.com (http://d-maps.com/carte.php?num_car=5973&lang=en).

dormancy rates with other orchids, I used data from three populations of *E. atrorubens* (two populations followed 2000-2014 and one 2002-2014) and five populations of *C. bulbosa* (followed 2002-2010) in Oulanka National Park, Kuusamo, that were collected by Anne Jäkäläniemi, Kirsi Alahuhta, and Hilde

Hens. The survey method was the same as for the study of *C. calceolus*, with the exception that for *C. bulbosa* and *E. atrorubens* we used the individual as the study unit.

Finnish climate data were obtained from the Kiutaköngäs weather station (within 13 km of the Finnish study populations) of the Finnish Meteorological Institute. Estonian climate data for the Ussisoo and Muhu populations were provided by the Estonian Weather Service from the Türi and Virtsu weather stations (located 25 km and 13 km from the populations), respectively.

2.2.2 Tree removal experiment

To evaluate selective tree removal as a management method, I used data from a total of twenty sites (ten managed tree removal experiment sites and ten control sites of similar habitat) that were established as a part of Metsähallitus' EU LIFE project in 2001 (Fig. 4, see details in Laitinen 2006). A randomly located 1×10 m permanent plot was established in the summer of 2001 at each site. If needed, an extra plot of varying size ($2.8 - 8 \text{ m}^2$) was established to obtain a sufficient sample size. Plot size therefore varied from 10 m^2 to 18 m^2 . Tree removal was conducted without heavy machinery in the winter of 2001, i.e. after the first summer survey. A thick snow cover protected the plants and ground from mechanical disturbance during cutting, and all logs and branches were removed from the sites. Managed sites were divided into three different intensities of selective tree removal depending on their forest type: (1) dense spruce forests, where half of the total tree basal area (TBA) was cut (mean = 48.9% , SD = 8.4%), (2) sparse spruce forests, where one-fourth of the spruce TBA was cut (mean reduction in TBA = 26.4%, SD = 7.4%), and (3) sparse broadleaf forests, where one-fourth of the total TBA was cut (mean reduction in TBA = 25.7%, SD = 0.7%). Control sites, in which no trees were cut, included the same forest types as the treated sites. The size of the managed areas varied from 600 m^2 to 1700 m^2 with the study plot in the center.

All twenty experimental sites were monitored by Metsähallitus in 2001-2004 (pre-harvest and immediate post-harvest period), by our research group in 2008-2010 (middle post-harvest period), and by me in 2014-2016 (late post-harvest period). During these years the numbers of ramets, flowers, and capsules; the demographic state of the clump; and the height of the tallest ramet of each state in the clump were recorded as in the long-term demographic surveys.

To explore how tree removal treatments affected light availability in the forest understory, photographs were taken during the pre-harvest period and then again in

the middle and late post-harvest periods. The camera was positioned straight up toward the sky at 1-m intervals along each plot (10 photographs in total per plot) and at the middle of the potential extra square. Using Adobe Photoshop, photographs were edited so that the open sky was filled with white and canopy was filled with black. The canopy cover was then calculated as the percentage of black in the photographs.

2.3 Statistical analyses

All analyses were conducted using the R statistical package (R Development Core Team 2015), with particular use of the function “`glmmadmb`” in the `glmmADMB` package (Fournier et al. 2012) and functions “`lmer`” and “`glmer`” in the `lme4` package (Bates et al. 2015). First, I tested for temporal trends in the flowering intensity and clump size of *C. calceolus*, and their correlations with weather factors (I) by using generalized linear mixed effects models (GLMMs) and step-wise model selection. Based on a previous study by Kaitala & Kull (2002), I tested for two-year cycles in flowering intensity and clump size within individuals (I) by studying temporal autocorrelations, specifically checking if the autocorrelation at a lag of one year was negative and significant (based on bootstrapped data sets). Synchrony in reproduction and size among individuals was studied by calculating pairwise correlation coefficients among clumps (I). The average strength of (auto) correlations in each country was then examined with general linear mixed effects models (GLMs), and the proportions of significant (auto) correlations in each country were analysed with GLMMs with a binomial distribution and logit link function (I). Second, I analyzed the relationships between dormancy and the past and future performance of the three orchid species with GLMs and GLMMs (II). Lastly, I studied the effect of tree removal on *C. calceolus*; specifically, I examined differences in ramet density, reproduction, survival, and dormancy between treated and control sites using GLMMs, taking into account the year and the initial level of a given response variable (III).

Larger sample of populations might have increased the statistical power and generalizability of our results. However, the number of populations we could sample was constrained by both availability of resources (funding, trained personnel) and the protected status of the study species. Ideally, the tree removal treatments would have been more evenly arranged among dry and wet sites and among regions, but this was impossible because of where the known *C. calceolus* sites with the given forest type happened to occur. It would have also been

interesting to have data on the soil properties and the understory vegetation layer of the tree removal sites, but unfortunately these were not recorded when the study was started in year 2001.

3 Results & discussion

The main result of this thesis is that the performance of northern, terrestrial orchids depends on both environmental factors (weather and canopy cover, I and III, respectively) and the demographic history of an individual (I, II, Fig. 5).

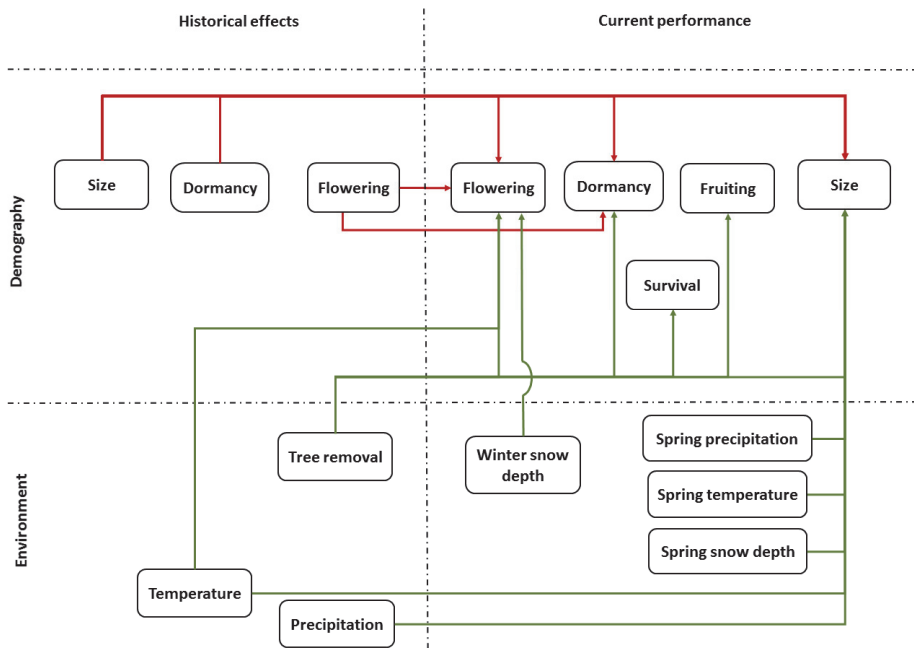


Fig. 5. A simplified schematic presentation of the results of the thesis. Effects of the environment (tree removal, weather of the previous growing season, winter and the current spring) are in green, and the interactions between past and current demographic variables are in red. Note that only the relationships observed in this study are presented; possible relationships that were not studied, or were studied and not observed, are left out for the sake of clarity. Note also that some of the effects indicated by the arrows are positive, some are negative, and some arrows include both positive and negative effects.

Furthermore, my results show that selective removal of trees increased the fruit production and ramet density of *C. calceolus*, and could thus be a suitable management method at herb-rich sites (III).

3.1 Effect of individual history

In this thesis, I show that the demographic history of a plant affects its current performance, presumably via effects on the plant's resource status (Cunningham, 1997; Ehrlén, 2000; Obeso, 2002; Sala et al., 2012). Plants which were large (measured as the number of ramets (I) or height of the plant (II)) in the previous year had a larger current size (I, II) and a higher probability of flowering (I) than plants that had previously been smaller. Furthermore, I observed that larger orchid individuals generally had a lower probability of going dormant than smaller individuals did (II). A similarly positive size effect had been previously observed in the orchids *Orphys sphegodes* (Hutchings, 1987) and *Orchis purpurea* (Jacquemyn & Brys, 2010), as well as in the clonal rhizomatous herb *Asarum canadensis* (Cain & Damman, 1997). These results are not surprising as large plants have more resources available to allocate to both flowering and growth than smaller plants do (Zimmerman, 1990). There was also a positive temporal trend in the number of ramets in *C. calceolus* clumps in both Finland and Estonia (I). This increase in clump size with time probably occurred via rhizome branching as the clones aged, and the extent of this branching can also explain the correlation between current and past size. My results further indicate that flowering and growth in *C. calceolus* depend on resources accumulated during the previous growing season rather than on the photosynthesis of the current growing season, as has also been observed for the epiphytic orchid *Catasetum viridianum* (Zimmerman, 1990).

3.1.1 Cycles and asynchrony

I observed putative two-year cycles in the reproduction of *C. calceolus* (I), which indicates that also non-masting herbs can have cyclic reproduction. Moreover, the existence of these cycles suggests that there is a trade-off between current and future reproduction in this orchid species. The likely mechanism for such cycles is that reproduction depletes an individual's resources, so that the plant needs to collect resources for a year or more before it is able to reproduce again (similar to the resource budget model for masting species, Isagi, Sugimura, Sumida, & Ito, 1997). A similar negative carryover effect of past reproduction on future reproduction has been previously observed in several other orchids of the genera *Cypripedium* (Kaitala & Kull, 2002; Primack & Stacy, 1998), *Spiranthes* (Willems & Dorland, 2000), and *Comparettia* (Meléndez-Ackerman et al., 2000), as well as

in other herbaceous plants such as the masting legume *Astragalus scaphoides* (Crone et al., 2009).

Here I also show that intensive vegetative growth can deplete resources and result in demographic costs, as revealed by two findings: *C. calceolus* also demonstrated two-year cycles in the number of ramets present, and all three studied orchids were more likely to go dormant after intensive growth (II). Similar results had been obtained by Ehrlén (2000), who observed that in the legume *Lathyrus vernus*, individuals that had in the past year transitioned to larger sizes were more likely to retrogress in size in the following year. Temporal cycles in ramet number could also arise due to self-shading, as discussed by Kaitala & Kull (2002). It is possible that fruiting results in even deeper resource depletion (Primack & Stacy, 1998) and creates more pronounced cycles than flowering or clonal growth. However, due to the consistently low fruiting probability of the populations of *C. calceolus* in Kuusamo, I was unable to test this. The low fruiting probability in these populations was most likely caused by pollen limitation, as hand-pollination resulted in significant increase in fruiting (S. Hurskainen, unpublished data).

There was virtually no synchrony in flowering among clones between or within populations of *C. calceolus* (I), and it seems likely that in deceptive orchids the disadvantages of synchronous flowering outweigh the advantages. If the environment were the main regulator of reproduction, synchrony in reproduction could be expected to arise if all plants reacted in a similar way to the common environment. However, this does not seem to be the case in orchids. For example, Hutchings (1987) observed no synchrony in flowering or dormancy rates in the sexually deceptive spider orchid *Orphys sphegodes*, and concluded that at least in this species, these functions are not under climatic control. Furthermore, in insect-pollinated species, the disadvantages of synchronous flowering include competition for pollinators (Parra-Tabla & Vargas, 2007) and the fact that pollinator learning is positively density-dependent (Smithson & MacNair, 1996). This may thus lead to negative frequency-dependent selection, which has been observed, for example, in the polymorphic deceptive orchid *Dactylorhiza sambucina* (Gigord, Macnair, & Smithson, 2001; Internicola et al., 2006) and in clusters of deceptive *Cypripedium japonicum* (Sun et al., 2009). On the other hand, the synchrony or asynchrony in flowering and the subsequent success of pollination may be of little importance for orchid fitness if the correlation between pollination and recruitment is low, for example due to microsite limitation for germination (Calvo, 1993). This seems to be the case for *C. calceolus*, as an increase in flowering and fruiting did not translate into an increase in the number of seedlings (III).

3.1.2 Dormancy

Like other vital rates, dormancy depends on both internal and external factors (Gremer, 2010; Lesica & Crone, 2007). In *Cypripedium calceolus*, *Calypso bulbosa*, and *Epipactis atrorubens*, the demographic state and the size of individual orchids after dormancy depended on their pre-dormancy state. Specifically, the size of the plant post-dormancy correlated positively with the size before dormancy, and the probability of flowering was the lowest for previously immature individuals and the highest for previously flowering individuals (II). In these orchids, large size and mature state before dormancy were therefore positively correlated with the probability of flowering after dormancy (II). Together with the tendency of smaller orchids to go dormant more often than larger individuals (unless the large size was a result of intensive growth spurt, II), this means that if analyses of dormancy do not take into account the pre-dormancy state, spurious costs may appear. For example, if dormant plants tend to be smaller upon emergence than plants that remained continuously sprouting, their smaller size may not necessarily represent the costs of dormancy. Instead, the same result could be found if plants that go dormant are on average smaller than those that keep sprouting, and this difference is reflected in their post-dormancy size as well.

However, there do seem to be real costs to dormancy, both in the absolute and relative senses, as revealed by two findings: dormant orchids regressed both in demographic state and size (the latter for large plants only), and this effect was either more common (state) or as common (size) than that observed in continuously sprouting individuals (II). Moreover, in all three studied orchid species, these effects of dormancy seem to be state- and size-dependent (Davison et al., 2013; Jäkäläniemi et al., 2011). In large and mature orchids, dormancy appeared to be a costly state associated with more shrinkage in size and retrogression in state compared to sprouting states (II). In small and young individuals, however, dormancy appears to be a passive state with no pronounced effects on the future fate of the plant. In other words, below-average-sized orchids tended to emerge from dormancy larger than they had been pre-dormancy, and a few young individuals emerged from dormancy in a mature state (II), but these absolute benefits were just as common in sprouting young orchids (II). Therefore, there is no evidence that dormancy in these young orchids has any benefits in the relative sense compared to sprouting. The results merely indicate that under some circumstances dormancy can be non-harmful. This low cost of dormancy in young plants, in addition to the fact that they do not yet pay the costs of lost opportunities

to reproduce, might explain their higher tendency to enter this state (II). In this, my results were similar to prior studies of the American slipper orchid, *Cypripedium candidum* (Shefferson, 2006), and the legume *Astragalus scaphoides* (Gremer, 2010), which likewise reported that small plants had the highest probability of dormancy.

Large plants, on the other hand, incurred both demographic costs (reduced future size and reproduction) as well as the costs of missed opportunities for reproduction. This raises questions about the evolution of dormancy, as it is expected to be advantageous over sprouting in situations in which (i) the performance of emergent plants is strongly suppressed and dormant plants will escape such adverse effects, and/or (ii) plants acquire resources during dormancy that will improve their expected future survival, growth, and/or reproduction, and this resource gain is greater than in sprouting plants. It is therefore likely that dormancy has some other fitness benefits (e.g., survival, Shefferson, Warren, & Pulliam, 2014) that I did not measure in this study. Dormancy may also improve fitness via the timing of reproduction: prolonged dormancy delays reproduction and growth, which functions as a bet-hedging trait (Gremer et al., 2012; Shefferson, 2009) and increases variability in mate choice (Jäkäläniemi et al., 2011).

3.2 Effect of environment

3.2.1 Weather factors

In addition to demographic history, the weather conditions of spring and of the previous growing season and winter also affected the flowering intensity and clonal growth of *C. calceolus* (I). In general, variation in flowering intensity and in clump size of this orchid was best explained by the previous size of the clump, temperature of the previous summer, as well as spring and winter snow depth (I). However, the effect of the weather variables on reproduction and growth varied between Finland and Estonia. My results were consistent with reports from two other orchids that the weather of the previous summer had an important effect: in *Orchis purpurea*, summer precipitation increased growth (Williams et al., 2015), and warm summers had a positive effect (increased population growth due to increased survival) on *Dactylorhiza lapponica* in Norway (Sletvold et al., 2013). It appears that, in Finland and Norway, the mean summer temperature is sub-optimal for these orchids and thus an increase in temperature is beneficial. Furthermore, increasing annual mean

temperature can be expected to decrease the depth of wintertime snow cover, which based on our results would be beneficial for flowering in Finland. However, at the warmer Estonian sites, warmer summer temperatures appeared to be actually detrimental to the growth of *C. calceolus* (I). Furthermore, both in Finland and Estonia, spring snow depth correlated positively with vegetative growth (I), possibly by sheltering and providing moisture to the plants. Vegetative growth was also a major predictor of flowering probability (I). Higher temperatures in springtime lead to earlier snowmelt and sprouting, and can expose plants to more frequent frost damage (Inouye, 2000). This seemed to be the case in Estonia, where high spring temperatures were indeed negatively correlated with vegetative growth (I). An increase in frost damage due to high spring temperatures was observed also in montane wildflowers in Colorado, USA (Inouye, 2008). Thus, the effects of climate warming are not straightforward, and even within the same species, populations at different latitudes are likely to respond differently to the expected increase in temperature. However, it should be noted that the observed correlations with weather variables did not result in synchrony among *C. calceolus* clumps either within or between populations in this study (I), which suggests that the carryover effect of demographic history, and possibly the effect of microsite factors, can override the synchronizing influence of weather.

3.2.2 Tree removal

In this thesis, I show that selective removal of trees can be used to manage populations of *C. calceolus* that are threatened by overshading from spruce, although the effect of tree removal depended on the forest type and time period in question (III). The observed increases in *C. calceolus*' survival, growth, and reproduction at tree removal sites (III) were probably the result of increases in ambient light and resource availability. Tree removal likely encouraged the release of nitrogen, which tends to be immobilized in spruce stands in acidic, slowly decomposing litter (Barbier et al., 2008; Hart & Chen, 2006) that is shaded and kept cool by mature trees (Abd Latif & Blackburn, 2010), which further reduces decomposition rates (Binkley, 1984).

Furthermore, the higher fruiting rates of *C. calceolus* at spruce forest sites with 25-50% TBA removal compared to unlogged control sites (III) can be explained by the pollinators' preference for light patches (Antonelli et al., 2009; Erneberg & Holm, 1999), which leads to increased pollination in canopy gaps compared to closed forest. My results are consistent with previous studies showing that light

correlates positively with flowering and fruiting in several herbaceous species, including a rare orchid (*Isotria medeoloides*, Brumback et al. 2011), a mycorrhizal fern (*Botrychium australe*, Kelly 1994), a small rhizomatous herb (*Trientalis europae*, Kirchner et al. 2009) and a primrose (*Primula vulgaris*, Valverde & Silvertown 1998). However, the effects of forest harvest on orchid survival and sexual reproduction were seen only during the immediate post-harvest period (up to three years after logging) (III). Furthermore, the initial increase in fruit production did not result in an increase in *C. calceolus* seedling production (III). This means that the initial positive effects of tree removal on this orchid's seed reproduction did not translate into lasting benefits for recruitment in the population.

The increase in ramet density of *C. calceolus* at the broad-leaf forest sites, on the other hand, appeared with a lag, but was still visible at the end of the study (III), which suggests that tree removal did increase ramet-level population size in the long-term. As seed set in *C. calceolus* is low and the species reproduces mainly vegetatively, this increase in ramet number is likely to markedly increase the number of offspring generated and therefore the fitness of this species. In a similar study, selective removal of 25% TBA more than doubled the number of stems of *Isotria medeoloides* over a ten-year period (Brumback et al., 2011), which indicates that tree removal has the potential to increase fruiting and shoot density also in other orchids. Furthermore, other endangered species with similar habitat requirements to *C. calceolus* are likely to benefit from the careful tree removal.

One possible reason why our tree removal treatments failed to increase orchid seedling density despite their positive effect on fruit production could be that the treatments were designed to minimize soil surface damage. Seedling recruitment of *C. calceolus* appears to be microsite limited (Kull, 1998), and small-scale disturbance of the moss layer may improve sprouting (Laitinen, 2006). Our tree removal treatments were more comparable to natural forest gaps created by snapped stems than those created by wind-throws, as treated sites lacked the pit-and-mound topography typical of wind-throw forest gaps (Ulanova, 2000). The beneficial effect of disturbance on the sprouting of *C. calceolus* was also seen in the long-term demography plots, where the dormancy rates dropped after the first study year. This likely occurred because the prodding of the thick moss layer in search of the plastic tags allowed more light to enter deep in the moss and break dormancy.

Although the rhizomes of *C. calceolus* are very close to the soil surface (often not more than 1 cm belowground, making the species easily damaged by any intensive mechanical disturbance), it seems that as long as the soil surface is not

severely damaged during logging, even an extensive reduction in tree basal area might not have long-term negative effects on this orchid. This is supported by the results of this tree removal experiment and the observation that, after an initial decrease, the population size of *C. calceolus* seems to increase at clear-cut sites in northern Finland, with populations being the largest in the open, young forest stage and then decreasing again as the canopy closes (A. Jäkäläniemi, personal observations). However, clear-cutting is unlikely to be a suitable management method: while harvesting tends to increase species richness in boreal forests, this is mainly due to an increase in early successional species and a shift in species composition (Pykälä, 2004). Therefore, some endangered species (such as the fairy's slipper orchid, *Calypso bulbosa*, Rytteri et al. 2012) co-occurring with the lady's slipper orchid would likely suffer from treatments that were too intensive. Still, Reier et al. (2005) suggested that a number of forest species are "lost" without a moderate level of disturbance, which is lacking in conventional forestry with clear-cuts, but also in conventional conservation sites, in which the policy is to leave the forest untouched.

4 Conclusions and future directions

Taken together, the findings of this thesis show that both the sexual and asexual reproduction of *C. calceolus* depend on environmental factors, such as weather and tree removal, as well as on an individual's own history, although the latter appears to be the more influential factor of the two. One consequence of the clonal growth strategy is that the number of offspring, and therefore fitness, of an individual depends not only on the number of seeds produced, but also on the number of daughter ramets generated, i.e. the extent of vegetative growth (Clarke, 2012; Sackville Hamilton et al., 1987). In general, *C. calceolus* has a low probability of fruiting and seedling production, so it reproduces mainly vegetatively (Kull, 1999). For this reason, any factor, environmental or historical, that affects vegetative growth in this species can be expected to have direct fitness consequences.

I observed a trade-off between current and future reproduction with respect to both flowering and clonal growth in *C. calceolus*. These reproductive costs may be mitigated in clonal plants by spreading the costs among several ramets. Furthermore, clonal plants can fine-tune their flowering effort by having some ramets flower and some remain vegetative (in contrast with a plant with one shoot which has only two options: to flower, or not to flower at all). A similar spreading of costs can be expected to occur also regarding dormancy, as clonal plants can control how many ramets they produce annually. In this study, I was unfortunately not able to estimate the within-clone degree of dormancy as the total number of available meristems cannot be counted without digging up the plants.

This thesis shows that orchids tend to delay their reproduction until conditions are suitable, with respect to both the environment and internal resource status. This means that these orchids will spend a large portion of their lifetimes as vegetative or dormant, which decreases momentary reproduction. However, this strategy likely increases survival, which elasticity analyses have identified as the most important demographic component for population growth in long-lived species (Franco & Silvertown, 2004; Heppell, Caswell, & Crowder, 2000). It is possible, then, that dormancy may have evolved due to long-term life-history trade-offs (Shefferson, 2009; Shefferson et al., 2018, 2014). Furthermore, fecundity tends to increase with size (Crone, 2016; Ehrlén & Van Groenendael, 2001), and delaying reproduction, e.g., by having vegetative and dormant periods, is therefore likely to maximize lifetime reproduction (Metcalf, Rose, & Rees, 2003; Miller et al., 2012; Orzack & Tuljapurkar, 1989; Tuljapurkar, 1990). Moreover, spreading reproduction over several years can also provide plants with a wider sample of available

environmental conditions. In temporally variable conditions (i.e. in environments with low temporal autocorrelation), trading off momentary reproduction for survival increases the geometric mean of the individual fitness by reducing the variation of the fitness, which is a central characteristic of evolutionary bet-hedging strategies (Childs, Metcalf, & Rees, 2010; Jäkäläniemi et al., 2011; Starrfelt & Kokko, 2012). However, to be a genuine bet-hedging trait, dormancy should also decrease the arithmetic mean of the fitness (Childs et al., 2010; Seger & Brockman, 1987). There is some evidence that a moderate amount of dormancy can fulfill all bet-hedging criteria (Gremer et al., 2012; Shefferson, 2009), although this may not always be the case (Shefferson et al., 2014). For example, in the shading experiment of Shefferson et al. (2012), dormancy increased both the arithmetic and geometric mean of the fitness of the shaded plants.

At the local or regional scale, weather is something that cannot be modified by conservation efforts. However, the effects of climate and climate change must be taken into account when making conservation plans. Furthermore, while we cannot reduce the resource costs of reproduction and dormancy, we can reduce the effects of these costs by improving the overall resource status of a plant. One way to do this is by providing favorable growing conditions, for example via selective tree removal treatments. Although forestry is a threat to several plant species, the positive effects of the tree removal experiment on *C. calceolus* show that the logging is not always harmful, and that preserving a site untouched does not automatically lead to successful nature conservation. However, in conservation management it is important to have a clear picture of what we are aiming to conserve. In this study, I evaluated the effect of tree removal only on one species, and the effect of these treatments on any other species or on the overall biodiversity of the understory remains unknown. However, as the young broadleaf-dominated forest is usually the most species-rich state in the succession cycle of an herb-rich forest (Alanen, Leivo, Lindgren, & Piri, 1995), spruce removal can be expected to benefit the majority of understory herbs. In this respect, it has been suggested that *C. calceolus* could serve as an umbrella species (Nicolè et al., 2005). In other words, providing enough quality habitat for this species would likely ensure that several other species dependent on the same rare habitat type would prosper as well (Caro & O'Doherty 1999). Irrespective of whether this orchid species offers any direct benefits to other species or can serve as an indicator of their health, *C. calceolus* can certainly be used as a flagship species (Devillers-Terschuren, 1999; Gale et al., 2018; Kull, 1999), i.e. a rallying point for nature conservation. Because of its charismatic yellow flowers, *C. calceolus* is a popular plant also in gardens (in fact,

collecting has been one of its main threats; Rassi et al., 2010) and it is a well-marketed attraction in the nature parks where it occurs, such as the Oulanka National Park where a large part of this study was conducted.

References

- Abd Latif, Z., & Blackburn, G. A. (2010). The effects of gap size on some microclimate variables during late summer and autumn in a temperate broadleaved deciduous forest. *International Journal of Biometeorology*, 54(2), 119–129. <https://doi.org/10.1007/s00484-009-0260-1>
- Abeli, T., Jäkäläniemi, A., Wannas, L., Mutikainen, P., & Tuomi, J. (2013). Pollen limitation and fruiting failure related to canopy closure in *Calypso bulbosa* (Orchidaceae), a northern food-deceptive orchid with a single flower. *Botanical Journal of the Linnean Society*, 171(4), 744–750. <https://doi.org/10.1111/boj.12014>
- Ackerman, J. D. (1986). Mechanisms and evolution of food deceptive pollination systems in orchids. *Lindleyana*, 1(2), 108–113.
- Alahuhta, K. (2013). *Neidonkengän (Calypso bulbosa) demografian ajallinen ja paikallinen vaihtelu* (master's thesis, University of Oulu), Oulu, Finland.
- Alanen, A., Leivo, A., Lindgren, L., & Piri, E. (1995). *Lehtojen hoito-opas* (Metsähallituksen luonnonosuojelujulkaisuja. Sarja B. No 26). Vantaa: Metsähallitus.
- Alexandersson, R., & Ågren, J. (1996). Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa*. *Oecologia*, 107, 533–540. <https://doi.org/10.1007/BF00333945>
- Allen, M. F. (1991). *The Ecology of Mycorrhizae*. Cambridge University Press.
- Alpert, P. (1991). Nitrogen sharing among ramets increases clonal growth in *Fragaria chiloensis*. *Ecology*, 72(1), 69–80. <https://doi.org/10.2307/1938903>
- Alpert, P. (1996). Nutrient sharing in natural clonal fragments of *Fragaria chiloensis*. *Journal of Ecology*, 84(3), 395–406. <https://doi.org/10.2307/2261201>
- Antonelli, A., Dahlberg, C. J., Carlgrén, K. H. I., & Appelqvist, T. (2009). Pollination of the lady's slipper orchid (*Cypripedium calceolus*) in Scandinavia - taxonomic and conservational aspects. *Nordic Journal of Botany*, 27(4), 266–273. <https://doi.org/10.1111/j.1756-1051.2009.00263.x>
- Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, 8(7), 343–351. [https://doi.org/10.1016/S1360-1385\(03\)00136-5](https://doi.org/10.1016/S1360-1385(03)00136-5)
- Barbier, S., Gosselin, F., & Balandier, P. (2008). Influence of tree species on understory vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. *Forest Ecology and Management*, 254(1), 1–15. <https://doi.org/10.1016/j.foreco.2007.09.038>
- Bartomeus, I., Ascher, J., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R. (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences*, 108(51), 20645–20649. <https://doi.org/10.1073/pnas.1115559108>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>

- Bazzaz, F. A. (1990). The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics*, 21(1990), 167–196. <https://doi.org/10.1146/annurev.ecolsys.21.1.167>
- Berry, P. M., Dawson, T. P., Harrison, P. A., Pearson, R., & Butt, N. (2003). The sensitivity and vulnerability of terrestrial habitats and species in Britain and Ireland to climate change. *Journal for Nature Conservation*, 11(1), 15–23. <https://doi.org/10.1078/1617-1381-00030>
- Bidartondo, M. I., Burghardt, B., Gebauer, G., Bruns, T. D., & Read, D. J. (2004). Changing partners in the dark: isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. *Proceedings of the Royal Society B – Biological Sciences*, 271, 1799–1806. <https://doi.org/10.1098/rspb.2004.2807>
- Bilz, M., Kell, S. P., Maxted, N., & Lansdown, R. V. (2011). *European red list of vascular plants*. Luxembourg: European Commission. Retrieved from <https://portals.iucn.org/library/sites/library/files/documents/RL-4-016.pdf>
- Binkley, D. (1984). Does forest removal increase rates of decomposition and nitrogen release? *Forest Ecology and Management*, 8(3–4), 229–233. [https://doi.org/10.1016/0378-1127\(84\)90055-0](https://doi.org/10.1016/0378-1127(84)90055-0)
- Blinova, I. (2004). Development of monocarpic shoots of *Cypripedium calceolus* L. (Orchidaceae) in the Arctic. *Journal Europäischer Orchideen*, 36(2), 455–464.
- Bowen-Jones, E., & Entwistle, A. (2002). Identifying appropriate flagship species: the importance of culture and local contexts. *Oryx*, 36(2), 189–195. <https://doi.org/10.1017/S0030605302000261>
- Brokaw, N. V. L. (1987). Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology*, 75, 9–19. <https://doi.org/10.2307/2260533>
- Brosfolske, K. D., Chen, J., & Crow, T. R. (2001). Understory vegetation and site factors: Implications for a managed Wisconsin landscape. *Forest Ecology and Management*, 146(1–3), 75–87. [https://doi.org/10.1016/S0378-1127\(00\)00447-3](https://doi.org/10.1016/S0378-1127(00)00447-3)
- Brumback, W. E., Cairns, S., Sperduto, M. B., & Fyler, C. W. (2011). Response of an *Isotrea medeoloides* population to canopy thinning. *Northeastern Naturalist*, 18(2), 185–196. <https://doi.org/10.1656/045.018.0205>
- Brzosko, E. (2002). Dynamics of island populations of *Cypripedium calceolus* in the Biebrza river valley (North-East Poland). *Botanical Journal of the Linnean Society*, 139(1), 67–77. <https://doi.org/10.1046/j.1095-8339.2002.00049.x>
- Bullock, J. M., Mortimer, A. M., & Begon, M. (1993). Carryover effects on the clonal growth of the grass *Holcus lanatus* L. *New Phytologist*, 124(2), 301–307. <https://doi.org/10.1111/j.1469-8137.1993.tb03820.x>
- Cain, M. L., & Damman, H. (1997). Clonal growth and ramet performance in the woodland herb, *Asarum canadense*. *Journal of Ecology*, 85(6), 883–897. <https://doi.org/10.2307/2960609>
- Calvo, R. N. (1993). Evolutionary demography of orchids : Intensity and frequency of pollination and the cost of fruiting. *Ecology*, 74(4), 1033–1042. <https://doi.org/10.2307/1940473>

- Caro, T. M., & Girling, S. (2010). *Conservation by proxy : indicator, umbrella, keystone, flagship, and other surrogate species*. Washington: Island Press.
- Caro, T. M., & O'Doherty, G. (1999). On the use of surrogate species in conservation biology. *Conservation Biology*, *13*(4), 805–814. <https://doi.org/10.1046/j.1523-1739.1999.98338.x>
- Chesson, P., & Peterson, A. G. (2002). The quantitative assessment of the benefits of physiological integration in clonal plants. *Evolutionary Ecology Research*, *4*(8), 1153–1176. Retrieved from http://www.eebweb.arizona.edu/Faculty/Chesson/Peter/Reprints/2002_Quantitative%20assessment%20of%20the%20benefits%20of%20physiological%20integration.pdf
- Childs, D. Z., Metcalf, C. J. E., & Rees, M. (2010). Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1697), 3055–3064. <https://doi.org/10.1098/rspb.2010.0707>
- Christenhusz, M. J. M., & Byng, J. W. (2016). The number of known plants species in the world and its annual increase. *Phytotaxa*, *261*(3), 201–217. <https://doi.org/10.11646/phytotaxa.261.3.1>
- Clarke, E. (2012). Plant individuality: a solution to the demographer's dilemma. *Biology & Philosophy*, *27*(3), 321–361. <https://doi.org/10.1007/s10539-012-9309-3>
- Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, *12*(1), 119–129. [https://doi.org/10.1016/0022-5193\(66\)90188-3](https://doi.org/10.1016/0022-5193(66)90188-3)
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*(4335), 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>
- Cozzolino, S., & Widmer, A. (2005). Orchid diversity: an evolutionary consequence of deception? *Trends in Ecology & Evolution*, *20*(9), 487–494. <https://doi.org/10.1016/j.tree.2005.06.004>
- Crone, E. E. (2013). Responses of social and solitary bees to pulsed floral resources. *The American Naturalist*, *182*(4), 465–473. <https://doi.org/10.1086/671999>
- Crone, E.E. (2016). Contrasting effects of spatial heterogeneity and environmental stochasticity on population dynamics of a perennial wildflower. *Journal of Ecology*, *104*, 281–291. <https://doi.org/10.1111/1365-2745.12500>
- Crone, E. E., Miller, E., & Sala, A. (2009). How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters*, *12*(11), 1119–1126. <https://doi.org/10.1111/j.1461-0248.2009.01365.x>
- Crone, E. E., & Rapp, J. M. (2014). Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences*, *1322*(2014), 21–34. <https://doi.org/10.1111/nyas.12465>
- Cunningham, S. A. (1997). The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understory palm. *Oecologia*, *111*(1), 36–44. <https://doi.org/10.1007/s004420050205>

- D'Odorico, P., Caylor, K., Okin, G. S., & Scanlon, T. M. (2007). On soil moisture-vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems. *Journal of Geophysical Research*, *112*(4), 1–10. <https://doi.org/10.1029/2006JG000379>
- Dafni, A. (1984). Mimicry and deception in pollination. *Annual Review of Ecology and Systematics*, *15*, 259–278. <https://doi.org/10.1146/annurev.ecolsys.15.1.259>
- Darwin, C. (1862). *On the contrivances by which British and foreign orchids are fertilized by insects, and on the good effects of intercrossing*. London: John Murray. <https://doi.org/10.1017/CBO9780511910197>
- Davison, R., Nicole, F., Jacquemyn, H., & Tuljapurkar, S. (2013). Contributions of covariance: decomposing the components of stochastic population growth in *Cypripedium calceolus*. *The American Naturalist*, *181*(3), 410–420. <https://doi.org/10.1086/669155>
- De Boever, M., Gabriels, D., Ouessar, M., & Cornelis, W. (2016). Influence of Acacia trees on near-surface soil hydraulic properties in arid Tunisia. *Land Degradation and Development*, *27*(8), 1805–1812. <https://doi.org/10.1002/ldr.2302>
- De Witte, L. C., & Stöcklin, J. (2010). Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany*, *106*, 859–870. <https://doi.org/10.1093/aob/mcq191>
- Dempster, E. R. (1955). Maintenance of genetic heterogeneity. In *Cold Spring Harbor symposia on quantitative biology*, *20*, 23–32. <https://doi.org/10.1101/SQB.1955.020.01.005>
- Devillers-Terschuren, J. (1999). *Action plan for Cypripedium calceolus in Europe* (No. 100-10). Council of Europe.
- Dirzo, R., Horvitz, C. C., Quevedo, H., & Lopez, M. A. (1992). The effects of gap size and age on the understory herb community of a tropical Mexican rain forest. *Journal of Ecology*, *80*(4), 809–822.
- Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>
- Ehrlén, J. (2000). The dynamics of plant populations: does the history of individuals matter? *Ecology*, *81*(6), 1675–1684. <https://doi.org/10.2307/177316>
- Ehrlén, J., & Van Groenendael, J. (2001). Storage and the delayed costs of reproduction in the understorey perennial *Lathyrus vernus*. *Journal of Ecology*, *89*(2), 237–246. <https://doi.org/10.1046/j.1365-2745.2001.00546.x>
- Erneberg, M., & Holm, B. (1999). Bee size and pollen transfer in *Cypripedium calceolus* (Orchidaceae). *Nordic Journal of Botany*, *19*(3), 363–367.
- Fitter, A.H., & Fitter, R.S.R. (2002). Rapid changes in flowering times in British plants. *Science*, *296*, 1689–1691. <https://doi.org/10.1126/science.1071617>
- Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., ... Sibert, J. (2012). AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*(2), 233–249. <https://doi.org/10.1080/10556788.2011.597854>

- Franco, M., & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology*, *85*(2), 531–538. <https://doi.org/10.1890/02-0651>
- Gale, S. W., Fischer, G. A., Cribb, P. J., & Fay, M. F. (2018). Orchid conservation: bridging the gap between science and practice. *Botanical Journal of the Linnean Society*, *186*(4), 425–434. <https://doi.org/10.1093/botlinnean/boy003>
- Galhidy, L., Mihok, B., Hagyo, A., Rajkai, K., & Standovar, T. (2006). Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecology*, *183*, 133–145. <https://doi.org/10.1007/s11258-005-9012-4>
- Gebauer, G., & Meyer, M. (2003). ^{15}N and ^{13}C natural abundance of autotrophic and myco-heterotrophic orchids provides insight into nitrogen and carbon gain from fungal association. *New Phytologist*, *160*(1), 209–223. <https://doi.org/10.1046/j.1469-8137.2003.00872.x>
- Geber, M. A., Kroon, H. De, & Watson, M. A. (2016). Organ preformation in mayapple as a mechanism for historical effects on demography. *Journal of Ecology*, *85*(2), 211–223. <https://doi.org/10.2307/2960652>
- Geiger, R., Aron, R. H., & Todhunter, P. (Eds.). (1995). *The climate near ground* (5th ed.). Lengerich, Germany: Vieweg.
- Gigord, L. D., Macnair, M. R., & Smithson, A. (2001). Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soo. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(11), 6253–6255. <https://doi.org/10.1073/pnas.111162598>
- Givnish, T. J., Spalink, D., Ames, M., Lyon, S. P., Hunter, S. J., Zuluaga, A., ... Cameron, K. M. (2015). Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151553. <https://doi.org/10.1098/rspb.2015.1553>
- Gough, L., Shaver, G. R., Carroll, J., Royer, D. L., & Laundre, J. A. (2000). Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. *Journal of Ecology*, *88*(1), 54–66. <https://doi.org/10.1046/j.1365-2745.2000.00426.x>
- Gregg, K. B., & Kéry, M. (2005). Comparison of size vs . life-state classification in demographic models for the terrestrial orchid *Cleistes bifaria*. *Biological Conservation*, *129*, 50–58. <https://doi.org/10.1016/j.biocon.2005.09.044>
- Gremer, J. R. (2010). *Causes and consequences of prolonged dormancy: why stay belowground?* (doctoral thesis, University of Montana) Missoula, MT. Retrieved from <https://scholarworks.umt.edu/etd/175/>
- Gremer, J. R., Crone, E. E., & Lesica, P. (2012). Are dormant plants hedging their bets? Demographic consequences of prolonged dormancy in variable environments. *American Naturalist*, *179*(3), 315–327. <https://doi.org/10.1086/664459>
- Gremer, J. R., & Sala, A. (2013). It is risky out there: the costs of emergence and the benefits of prolonged dormancy. *Oecologia*, *172*(4), 937–947. <https://doi.org/10.1007/s00442-012-2557-8>

- Gremer, J. R., Sala, A., & Crone, E. E. (2010). Disappearing plants: why they hide and how they return. *Ecology*, *91*(11), 3407–3413. <https://doi.org/10.1890/09-1864.1>
- Harper, J. L. (1987). *Population Biology of Plants. Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences* (7th ed., Vol. 330). London : Academic Press.
- Hart, S. A., & Chen, H. Y. H. (2006). Understory vegetation dynamics of North American boreal forests. *Critical Reviews in Plant Sciences*, *25*, 381–397. <https://doi.org/10.1080/07352680600819286>
- Hartnett, D. C., & Bazzaz, F. A. (1983). Physiological integration among intraclonal ramets in *Solidago canadensis*. *Ecology*, *64*(4), 779–788. <https://doi.org/10.2307/1937201>
- Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, *12*(2), 184–195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Hens, H., Pakanen, V.-M., Jäkäläniemi, A., Tuomi, J., & Kvist, L. (2017). Low population viability in small endangered orchid populations: genetic variation, seedling recruitment and stochasticity. *Biological Conservation*, *210*, 174–183. <https://doi.org/10.1016/j.biocon.2017.04.019>
- Heppell, S. S., Caswell, H., & Crowder, L. B. (2000). Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, *81*(3), 654–665. [https://doi.org/10.1890/0012-9658\(2000\)081\[0654:LHAEPP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0654:LHAEPP]2.0.CO;2)
- Hultén, E., & Fries, M. (1986). *Atlas of North European vascular plants* (Vol. I–III). Königstein, Germany: Koeltz Scientific Books.
- Hutchings, M. J. (1987). The population biology of the early spider orchid , *Ophrys sphegodes* Mill. II. Temporal patterns in behaviour. *Journal of Ecology*, *75*(3), 729–742. <https://doi.org/10.2307/2260202>
- Hutchings, M. J., & Mogie, M. (1990). The spatial structure of clonal plants: control and consequences. In J. van Groenendael & H. de Kroon (Eds.), *Clonal growth in plants: Regulation and function* (pp. 57–76). Hague, Netherlands: SPB Academic.
- Inouye, D. W. (2000). The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, *3*(5), 457–463. <https://doi.org/10.1046/j.1461-0248.2000.00165.x>
- Inouye, D. W. (2008). Effects of climate change on phenology, frost damage and floral abundance of montane wildflowers. *Ecology*, *89*(2), 353–362. <https://doi.org/10.1890/06-2128.1>
- Internicola, A. I., Juillet, N., Smithson, A., & Gigord, L. D. B. (2006). Experimental investigation of the effect of spatial aggregation on reproductive success in a rewardless orchid. *Oecologia*, *150*(3), 435–441. <https://doi.org/10.1007/s00442-006-0530-0>
- IPCC. (2014). Fifth Assessment Report. Summary for Policy Makers. *Climate Change 2014: Impacts, Adaptation and Vulnerability - Contributions of the Working Group II to the Fifth Assessment Report*, 1–32. Retrieved from <http://www.ipcc.ch/report/ar5/syr/>
- Isagi, Y., Sugimura, K., Sumida, A., & Ito, H. (1997). How does masting happen and synchronize? *Journal of Theoretical Biology*, *187*(2), 231–239. <https://doi.org/10.1006/jtbi.1997.0442>

- Isogimi, T., Matsushita, M., Watanabe, Y., & Nakagawa, M. (2011). Sexual differences in physiological integration in the dioecious shrub *Lindera triloba*: a field experiment using girdling manipulation. *Annals of Botany*, 107(6), 1029–1037. <https://doi.org/10.1093/aob/mcr043>
- IUCN. (2017). Summary Statistics. Retrieved August 14, 2017, from <http://www.iucnredlist.org/about/summary-statistics>
- Jacquemyn, H., & Brys, R. (2010). Temporal and spatial variation in flower and fruit production in a food-deceptive orchid: a five-year study. *Plant Biology*, 12(1), 145–153. <https://doi.org/10.1111/j.1438-8677.2009.00217.x>
- Jakubska-Busse, A., & Kadej, M. (2011). The pollination of *Epipactis* Zinn, 1757 (Orchidaceae) species in Central Europe - the significance of chemical attractants, floral morphology and concomitant insects. *Acta Societatis Botanicorum Poloniae*, 80(1), 49–57. <https://doi.org/10.5586/asbp.2011.007>
- Jersáková, J., Johnson, S. D., & Kindlmann, P. (2006). Mechanisms and evolution of deceptive pollination in orchids. *Biological Reviews*, 81(2), 219–235. <https://doi.org/10.1017/S1464793105006986>
- Johnson, S. D., & Edwards, T. J. (2000). The structure and function of orchid pollinaria. *Plant Systematics and Evolution*, 222(1–4), 243–269. <https://doi.org/10.1007/BF00984105>
- Julou, T., Burghardt, B., Gebauer, G., Berveiller, D., Damesin, C., & Selosse, M. A. (2005). Mixotrophy in orchids: insights from a comparative study of green individuals and nonphotosynthetic individuals of *Cephalanthera damasonium*. *New Phytologist*, 166(2), 639–653. <https://doi.org/10.1111/j.1469-8137.2005.01364.x>
- Jäkäläniemi, A. (2003). *Epipactis atrorubens* (Hoffm, ex Bernh.) Besser. In T. Rytteri, Ü. Kukk, T. Kull, A. Jäkäläniemi, & M. Reitalu (Eds.), *Monitoring of threatened vascular plants in Estonia and Finland – methods and experiences* (pp. 87–98). Helsinki: Suomen ympäristökeskus.
- Jäkäläniemi, A. (2011). Narrow climate and habitat envelope affect the survival of relict populations of a northern *Arnica angustifolia*. *Environmental and Experimental Botany*, 72, 415–421. <https://doi.org/10.1016/j.envexpbot.2011.03.013>
- Jäkäläniemi, A., Crone, E. E., Närhi, P., & Tuomi, J. (2011). Orchids do not pay costs at emergence for prolonged dormancy. *Ecology*, 92(7), 1538–1543. <https://doi.org/10.1890/10-1957.1>
- Jäkäläniemi, A., Illarionova, I., & Rankou, H. (2011). *Calypso bulbosa*. Retrieved April 17, 2018, from <http://www.iucnredlist.org/details/161965/1>
- Kaitala, V., & Kull, T. (2002). Temporal auto-correlation structures in population of *Cypripedium calceolus*: a two-year rhythm in flowering. In P. Kindlmann, J. Willems, & D. Whigham (Eds.), *Trends and fluctuations and underlying mechanisms in terrestrial orchid populations* (pp. 43–52). Leiden, Netherlands: Backhuys.
- Kelly, D. (1994). Demography and conservation of *Botrychium australe*, a peculiar, sparse mycorrhizal fern. *New Zealand Journal of Botany*, 32(4), 393–400. <https://doi.org/10.1080/0028825X.1994.10412925>

- Kéry, M., & Gregg, K. B. (2004). Demographic analysis of dormancy and survival in the terrestrial orchid *Cypripedium reginae*. *Journal of Ecology*, 92, 686–695. <https://doi.org/10.1111/j.0022-0477.2004.00885.x>
- Kéry, M., Gregg, K. B., & Schaub, M. (2005). Demographic estimation methods for plants with unobservable life-states. *Oikos*, 108(2), 307–320. <https://doi.org/10.1111/j.0030-1299.2005.13589.x>
- Kirchner, K., Kammermeier, S., & Bruelheide, H. (2009). The response of the pseudoannual species *Trientalis europaea* L. to forest gap dynamics in a near-natural spruce forest. *Forest Ecology and Management*, 257(3), 1070–1077. <https://doi.org/10.1016/j.foreco.2008.11.013>
- Kon, H., Noda, T., Terazawa, K., Koyama, H., & Yasaka, M. (2005). Proximate factors causing mast seeding in *Fagus crenata*: the effects of resource level and weather cues. *Canadian Journal of Botany*, 83(11), 1402–1409. <https://doi.org/10.1139/b05-120>
- Kujala, V. (1979). *Suomen metsätyypit [Forest types of Finland]*. Helsinki: Metsäntutkimuslaitos.
- Kull, T. (1998). Fruit-set and recruitment in populations of *Cypripedium calceolus* L. in Estonia. *Botanical Journal of the Linnean Society*, 126, 27–38. <https://doi.org/10.1111/j.1095-8339.1998.tb02513.x>
- Kull, T. (1999). Biological flora of the British Isles. *Cypripedium calceolus* L. *Journal of Ecology*, 87, 913–924. Retrieved from <http://www.jstor.org/stable/2648646>
- Kull, T., & Kull, K. (1991). Preliminary results from a study of populations of *Cypripedium calceolus* in Estonia. In T. C. E. Wells & J. H. Willems (Eds.), *Population ecology of terrestrial orchids* (pp. 69–76). Hague, Netherlands: SPB Academic.
- Kull, T. (2003). *Cypripedium calceolus* L. – Interpreting population trends through short-term and long-term monitoring. In T. Rytteri, Ü. Kukk, T. Kull, A. Jäkäläniemi, & M. Reitalu (Eds.), *Monitoring of threatened vascular plants in Estonia and Finland – methods and experiences* (pp. 71–75). Helsinki: Suomen ympäristökeskus. Retrieved from <http://hdl.handle.net/10138/40538>
- Kuusik V. 1984. *Orchidaceae. Flora of the Estonian SSR IX*. Tallinn, Estonia: Valgus.
- Laitinen, T. (2006). *Tikankontin tila Suomessa [The conservation status of the Lady's slipper orchid (Cypripedium calceolus L.) in Finland]*. Vantaa: Metsähallitus. Retrieved from <https://julkaisut.metsa.fi/assets/pdf/lp/Asarja/a154.pdf>
- Laitinen, T., & Ilmonen, J. (2009). *Metsähallituksen vastuulajien tila ja suojeletaso vuonna 2006: Tummaneidonvaippa - Epipactis atrorubens (Hoffm. ex Bernh.) Besser*. Vantaa: Metsähallitus. Retrieved from <https://julkaisut.metsa.fi/julkaisut/show/509>
- Leake, J. R. (1994). The biology of myco-heterotrophic ('saprophytic') plants. *New Phytologist*, 127(69), 171–216. <https://doi.org/10.1111/j.1469-8137.1994.tb04272.x>
- Lee, Y. I., Yang, C. K., & Gebauer, G. (2015). The importance of associations with saprotrophic non-*Rhizoctonia* fungi among fully mycoheterotrophic orchids is currently under-estimated: novel evidence from sub-tropical Asia. *Annals of Botany*, 116(3), 423–435. <https://doi.org/10.1093/aob/mcv085>

- Lesica, P., & Crone, E. E. (2007). Causes and consequences of prolonged dormancy for an iteroparous geophyte, *Silene spaldingii*. *Journal of Ecology*, *95*(6), 1360–1369. <https://doi.org/10.1111/j.1365-2745.2007.01291.x>
- Lesica, P., & Crone, E. E. (2017). Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains. *Ecology Letters*, *20*(2), 166–174. <https://doi.org/10.1111/ele.12718>
- Lesica, P., & McCune, B. (2004). Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science*, *15*(5), 679–690. <https://doi.org/10.1111/j.1654-1103.2004.tb02310.x>
- Lesica, P., & Steele, B. M. (1994). Prolonged dormancy in vascular plants and implications for monitoring studies. *Natural Areas Journal*, *14*(3), 209–212. Retrieved from <http://www.jstor.org/stable/4496087>
- Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., & Comeau, P. G. (1999). Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research*, *29*(6), 796–811. <https://doi.org/10.1139/x98-165>
- Lindenmayer, D. B., Fischer, J., Felton, A., Montague-Drake, R., Manning, A. D., Simberloff, D., ... Elliott, C. P. (2007). The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos*, *116*(7), 1220–1226. <https://doi.org/10.1111/j.2007.0030-1299.15683.x>
- Ma, S., Concilio, A., Oakley, B., North, M., & Chen, J. (2010). Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *Forest Ecology and Management*, *259*(5), 904–915. <https://doi.org/10.1016/j.foreco.2009.11.030>
- Marchand, F. L., Nijs, I., Heuer, M., Mertens, S., Kockelbergh, F., Pontailier, J.-Y., ... Beyens, L. (2004). Climate warming postpones senescence in high arctic tundra. *Arctic, Antarctic, and Alpine Research*, *36*(4), 390–394. [https://doi.org/10.1657/1523-0430\(2004\)036\[0390:CWPSIH\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2004)036[0390:CWPSIH]2.0.CO;2)
- Maria, J. E., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B., & Retana, J. (2011). Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. *Ecology*, *89*(3), 805–817. <https://doi.org/10.1890/07-0217.1>
- Martikainen, P., Kaila, L., & Haila, Y. (1998). Threatened beetles in white-backed woodpecker habitats. *Conservation Biology*, *12*(2), 293–301. <https://doi.org/10.1111/j.1523-1739.1998.96484.x>
- McCormick, M. K., Taylor, D. L., Juhaszova, K., Burnett Jr, R. K., Whigham, D. F., & O'Neill, J. P. (2012). Limitations on orchid recruitment: not a simple picture. *Molecular Ecology*, *21*(6), 1511–1523. <https://doi.org/10.1111/j.1365-294X.2012.05468.x>
- McEwan, R. W., Brecha, R. J., Geiger, D. R., & John, G. P. (2011). Flowering phenology change and climate warming in southwestern Ohio. *Plant Ecology*, *212*(1), 55–61. <https://doi.org/10.1007/s11258-010-9801-2>

- McKendrick, S. L., Leake, J. R., & Read, D. J. (2000). Symbiotic germination and development of myco-heterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and *Betula pendula* to the orchid *Corallorhiza trifida* through shared hyphal connections. *New Phytologist*, *145*(3), 539–548. <https://doi.org/10.1046/j.1469-8137.2000.00592.x>
- Meléndez-Ackerman, E. J., Ackerman, J. D., & Rodríguez-Robles, J. A. (2000). Reproduction in an orchid can be resource-limited over its lifetime. *Biotropica*, *32*(2), 282–290. <https://doi.org/10.1111/j.1744-7429.2000.tb00471.x>
- Metcalf, J. C., Rose, K. E., & Rees, M. (2003). Evolutionary demography of monocarpic perennials. *Trends in Ecology and Evolution*, *18*(9), 471–480. [https://doi.org/10.1016/S0169-5347\(03\)00162-9](https://doi.org/10.1016/S0169-5347(03)00162-9)
- Micheneau, C., Johnson, S. D., & Fay, M. F. (2009). Orchid pollination: from Darwin to the present day. *Botanical Journal of the Linnean Society*, *161*(1), 1–19. <https://doi.org/10.1111/j.1095-8339.2009.00995.x>
- Miller, T. E. X., Williams, J. L., Jongejans, E., Brys, R., & Jacquemyn, H. (2012). Evolutionary demography of iteroparous plants: incorporating non-lethal costs of reproduction into integral projection models. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1739), 2831–2840. <https://doi.org/10.1098/rspb.2012.0326>
- Moreira, X., Abdala-Roberts, L., Linhart, Y. B., & Mooney, K. A. (2014). Masting promotes individual- and population-level reproduction by increasing pollination efficiency. *Ecology*, *95*(4), 801–807. <https://doi.org/10.1890/13-1720.1>
- Motomura, H., Selosse, M.-A., Martos, F., Kagawa, A., & Yukawa, T. (2010). Mycoheterotrophy evolved from mixotrophic ancestors: evidence in *Cymbidium* (Orchidaceae). *Annals of Botany*, *106*, 573–581. <https://doi.org/10.1093/aob/mcq156>
- Neiland, M. R. M., & Wilcock, C. C. (1998). Fruit set, nectar reward, and rarity in the Orchidaceae. *American Journal of Botany*, *85*(12), 1657–1671. <https://doi.org/10.2307/2446499>
- Nicolè, F., Brzosko, E., & Till-Bottraud, I. (2005). Population viability analysis of *Cypripedium calceolus* in a protected area: longevity, stability and persistence. *Journal of Ecology*, *93*(4), 716–726. <https://doi.org/10.1111/j.1365-2745.2005.01010.x>
- Nicolè, F., Dahlgren, J. P., Vivat, A., Till-Bottraud, I., & Ehrlén, J. (2011). Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology*, *99*, 1211–1218. <https://doi.org/10.1111/j.1365-2745.2011.01852.x>
- Nygaard, P. H., & Odegaard, T. (1999). Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. *Journal of Vegetation Science*, *10*(1994), 5–16. <https://doi.org/10.2307/3237155>
- Obeso, J. R. (2002). The costs of reproduction in plants. *New Phytologist*, *155*, 321–348. <https://doi.org/10.1046/j.1469-8137.2002.00477.x>
- Oostra, S., Majdi, H., & Olsson, M. (2006). Impact of tree species on soil carbon stocks and soil acidity in southern Sweden. *Scandinavian Journal of Forest Research*, *21*(5), 364–371. <https://doi.org/10.1080/02827580600950172>

- Orzack, S. H., & Tuljapurkar, S. (1989). Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *The American Naturalist*, 133(6), 901–923. <https://doi.org/10.1086/284959>
- Paalamo, P., Eeronheimo, H., & Ilmonen, J. (2009). *Metsähallituksen vastuulajien tila ja suojeletaso vuonna 2006. Neidonkenkä - Calypso bulbosa (L.) Oakes*. Vantaa: Metsähallitus. Retrieved from <https://julkaisut.metsa.fi/julkaisut/show/498>
- Parmesan, C., & Yohe, G. (2002). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42. <https://doi.org/10.1038/nature01286>
- Parra-Tabla, V., & Vargas, C. F. (2007). Flowering synchrony and floral display size affect pollination success in a deceit-pollinated tropical orchid. *Acta Oecologica*, 32(1), 26–35. <https://doi.org/10.1016/j.actao.2007.02.002>
- Parviainen, M., Luoto, M., Rytteri, T., & Heikkinen, R. K. (2008). Modelling the occurrence of threatened plant species in taiga landscapes: methodological and ecological perspectives. *Journal of Biogeography*, 35(10), 1888–1905. <https://doi.org/10.1111/j.1365-2699.2008.01922.x>
- Pauw, A., & Bond, W. J. (2011). Mutualisms matter: pollination rate limits the distribution of oil-secreting orchids. *Oikos*, 120(10), 1531–1538. <https://doi.org/10.1111/j.1600-0706.2011.19417.x>
- Pearce-Higgins, J. W., Ockendon, N., Baker, D. J., Carr, J., White, E. C., Almond, R. E. A., ... Tanner, E. V. J. (2015). Geographical variation in species' population responses to changes in temperature and precipitation. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151561. <https://doi.org/10.1098/rspb.2015.1561>
- Pesendorfer, M. B., Koenig, W. D., Pearse, I. S., Knops, J. M. H., & Funk, K. A. (2016). Individual resource-limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*). *Journal of Ecology*, 104(3), 637–645. <https://doi.org/10.1111/1365-2745.12554>
- Peterson, C. J., & Pickett, S. T. A. (1995). Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology*, 76(3), 763–774. <https://doi.org/10.2307/1939342>
- Phillips, R. D., Peakall, R., Hutchinson, M. F., Linde, C. C., Xu, T., Dixon, K. W., & Hopper, S. D. (2014). Specialized ecological interactions and plant species rarity: the role of pollinators and mycorrhizal fungi across multiple spatial scales. *Biological Conservation*, 169, 285–295. <https://doi.org/10.1016/j.biocon.2013.11.027>
- Primack, R., & Stacy, E. (1998). Cost of reproduction in the Pink Lady's Slipper Orchid (*Cypripedium acaule*, Orchidaceae): an eleven-year experimental study of three populations. *American Journal of Botany*, 85(12), 1672–1679. <https://doi.org/10.2307/2446500>
- Pykälä, J. (2004). Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. *Applied Vegetation Science*, 7(1), 29–34. [https://doi.org/10.1658/1402-2001\(2004\)007\[0029:IIIPSR\]2.0.CO;2](https://doi.org/10.1658/1402-2001(2004)007[0029:IIIPSR]2.0.CO;2)
- R Development Core Team. (2015). R: a language and environment for statistical computing. *R Foundation for Statistical Computing*. Vienna, Austria.

- Rankou, H., & Bilz, M. (2014). *Cypripedium calceolus*. Retrieved April 19, 2017, from <http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T162021A43316125.en>.
- Rasmussen, H. N. (2002). Recent developments in the study of orchid mycorrhiza. *Plant and Soil*, 244(1–2), 149–163. <https://doi.org/10.1023/A:1020246715436>
- Rasmussen, H. N., Dixon, K. W., Jersáková, J., & Těšitelová, T. (2015). Germination and seedling establishment in orchids: a complex of requirements. *Annals of Botany*, 116(3), 391–402. <https://doi.org/10.1093/aob/mcv087>
- Rasmussen, H. N., & Rasmussen, F. N. (2009). Orchid mycorrhiza : implications of a mycophagous life style. *Oikos*, 118, 334–345. <https://doi.org/10.1111/j.1600-0706.2008.17116.x>
- Rassi, P., Hyvärinen, E., Juslén, A., & Mannerkoski, I. (Eds.). (2010). *Suomen lajien uhanalaisuus – Punainen kirja 2010 [The 2010 Red List of Finnish Species]*. Ympäristöministeriö & Suomen ympäristökeskus. Helsinki: Ympäristöministeriö & Suomen ympäristökeskus. Retrieved from www.environment.fi/redlist
- Reddy, V. R., Reddy, K. R., & Hodges, H. F. (1995). Carbon dioxide enrichment and temperature effects on cotton canopy photosynthesis, transpiration, and water-use efficiency. *Field Crops Research*, 41(1), 13–23. [https://doi.org/10.1016/0378-4290\(94\)00104-K](https://doi.org/10.1016/0378-4290(94)00104-K)
- Rees, M., Kelly, D., & Bjørnstad, O. N. (2002). Snow tussocks, chaos, and the evolution of mast seeding. *The American Naturalist*, 160(1), 44–59. <https://doi.org/10.1086/340603>
- Reier, Ü., Tuvi, E., Pärtel, M., Kalamees, R., & Zobel, M. (2005). Threatened herbaceous species dependent on moderate forest disturbances : a neglected target for ecosystem-based silviculture. *Scandinavian Journal of Forest Research*, 20:S6, 145–152. <https://doi.org/10.1080/14004080510042128>
- Roiloa, S. R., & Retuerto, R. (2005). Presence of developing ramets of *Fragaria vesca* L. increases photochemical efficiency in parent ramets. *International Journal of Plant Sciences*, 166(5), 795–803. <https://doi.org/10.1086/431804>
- Romme, W. H., Everham, E. H., Frelich, L. E., Moritz, M. A., & Sparks, R. E. (1998). Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems*, 1(6), 524–534. <https://doi.org/10.1007/s100219900048>
- Ryan, M. G. (1991). Effects of climate change on plant respiration. *Ecological Applications*, 1(2), 157–167. <https://doi.org/10.2307/1941808>
- Rydgren, K. (1996). Vegetation-environment relationships of old-growth spruce forest vegetation in Østmarka Nature Reserve, SE Norway, and comparison of three ordination methods. *Nordic Journal of Botany*, 16(4), 421–439. <https://doi.org/10.1111/j.1756-1051.1996.tb00254.x>
- Ryttäri, T., Kalliovirta, M., & Lampinen, R. (Eds.). (2012). *Suomen uhanalaiset kasvit*. Helsinki: Tammi.
- Sackville Hamilton, N. R., Schmid, B., & Harper, J. L. (1987). Life-history concepts and the population biology of clonal organisms. *Proceedings of the Royal Society B: Biological Sciences*, 232(1266), 35–57. <https://doi.org/10.1098/rspb.1987.0060>

- Saitoh, T., Seiwa, K., & Nishiwaki, A. (2002). Importance of physiological integration of dwarf bamboo to persistence in forest understorey : a field experiment. *Journal of Ecology*, *90*(1), 78–85. <https://doi.org/10.1046/j.0022-0477.2001.00631.x>
- Sala, A., Hopping, K., McIntire, E. J. B., Delzon, S., & Crone, E. E. (2012). Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *The New Phytologist*, *196*(1), 189–199. <https://doi.org/10.1111/j.1469-8137.2012.04257.x>
- Satake, A., & Iwasa, Y. (2002). The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. *Journal of Ecology*, *90*(5), 830–838. <https://doi.org/10.1046/j.1365-2745.2002.00721.x>
- Seger, J., & Brockman, H. J. (1987). What is bet-hedging? *Oxford Surveys in Evolutionary Biology*, *4*, 182–211.
- Sergio, F., Newton, I., Marchesi, L., & Pedrini, P. (2006). Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, *43*(6), 1049–1055. <https://doi.org/10.1111/j.1365-2664.2006.01218.x>
- Shefferson, R. P. (2006). Survival costs of adult dormancy and the confounding influence of size in lady’s slipper orchids, genus *Cypripedium*. *Oikos*, *115*(2), 253–262. <https://doi.org/10.1111/j.2006.0030-1299.15231.x>
- Shefferson, R. P. (2009). The evolutionary ecology of vegetative dormancy in mature herbaceous perennial plants. *Journal of Ecology*, *97*(5), 1000–1009. <https://doi.org/10.1111/j.1365-2745.2009.01525.x>
- Shefferson, R. P., Kull, T., Hutchings, M. J., Selosse, M.-A., Jacquemyn, H., Kellett, K. M., ... Whigham, D. F. (2018). Drivers of vegetative dormancy across herbaceous perennial plant species. *Ecology Letters*, *21*, 724–733. <https://doi.org/10.1111/ele.12940>
- Shefferson, R. P., Kull, T., Tali, K., & Kellett, K. M. (2012). Linking vegetative dormancy to fitness in two long-lived herbaceous perennials. *Ecosphere*, *3*(2), 1–19. <https://doi.org/10.1890/es11-00328.1>
- Shefferson, R. P., Mizuta, R., & Hutchings, M. J. (2017). Predicting evolution in response to climate change: the example of sprouting probability in three dormancy-prone orchid species. *Royal Society Open Science*, *4*, 160647. <https://doi.org/10.1098/rsos.160647>
- Shefferson, R. P., Sandercock, B. K., Proper, J., & Beissinger, S. R. (2001). Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. *Ecology*, *82*(1), 145–156. <https://doi.org/10.2307/2680092>
- Shefferson, R. P., & Tali, K. (2007). Dormancy is associated with decreased adult survival in the burnt orchid, *Neotinea ustulata*. *Journal of Ecology*, *95*(1), 217–225. <https://doi.org/10.1111/j.1365-2745.2006.01195.x>
- Shefferson, R. P., Warren, R. J., & Pulliam, R. H. (2014). Life-history costs make perfect sprouting maladaptive in two herbaceous perennials. *Journal of Ecology*, *102*(5), 1318–1328. <https://doi.org/10.1111/1365-2745.12281>
- Shefferson, R. P., Weiß, M., Kull, T., & Taylors, D. L. (2005). High specificity generally characterizes mycorrhizal association in rare lady’s slipper orchids, genus *Cypripedium*. *Molecular Ecology*, *14*(2), 613–626. <https://doi.org/10.1111/j.1365-294X.2005.02424.x>

- Shefferson, R., Proper, J., & Beissinger, S. (2003). Life history trade-offs in a rare orchid: the costs of flowering, dormancy, and sprouting. *Ecology*, *84*(5), 1199–1206. [https://doi.org/10.1890/0012-9658\(2003\)084\[1199:lhtiar\]2.0.co;2](https://doi.org/10.1890/0012-9658(2003)084[1199:lhtiar]2.0.co;2)
- Shibata, M., Tanaka, H., & Nakashizuka, T. (1998). Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. *Ecology*, *79*(1), 54–64. <https://doi.org/10.2307/176864>
- Simberloff, D. (1998). Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? *Biological Conservation*, *83*(3), 247–257. [https://doi.org/10.1016/s0006-3207\(97\)00081-5](https://doi.org/10.1016/s0006-3207(97)00081-5)
- Similä, M., & Juninen, K. (2011). *Metsien ennallistamisen ja luonnonhoidon opas [Guide for forest habitat restoration and management] Nature Protection Publications of Metsähallitus. Series B 157*. Helsinki: Erweko Painotuote Oy.
- Sjöberg, K., & Ericson, L. (1992). Forested and open wetland complexes. In L. Hansson (Ed.), *Ecological Principles of Nature Conservation* (pp. 326–351). London: Elsevier.
- Slatkin, M. (1974). Hedging ones evolutionary bets. *Nature*, *250*, 704–705. <https://doi.org/10.1038/250704b0>
- Sletvold, N., Dahlgren, J. P., Øien, D. I., Moen, A., & Ehrlén, J. (2013). Climate warming alters effects of management on population viability of threatened species: results from a 30-year experimental study on a rare orchid. *Global Change Biology*, *19*, 2729–2738. <https://doi.org/10.1111/gcb.12167>
- Smithson, A., & MacNair, M. R. (1996). Frequency-dependent selection by pollinators: mechanisms and consequences with regard to behaviour of bumblebees *Bombus terrestris* (L.) (Hymenoptera: Apidae). *Evolution*, *51*(3), 571–588. <https://doi.org/10.1046/j.1420-9101.1996.9050571.x>
- Starrfelt, J., & Kokko, H. (2012). Bet-hedging – a triple trade-off between means, variances and correlations. *Biological Reviews*, *87*(3), 742–755. <https://doi.org/10.1111/j.1469-185X.2012.00225.x>
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*(3), 259–268. <https://doi.org/10.2307/2389364>
- Stuefer, J. F., During, H. J., & de Kroon, H. (1994). High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *Journal of Ecology*, *82*(3), 511–518. <https://doi.org/10.2307/2261260>
- Suetsugu, K., & Fukushima, S. (2014). Pollination biology of the endangered orchid *Cypripedium japonicum* in a fragmented forest of Japan. *Plant Species Biology*, *29*(3), 294–299. <https://doi.org/10.1111/1442-1984.12016>
- Sun, H. Q., Cheng, J., Zhang, F. M., Luo, Y. B., & Ge, S. (2009). Reproductive success of non-rewarding *Cypripedium japonicum* benefits from low spatial dispersion pattern and asynchronous flowering. *Annals of Botany*, *103*(8), 1227–1237. <https://doi.org/10.1093/aob/mcp066>
- Suter, W., Graf, R. F., & Hess, R. (2002). Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology*, *16*(3), 778–788. <https://doi.org/10.1046/j.1523-1739.2002.01129.x>

- Swarts, N. D., & Dixon, K. W. (2009). Perspectives on orchid conservation in botanic gardens. *Trends in Plant Science*, *14*(11), 590–598. <https://doi.org/10.1016/j.tplants.2009.07.008>
- Swarts, N. D., Sinclair, E. A., Francis, A., & Dixon, K. W. (2010). Ecological specialization in mycorrhizal symbiosis leads to rarity in an endangered orchid. *Molecular Ecology*, *19*(15), 3226–3242. <https://doi.org/10.1111/j.1365-294X.2010.04736.x>
- Taylor, D. L., & Bruns, T. D. (1997). Independent, specialized invasions of ectomycorrhizal mutualism by two nonphotosynthetic orchids. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 4510–4515. <https://doi.org/10.1073/pnas.94.9.4510>
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K., & Kouki, J. (2006). Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Annales Zoologici Fennici*, *43*, 373–383. Retrieved from http://www.jstor.org/stable/23736858?seq=1#page_scan_tab_contents
- Tremblay, R. L., Ackerman, J. D., Zimmerman, J. K., & Calvo, R. N. (2005). Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biological Journal of the Linnean Society*, *84*(1), 1–54. <https://doi.org/10.1111/j.1095-8312.2004.00400.x>
- Tuljapurkar, S. (1990). Delayed reproduction and fitness in variable environments. *Proceedings of the National Academy of Science*, *87*, 1139–1143. <https://doi.org/10.1073/pnas.87.3.1139>
- Ulanova, N. G. (2000). The effects of windthrow on forests at different spatial scales : a review. *Forest Ecology and Management*, *135*, 155–167. [https://doi.org/10.1016/S0378-1127\(00\)00307-8](https://doi.org/10.1016/S0378-1127(00)00307-8)
- Valverde, T., & Silvertown, J. (1998). Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *Journal of Ecology*, *86*(4), 545–562. <https://doi.org/10.1046/j.1365-2745.1998.00280.x>
- Veríssimo, D., Fraser, I., Groombridge, J., Bristol, R., & MacMillan, D. C. (2009). Birds as tourism flagship species: a case study of tropical islands. *Animal Conservation*, *12*(6), 549–558. <https://doi.org/10.1111/j.1469-1795.2009.00282.x>
- Ward, M., Johnson, S. D., & Zalucki, M. P. (2013). When bigger is not better: intraspecific competition for pollination increases with population size in invasive milkweeds. *Oecologia*, *171*(4), 883–891. <https://doi.org/10.1007/s00442-012-2463-0>
- Willems, J. H., & Dorland, E. (2000). Flowering frequency and plant performance and their relation to age in the perennial orchid *Spiranthes spiralis* (L.) Chevall. *Plant Biology*, *2*(3), 344–349. <https://doi.org/10.1055/s-2000-3707>
- Williams, J. L., Jacquemyn, H., Ochocki, B. M., Brys, R., & Miller, T. E. X. (2015). Life history evolution under climate change and its influence on the population dynamics of a long-lived plant. *Journal of Ecology*, *103*(4), 798–808. <https://doi.org/10.1111/1365-2745.12369>

- Worley, A. C., & Harder, L. D. (1996). Size-dependent resource allocation and costs of reproduction in *Pinguicula vulgaris* (Lentibulariaceae). *Journal of Ecology*, *84*, 195–206. <https://doi.org/10.2307/2261355>
- Worley, A. C., & Harder, L. D. (1999). Consequences of preformation for dynamic resource allocation by a carnivorous herb, *Pinguicula vulgaris* (Lentibulariaceae). *American Journal of Botany*, *86*(8), 1136–1145. <https://doi.org/10.2307/2656977>
- Zimmerman, J. K. (1990). Role of pseudobulbs in growth and flowering of *Catasetum viridiflavum* (Orchidaceae). *American Journal of Botany*, *77*(4), 533–542. <https://doi.org/10.2307/2656977>

List of original publications

- I Hurskainen, S., Jäkäläniemi, A., Kaitala, V., Kull, T., Mötler, M., Ramula, S., & Tuomi, J. (2017). Temporal cycles and spatial asynchrony in the reproduction and growth of a rare nectarless orchid, *Cypripedium calceolus*. *Botanical Journal of the Linnean Society*, 183(2), 316-326.
- II Hurskainen, S., Alahuhta, A., Hens, H., Jäkäläniemi, A., Kull, T., Shefferson R.P., & Tuomi, J. (in press). Prolonged dormancy in orchids incurs absolute and relative costs in large, but not in small plants. *Botanical Journal of the Linnean Society*.
- III Hurskainen, S., Jäkäläniemi, A., Ramula, S., & Tuomi, J. (2017). Tree removal as a management strategy for the lady's slipper orchid, a flagship species for herb-rich forest conservation. *Forest Ecology and Management*, 406, 12-18.

Reprinted with permission from Oxford University Press (I, II) and Elsevier (III).

Original publications are not included in the electronic version of the dissertation.

ACTA UNIVERSITATIS OULUENSIS
SERIES A SCIENTIAE RERUM NATURALIUM

711. Lehosmaa, Kaisa (2018) Anthropogenic impacts and restoration of boreal spring ecosystems
712. Sarremejane, Romain (2018) Community assembly mechanisms in river networks : exploring the effect of connectivity and disturbances on the assembly of stream communities
713. Oduor, Michael (2018) Persuasive software design patterns and user perceptions of behaviour change support systems
714. Tolvanen, Jere (2018) Informed habitat choice in the heterogeneous world: ecological implications and evolutionary potential
715. Hämälä, Tuomas (2018) Ecological genomics in *Arabidopsis lyrata* : local adaptation, phenotypic differentiation and reproductive isolation
716. Edesi, Jaanika (2018) The effect of light spectral quality on cryopreservation success of potato (*Solanum tuberosum* L.) shoot tips *in vitro*
717. Seppänen, Pertti (2018) Balanced initial teams in early-stage software startups : building a team fitting to the problems and challenges
718. Kinnunen, Sanni (2018) Molecular mechanisms in energy metabolism during seasonal adaptation : aspects relating to AMP-activated protein kinase, key regulator of energy homeostasis
719. Flyktman, Antti (2018) Effects of transcranial light on molecules regulating circadian rhythm
720. Maliniemi, Tuija (2018) Decadal time-scale vegetation changes at high latitudes : responses to climatic and non-climatic drivers
721. Giunti, Guido (2018) 3MD for chronic conditions : a model for motivational mHealth design
722. Asghar, Muhammad Zeeshan (2018) Remote activity guidance for the elderly utilizing light projection
723. Hopkins, Juhani (2018) The costs and consequences of female sexual signals
724. Nurmesniemi, Emma-Tuulia (2018) Experimental and computational studies on sulphate removal from mine water by improved lime precipitation
725. Tyni, Teemu (2018) Direct and inverse scattering problems for perturbations of the biharmonic operator
726. Kuismin, Markku (2018) On regularized estimation methods for precision and covariance matrix and statistical network inference

Book orders:
Granum: Virtual book store
<http://granum.uta.fi/granum/>

S E R I E S E D I T O R S

A
SCIENTIAE RERUM NATURALIUM
University Lecturer Tuomo Glumoff

B
HUMANIORA
University Lecturer Santeri Palviainen

C
TECHNICA
Postdoctoral research fellow Sanna Taskila

D
MEDICA
Professor Olli Vuolteenaho

E
SCIENTIAE RERUM SOCIALIUM
University Lecturer Veli-Matti Ulvinen

E
SCRIPTA ACADEMICA
Planning Director Pertti Tikkanen

G
OECONOMICA
Professor Jari Juga

H
ARCHITECTONICA
University Lecturer Anu Soikkeli

EDITOR IN CHIEF
Professor Olli Vuolteenaho

PUBLICATIONS EDITOR
Publications Editor Kirsti Nurkkala

