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The abundance and reproductive success of the orchid *Calypso bulbosa* L. in relation to forest structure

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ABSTRACT
This seven-year study investigated the effects of forest structure and fragmentation on the Calypso orchid (*Calypso bulbosa*) (Orchidaceae). The species was found to prefer growing sites in the interior of the forest and near small openings. Proximity to clear-cuts and to openings had no effect on reproductive success. High canopy cover and shrub cover reduced the number of plants, while high shrub cover reduced the number of flowering plants. This in turn may affect the behaviour of bumblebees (*Bombus* spp.), the main pollinators of the Calypso orchid, and their ability to find and pollinate a plant. The number of flowering and pollinated plants was higher in large populations than in small ones. The long-term reproductive success of large populations, as measured by flower and fruit production, was more stable than that of small populations. Despite its status as a strictly protected species, the Calypso orchid is threatened by forest management, particularly in privately owned forests. Nature-friendly harvesting methods, such as selection harvesting and small-gap harvesting without soil preparation, may prove to be appropriate forest management practices in the species' sites.

RÉSUMÉ
Cette étude sur sept ans s'est intéressée aux effets de la structure forestière et de la fragmentation sur le calypso bulbeux (*Calypso bulbosa*) (Orchidaceae). L'espèce préfère les sites au cœur des forêts et près de petites ouvertures. La proximité de coupes totales et d'ouvertures du couvert forestier n'avait pas d'effet sur le succès reproducteur. Un couvert élevé d'arbres et d'arbustes diminue le nombre de plantes, tandis qu'un couvert élevé d'arbustes diminue le nombre de plantes en floraison. Cela peut affecter le comportement des bourdons (*Bombus* spp.), les principaux pollinisateurs du calypso bulbeux, ainsi que leur capacité à trouver et polliniser les plantes. Le nombre de plantes en floraison et pollinisées était plus élevé dans les grandes populations que dans les petites. Le succès reproducteur à long terme des grandes populations, tel que mesuré par la production de fleurs et de fruits, était plus stable que celui des petites populations. En dépit de son statut d'espèce protégée, le calypso bulbeux est menacé par l'aménagement forestier, particulièrement dans les forêts privées. Des méthodes d'aménagement moins intensives, telles que les coupes sélectives et par petites trouées sans préparation de sol, pourraient être plus appropriées dans les sites où l'espèce se trouve.

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Introduction

Human land use, in particular, forest management and the resulting fragmentation of forests, has a negative effect on forest biota. This includes birds, mammals, insects, and also plants (Prugh et al. 2008; Hens et al. 2017; Kotilinek et al. 2020). In particular, deforestation has been shown to result in significant habitat loss and fragmentation, which in turn poses a significant threat to the diversity and functionality of forest plant species and the ability of pollinators to function effectively in altered environments (Prugh et al. 2008; Nayak and Davidar 2010; Potts et al. 2010). Forest fragmentation reduces the size of plant populations and increases the degree of population isolation, which also affects plant–animal interactions and ultimately reduces overall plant fitness (Damschen et al. 2006; Tsaliki et al. 2010; Kotilinek et al. 2020).

Orchidaceae is a family of plants with a very high diversity of species. Orchids are cosmopolitan plants, occurring on all continents except Antarctica and in almost all habitats, from arctic-alpine zones to equatorial rainforests. The greatest diversity is found in the humid tropics. This is reflected in the fact that about 70% of the species in the tribe are epiphytes (Nilsson 1992; Chase 2005). Orchids are one of the most threatened plant families in the world. Conservation of these species requires comprehensive studies of their ecology and habitat requirements, and long-term demographic studies are particularly valuable in this regard.

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The Calypso orchid (*Calypso bulbosa*, Orchidaceae) is a species threatened by forest management, with about half of the Finnish population occurring in state forests and the rest in private forests. A total of 47% of the existing Calypso habitats are located in nature reserves or protected areas; 44% of the habitats are located within Natura-2000 sites (Paalamo et al. 2009). In addition, sites within state forests that are not located within protected areas are also well conserved, as the relevant information is stored in the information system used to plan the actions to be taken to conserve these sites.

In private forests, the Finnish Forestry Act (Ministry of Agriculture and Forestry 1996) protects growing sites of Calypso orchid to some extent. Nevertheless, growth sites on private land outside protected areas (30% of all sites) remain vulnerable to the effects of forest management activities, as these sites may not be identified. In the long term, threats associated with land use (e.g., land clearing, timber harvesting, mining, roads and recreational facilities) will persist. However, these threats will generally affect only a small proportion of growth sites.

The objective of this study was to obtain insight into the habitat requirements of the Calypso orchid through a long-term study. The aim was to find out how forest structure and fragmentation affect the occurrence and reproduction of the species.

Material and methods

Study species

The Calypso orchid is a perennial plant species with a circumboreal distribution (Hultén and Fries 1986). It is characterised by self-compatibility and non-autogamy (Mosquin 1970; Ackerman 1981; Alexandersson and Ågren 2000). It is a rare and fully protected species in Finland and is one of the vascular flora species listed in Annexes II and IV of the EU Habitats Directive (Council Directive 92/43/EEC).

The Calypso orchid is restricted to the northern part of Finland, where it grows in calcareous, nutrient-rich, mesic to moist spruce (*Picea abies* (L.) H. Karst.) and spruce-pine (*P. abies*-*Pinus sylvestris* L.) forests. The plant produces a single leaf from an underground corm in late summer. In spring, flowering plants develop a 4–15 cm inflorescence consisting of a single flower with a pink tepal. The flower has a pouch-like lip and a two-cornered spur. The Calypso orchid flowers for about three to 4 weeks in late May or early June. If not pollinated, the flower can remain open for up to 2 weeks. After pollination, the flower usually withers within 4 days (Proctor and Harder 1995). The fruit ripens in late July and contains a large number of seeds (Kirillova and Kirillov 2023). The leaf undergoes a process of senescence, while the fruit is developing. A new corm is formed in August from which a new leaf is produced towards the end of the growing season (Kozhevnikova and Vinogradova 1999).

Study design

The study area was located in the south-western part of the province of Lapland at about 66° 10′ N, 24° 80′ E. The area consisted of mesic moist spruce and spruce-pine forests. The ground vegetation included *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Gymnocarpium dryopteris* (L.) Newm., and frequently *Geranium sylvaticum* L. and other vascular plants. To quantify the relationship between forest structure and site preference and reproductive success (number of flowering and fruiting plants), a seven-year study (2004–2010) was conducted on 55 populations of Calypso orchid, representing a wide range of population sizes.

The selection of study sites was based on the criterion of a minimum distance of 500 m between study sites. At each study site, an orchid local population was defined as a group of plants separated by a minimum of 100 m from the nearest conspecific. This ensured that populations were clearly distinct. Population boundaries and size were estimated by a systematic survey of the study site, where individual plants were identified and mapped using GPS. The study included 55 populations of different sizes: large (over 100 plants; $N = 21$); medium (21–100 plants; $N = 18$); and small (1–20 plants; $N = 16$). During the study, eight populations were destroyed by forest logging.

In each of the 55 populations, a 4 × 4 m sampling frame was placed in the centre of the plant group. The number of plants in a frame was a reliable indicator of population size, as frames placed in larger populations contained more plants than those placed in smaller populations ($F = 40.2$, $df = 2$, $p < 0.01$). In the field, a sampling frame was delineated using four 50 cm poles placed at each corner of the frame.

Each sampling frame was visited twice a year: once during the flowering season (late May and early June) and once close to fruit ripening (late July). The number of above-ground shoots and the status (flowering or vegetative) was recorded during the flowering season. In each year, the location of flowering plants within the frame was marked with small plastic markers. For each frame, the total number of flowering plants, the total number of non-flowering plants and the number of plants that produced a mature fruit were recorded. The potential effects of herbivory, frost and drought were observed. In general, flowers damaged by frost quickly turn black, while those affected by drought have a shrivelled and brown appearance. In this study, all damage observed was caused by herbivores, with no evidence of frost or drought damage.

Vegetation characteristics

Forest structure was measured using the relascope method (Bitterlich 1984). The characteristics measured were tree basal area (m^2/ha), mean stem diameter (cm) at breast height (1.5 m) and mean stem height (m) by tree species (spruce, pine, deciduous tree). Tree basal area is the area of a given land occupied by the cross-section of tree stems and trunks at their base. Measurements of diameter were taken at breast height (DBH) for each tree, including the bark. To estimate the basal area of a tree, the following formula was used: basal area = 0.00007854 × DBH^2. The resulting value is expressed in $m^2\ ha^{-1}$ (Bitterlich 1984). All forest structure measurements were derived from an area with a radius of 50 m from the centre of a Calypso sampling frame.

Within each sampling frame, the percentage of shrub cover (height <0.5 m) was estimated visually. Tree canopy cover (%) was measured at 10 points. Nine points were distributed in a regular pattern around the circumference of a 50 m radius forest structure measurement circle located in the centre of the frame. In addition, one point was located directly above the central point of the frame. To quantify the degree of tree shading, the canopy cover was measured at each point using a sighting tube (11.2 × 4.5 cm). The mean of these 10 points was used as a measure of canopy cover for each sampling frame.

The distance of each sampling frame to the nearest large clear-cut of several hectares was determined (5–≥100 m). The presence of a small opening (diameter max. 20 m) in the forest in the immediate vicinity of a sampling frame was recorded (0/1). In addition, the presence of decayed wood on the ground in a sampling frame was documented (0/1). Some empirical observations have indicated a possible preference for Calypso orchids to grow on highly decayed wood.

Statistical analyses

Mixed models were used to examine the relationships between total number of plants, number of flowering plants, fruit production and habitat structure. Total number of plants, number of flowering plants and number of fruit-bearing plants in populations were treated as dependent variables. Habitat variables and population size were treated as fixed variables, while year was treated as a random variable. ANOVA was used to test for homogeneity of variances. All statistical analyses were performed using IBM SPSS Statistics 29.0.0.0. The reported significance level is $p < 0.05$.

Results

The mean percentage of flowering plants was 30.11%, ± S.D. = 21.10, the mean percentage of flowering plants bearing fruit was 28.84%, ± S.D. = 28.91 and the mean percentage of plants bearing fruit per total number of plants was 9.28%, ± S.D. = 13.45. In general, the number of flowering and fertile plants was higher in the large populations than in the small populations (Tables 1, 3 and 4), although the percentages were not different ($p > 0.1$). However, compared to the large populations, there was more annual variation in the small populations in the percentage of flowering plants, the percentage of flowers bearing fruit and the percentage of plants bearing fruit per total number of plants, all $p < 0.001$ (Levene's test for homogeneity of variances, Table 1). Only a small amount

Table 1. Reproductive parameters of populations of different sizes as described by the percentage of flowering plants, the percentage of flowers bearing fruit and the percentage of plants bearing fruit per total number of plants. N which refers to the number of plants in the sampling frames, means, standard errors (S.E.) and standard deviations (S.D.) are shown.

	N	Mean	S.E.	S.D.
Population size: small				
Flowering plants %	92	32,13	2,87	27,49
Flowers bearing fruit %	68	31,22	4,51	37,19
Plants bearing fruit %	92	10,55	2,00	19,19
Population size: medium				
Flowering plants %	116	27,00	1,63	17,60
Flowers bearing fruit %	112	29,86	2,53	26,79
Plants bearing fruit %	116	8,74	0,91	9,82
Population size: large				
Flowering plants %	136	31,39	1,59	18,56
Flowers bearing fruit %	127	26,19	2,27	25,54
Plants bearing fruit %	135	8,75	0,97	11,26

Table 2. Results of a mixed model for the total number of calypso orchid in the sampling frames and forest structure. Year as a random variable.

	Numerator df	Denominator df	F	Sig.
Intercept	1	324,7	29,8	<0.001
Decayed tree	1	324,6	10,9	0.001
Opening	1	324,6	6,2	<0.05
Distance to an open area	1	324,6	7,7	<0.01
Spruce basal area m^2/ha	1	324,6	0,0	0.873
Pine basal area m^2/ha	1	324,6	5,0	<0.05
Deciduous trees basal area m^2/ha	1	324,6	1,3	0.247
Shrub cover %	1	324,6	6,7	0.01
Tree cover %	1	324,6	4,8	<0.05

Table 3. Results of a mixed model for the number of flowering plants in the sampling frames and forest structure. Year as a random variable.

	Numerator df	Denominator df	F	Sig.
Intercept	1	65,6	9,0	<0.01
Decayed tree	1	317,0	11,9	0.001
Opening	1	317,1	2,1	0.149
Distance to an open area	1	317,1	2,5	0.116
Spruce basal area m^2/ha	1	317,2	0,8	0.367
Pine basal area m^2/ha	1	317,1	1,6	0.204
Deciduous trees basal area m^2/ha	1	317,1	0,6	0.437
Shrub cover %	1	317,1	6,1	<0.05
Tree cover %	1	317,1	1,6	0.210
Population size	2	317,1	24,8	<0.001

of leaf damage by herbivores was observed (damaged plants %, annual mean 9.34, ± S.D. = 11.30, damaged leaf area %, mean 12.01, ± S.D. = 16.63).

The number of Calypso orchids observed in the sampling frames increased from the edge of the forest towards the interior (Table 2). Furthermore, the size of the plant population did not depend on the distance of the population from the forest edge (size × distance, $p > 0.1$). About 40.0–73.7% of the populations were located in the interior of the forest, at a distance of at least 100 m from the forest edge. The number of plants was higher in sampling frames located near small openings in the forest than in more distant frames (Table 2). However, reproductive parameters were not influenced by the distance to clear-cuts or small openings (Tables 3 and 4). Plants did not favour decaying wood as a growth site nor was the number of flowering plants higher in sampling frames with decaying wood. The high percentage of shrub ($\beta = -0.281$) and tree canopy cover ($\beta = -0.393$) reduced the number of plants (Tables 2 and 3). Similarly, the high percentage of shrub cover ($\beta = -0.075$) reduced the number of flowering plants (Table 3).

Discussion

The presence of large canopy cover and shrub cover reduced plant abundance and reproductive success. It can be difficult for pollinating bumblebees to find plants when they are under dense foliage. Canopy cover has been shown to have a significant influence on the incidence of fruit failure, which is more pronounced under a dense canopy (Abeli et al. 2013). Calypso orchid also preferred sites near small openings in the forest, which may be due to favourable exposure conditions within the forest.

Table 4. Results of a mixed model for the total number of plants producing fruit in the sampling frames and forest structure. Year as a random variable.

	Numerator df	Denominator df	F	Sig.
Intercept	1	136,3	14,9	<0.001
Decayed tree	1	316,0	4,3	<0.05
Opening	1	316,1	0,6	0.435
Distance to an open area	1	316,1	0,7	0.415
Spruce basal area m^2/ha	1	316,1	1,1	0.306
Pine basal area m^2/ha	1	316,1	2,2	0.136
Deciduous tress basal area m^2/ha	1	316,0	1,0	0.331
Shrub cover %	1	316,0	2,8	<0.10
Tree cover %	1	316,0	0,9	0.320
Population size	2	316,1	12,2	<0.001

Despite possibly better light conditions at the forest edges, the Calypso orchid appeared to prefer the interior of the forest as a growth site. Microclimatic conditions may be more conducive to plant viability in the interior of the forest, as forest edges of large open areas often have more extreme and variable microclimates than interior areas (Matlack 1993). The calypso habitats are typically characterised by microclimatic moisture and shade, with a dominance of spruce. Such an environment also provides an abundance of large trees that facilitate mycorrhizal root formation. The Calypso orchid can form a mycorrhizal root with several fungal species (Currah 1987; Currah et al. 1987), which are subsequently digested by specialised plant cells (Arditti et al. 1981; Currah 1987; Currah et al. 1987; Vinogradova and Andronova 2002).

The presence of the Calypso orchid in the interior of the forest is corroborated by the presence of blueberries (*Vaccinium myrtillus* L.) in the same habitats. The blueberry, which flowers concurrently with the Calypso orchid, serves as a crucial source of nectar for bumblebees, which also facilitate pollination of Calypso orchids (Wollin 1975; Alexandersson and Ågren 1996). The Calypso orchid has nectarless flowers and a deceptive pollination system (Mosquin 1970; Wollin 1975; Ackerman 1981). The pink colour of the calypso flower imitates that of the blueberry flower and gives off a sweet scent (Wollin 1975). Many insect-pollinated plant species attract their pollinators with rewards, usually nectar or pollen, or a combination of the two. In the case of a nectarless plant, proximity to a nectar-rich species may prove beneficial, as postulated by the magnet species theory (Lammi and Kuitunen 1995).

The annual variation in reproductive parameters was more pronounced in small populations than in large populations. This shows that large populations have greater viability over time than smaller ones. It has been shown that bumblebees prefer larger populations and that an increase in the number of flowering plants in orchids leads to an increase in both total pollinia removal and seed production of the population (Mustajärvi et al. 2001; Vallius et al. 2007; Hens et al. 2017). There is expected to be a correlation between the level of population genetic diversity and both population size and long-term population viability (Alexandersson and Ågren 2000; Hens et al. 2017). The lifetime seed production of the Calypso orchid may be limited by pollen limitation (e.g., Alexandersson and Ågren 1996). It is therefore important to understand how pollinators can function in a human-modified and fragmented environment.

This study suggests that the forest edge effect has an influence on the persistence of the Calypso orchid but not on its reproductive success. However, the study did not assess the direct effect of forest patch size on populations. A common consequence of habitat fragmentation is a reduction in habitat patch area and the resulting reduction in population size. Fragmentation may affect the reproductive success of Calypso orchid, as the reproductive success of small populations was more unstable than that of large populations. This in turn may reduce the long-term survival of small populations in fragmented habitats.

Conservation of the Calypso orchid has focused on protecting plant populations, designating protected areas, and conducting surveys (Alavuotunki and Ulvinen 1992; Ryttäri et al. 2001). However, no active management strategies or plans have been proposed for the Calypso orchid. In the conservation of endangered plant species, it is also important to ensure the pollination success of the plant by improving the living conditions of pollinators (Sipes and Tepedino 1995; Sun et al. 2006). When considering habitat, it is important to consider land use planning and management of food plants and nesting sites (Sipes and Tepedino 1995). It is also clear that the conservation of the Calypso orchid should take into account its pollinators and assess the impact of herbivory on the plant.

Conclusion

The implementation of intensive forest management practices, particularly clear-cutting with extensive soil preparation, results in changes in forest habitat and quality, which in turn results in the extirpation of Calypso orchids from logged sites. In principle, many Calypso sites in private forests are protected by the Forest Act. However, not all private land can be set aside as protected areas to conserve the species, so the Calypso orchid should be considered in forest management. Therefore, it may be advisable to consider the use of nature-friendly harvesting methods, such as selection harvesting and small gap harvesting without soil preparation, as a means of minimising the effect of forest management activities on calypso occurrences in private forests. By using these methods on Calypso sites, it may be possible to maintain the sites in a condition suitable for the plant, despite the presence of forest management activities.

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