Folia Geobot (2015) 50:13–23
DOI 10.1007/s12224-015-9212-1

Population size and reproduction in the declining endangered forest plant *Chimaphila umbellata* in Sweden

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Received: 4 June 2014 / Accepted: 10 March 2015 / Published online: 16 May 2015

Abstract The rare forest plant *Chimaphila umbellata* (Ericaceae) has decreased drastically during the last century, approximately by 80 % in some regions in Sweden. We examined associations between various biotic and abiotic conditions related to changes in forest management and nitrogen deposition, and *C. umbellata* population size, flowering frequency, fruit set and seed production. Environmental conditions at 38 *C. umbellata* sites in the provinces of Uppland and Södermanland, Sweden, included light inflow, cover of competitive species, soil nitrogen, continuity of forest cover and soil texture. The results suggested that population size was negatively affected by cover of competitive species. Population size was not related to light availability although increased shading was associated with decreased flowering frequency. Fruit set was negatively affected by cover of competitive species, and seed production decreased with increasing soil nitrogen content. Fruit set and seed production increased with increasing population size. This study shows that denser forest stands and increased abundance of *Vaccinium myrtillus* and graminoid species may have strong negative effects on *C. umbellata*. This species' longevity and clonal propagation may buffer some negative impacts, which in turn might contribute to an extinction debt. To maintain viable populations of *Chimaphila umbellata* in Swedish forests, there is a need for targeted management in forest habitats, i.e. reintroducing moderate disturbance regimes to reduce competition and increase light inflow.

Keywords clonal plants · demography · dust seeds · forest management · fruit set · plant conservation · seed production

Introduction

The gradual introduction of modern forest management in Sweden at the beginning of the 20th century combined with intensified forestry after the 1950s has entailed major transformations of forest ecosystems. Previously, Swedish forests were subjected to small-scale management actions like occasional clearing and burning, and forest ecosystems were subjected to natural fire regimes (Ericsson et al. 2000). In modern forests, wildfires are suppressed (Ericsson et al. 2000), and modern management with practices like clear-cutting, thinning, fertilization, draining, and planting pine and spruce have resulted in stands that are relatively dense, young, even-aged and single-layered, and dominated by a single tree species, i.e. Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* L.; Östlund et al. 1997). Grazing of livestock in forests was banned in Sweden 1928, but continued to some extent until the middle of the 20th century, when the practice was eventually

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abandoned (Eriksson and Cousins 2014). These changes in management have resulted in the fast regrowth of forests and hence darker understorey conditions (Maad et al. 2009). Light availability in forests has been further reduced by the large-scale planting of Norway spruce, a late-successional species with a great shading capacity (Hedwall et al. 2013). Furthermore, clearcut logging has been found to influence the species composition and diversity of ectomycorrhizal fungal communities (Jones et al. 2003).

Beside the changes in land use, a large increase in atmospheric emissions of nitrogen and sulfur compounds have also influenced the forest field layer. The atmospheric deposition of nitrogen as well as the resulting nutrient input into terrestrial and marine ecosystems has risen sharply since the 1950s (Bobbink et al. 2010). Swedish boreal forests are nitrogen-limited, and species native to these habitats are hence adapted to low levels of nutrients (Tamm 1991). The deposition of nitrogen in East Central Sweden was 200–500 mg/m^2 in 2011 (SMHI 2013). Input of nutrients alters the species composition due to differences in competitive ability, i.e. species adapted to environments with nutrient limitations are replaced with species that can utilize high nutrient levels (Kellner and Redbo-Torstensson 1995). Shifts from a lichen-dominated flora to dominance of a dwarf shrub flora, like *Vaccinium* species, and eventually to graminoid species have been documented (Tamm 1991; Kellner and Redbo-Torstensson 1995; Strengbom et al. 2001; Manninen et al. 2009).

Thus, present forest management regimes disfavour species that are dependent on features of old-growth forests and those adapted to forests with a sparse tree cover and lighter conditions, and this has led to a reduction in many forest species populations and biodiversity loss (Berg et al. 1994; Östlund et al. 1997; Bengtsson et al. 2000; Larsson and Thor 2010). There are currently 2,131 species associated with forest habitats on the Swedish national red data list, corresponding to 52 % of the listed species (Gärdenfors 2010).

Maad et al. (2009) reported changes in plant species distribution in the province of Uppland in eastern Sweden (Fig. 1) during the last century. The study included 451 species from various habitats, of which seven were restricted to coniferous forests: *Pulsatilla vernalis* (L.) Mill., *Geranium lanuginosum* Lam., *G. bohemicum* L., *Diphasiastrum complanatum* (L.) Holub, *Arctostaphylos uva-ursi* (L.) Sprengel, *Monotropa hypopitys* L. and *Chimaphila umbellata* (L.) W.P.C. Barton. The results show a sharp and statistically significant decline in these species, except for *M. hypopitys*, of 40 % on average. One of the largest reductions was observed in *Chimaphila umbellata* (Pipsissewa, Sw. Ryl, tribe Pyroleae, Ericaceae), which had decreased with 75–81 % in Uppland since the beginning of the 20th century. Declines of *C. umbellata* and additional forest species are reported also for the province of Södermanland, south of Uppland (Rydberg and Wanntorp 2001), and it is likely that a similar decline occurs across the distribution range of *C. umbellata* in Sweden. *Chimaphila umbellata* is currently red-listed as endangered in Sweden (Gärdenfors 2010), and it is suggested to become classified as vulnerable in the IUCN European regional assessment (D. Allen, IUCN, pers. comm.).

In this study, we have investigated the population size and reproduction of *C. umbellata*. The main objectives were: (1) to examine the effects of biotic and abiotic conditions on *C. umbellata* populations with regard to population size, plant reproduction (flowering frequency, fruit set, seed production) and plant growth (leaf length). The examined conditions included: (i) light inflow, (ii) cover of *Vaccinium myrtillus* L. and graminoid species, (iii) soil nutrients, (iv) continuity of forest cover, and (v) soil texture; (2) to examine the impact of *C. umbellata* population size on fruit set and seed production; and (3) to suggest management actions to promote maintenance of *C. umbellata* as a representative of species declining under current forestry regimes.

Material and methods

Study species

The genus *Chimaphila* is placed in the tribe Pyroleae along with the genera *Pyrola*, *Orthilia* and *Moneses* within the family Ericaceae (Kron et al. 2002). It consists of seven species (Freudenstein 1999), of which one, *C. umbellata*, occurs in Sweden. The distribution in Sweden is limited to the southern and central parts, with the northern range found along the eastern coastline (62°33′N; Delin 2013).

Chimaphila umbellata is a perennial evergreen dwarf shrub, 10–20 cm in height. Its leaves are coriaceous, bright green and shiny, shallowly serrated and typically arranged in whorls, in general two on each stem. The

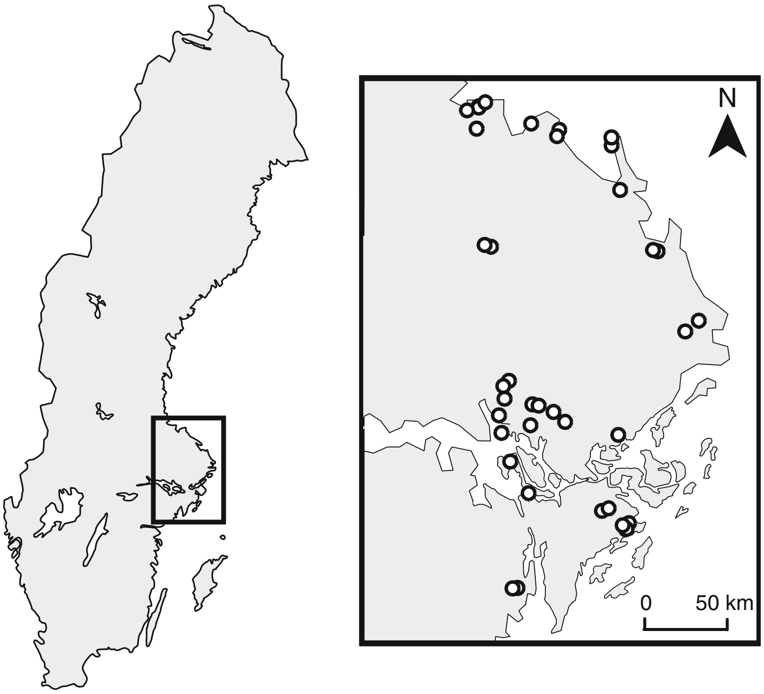

Fig. 1 The 38 study sites of *Chimaphila umbellata* in the provinces of Uppland and Södermanland, Sweden.

long, creeping rhizome is yellowish with growths of thin roots, and the shoot produces 3–6 pink flowers in an umbel (Fig. 2; Warming 1918). *Chimaphila umbellata* reproduces both by seeds and clonally by rhizomes. Thus, a population consists of one or more genets (genetic individuals) that are producing vegetative ramets (Fig. 2). *Chimaphila umbellata* produces nectar and is mainly pollinated by bumblebees, but is not buzz-pollinated as other members of the Pyroleae studied (Knudsen and Olesen 1993).

All species of the tribe Pyroleae have extremely small dust seeds, which are produced in large numbers (Eriksson and Kainulainen 2011). Johansson et al. (2014) estimated the seed production in six members of the Pyroleae species and found the highest number in *C. umbellata*, with an average of around 7,800 seeds/capsule. Seeds of *C. umbellata,* with a mean size of 0.55 × 0.10 mm, are among the smallest of the Pyroleae (Johansson et al. 2014). Due to their small size, dust seeds contain only a minimal nutrient reserve, and are

Fig. 2 Morphology in *Chimaphila umbellata* (from left to right): rhizome with ramets (vegetative units), flowers and fruit capsules.

hence dependent on fungal hosts to germinate and develop into seedlings. All species belonging to the Pyroleae with the exception of *Pyrola aphylla* Sm. (Hynson et al. 2009) are photosynthetic as adults. This strategy is termed partial mycoheterotrophy and enables the species to establish in deeply shaded understorey habitats (Tedersoo et al. 2007; Zimmer et al. 2007; Selosse and Roy 2009). Whether *C. umbellata* continues to parasitize on fungi as an adult is unclear. Hynson et al. (2012) found no support for carbon gain in the species, and Johansson et al. (2015) also supports that *C. umbellata* is fully autotrophic as an adult. However, Zimmer et al. (2007) reported that 40 % of the nitrogen in leaves of *C. umbellata* was gained from fungi.

The habitat preference of the species is generally described as sparse pine forests or old-growth boreal forests and on sandy, calcareous and nutrient-poor soils (Rydberg and Wanntorp 2001; Jonsell 2010). An analysis of the geographic distribution of *C. umbellata* in the provinces of Uppland and Södermanland, based on findings reported to the Species Observation System (2013) of *C. umbellata* between 1913 and 2013, and in relation to soil type, supports the claims of the species' affiliation to sandy soils. Our results showed that 51 % of the reported *C. umbellata* sites were on sandy soils, 23 % on thin soils on top of bedrock, 6 % on clay soils and 11 % on mixed soils (Table 1).

Table 1 Distribution of 214 reported *Chimaphila umbellata* sites in the provinces of Uppland and Södermanland, Sweden, on various soil types. Data on soil type (scale 1:50,000) was provided by the Geological Survey of Sweden (SGU, Uppsala, Sweden, www.sgu.se). The soil type of each site was extracted using QGIS (Quantum GIS Development Team 2013).

Soil type[a]	%	n
Sandy soils[b]	51.4	110
Clay soils[c]	6.1	13
Mixed soils[d]	11.2	24
Bedrock	23.4	50
Peat	3.7	8
Other	4.2	9

[a] At 50 cm depth

[b] Sandy moraine; glaciofluvial sediment of fine sand, sand, medium sand, gravel; postglacial sediment of fine sand, medium sand to coarse sand, gravel, cobble to boulder; dunes; postglacial sand

[c] Glacial clay; postglacial fine clay; clay; sandy silty moraine

[d] Glaciofluvial sediment of coarse silt to boulder

Data collection

Findings of *C. umbellata* in Uppland and Södermanland were retrieved from the Species Observation System (2013) or obtained by personal communication from the discoverers of sites. Potential sites of *C. umbellata* populations were visited in May 2013, when the evergreen plants were relatively easy to track. In total, 38 sites were selected for the study (Fig. 1), including 34 sites with extant *C. umbellata* populations and four sites with recently extinct populations. Only sites where the estimated locations of extinct populations were certain were included.

The sites consisted of mixed coniferous forests of Scots pine and Norway spruce, to a varying extent intermixed with deciduous tree species, or pure pine stands. The most common deciduous trees included *Betula pendula* Roth., *Populus tremula* L., *Quercus robur* L. and *Sorbus aucuparia* L. Ground vegetation was typically dominated by dwarf shrubs, mainly *Vaccinium myrtillus,* but also some *Vaccinium vitis-idea* L. and *Calluna vulgaris* (L.) Hull, reindeer lichens (*Cladina* spp.), feather mosses (*Pleurozium schreberi* [Brid.] Mitt and *Hylocomium splendens* [Hedv.] Schimp.) and graminoids.

The field sites were visited on two occasions in 2013, at flowering time in July and at fruit set in September. At the first visit, the *C. umbellata* population was delineated and patch area measured. When sites consisted of multiple patches, the one that was estimated to have the largest population size was chosen. All shoots, as well as all flowering shoots, were counted. At one site, the population was very large and the flowering frequency high. In this case, all shoots were counted, but to estimate flowering frequency, 100 shoots were sampled by placing a one-metre stick through the patch and at every 10th cm, noting whether the shoot closest was flowering or not. To estimate forthcoming fruit set, 25 of the flowering shoots were randomly selected, permanently marked and the number of flowers was noted. The length of the longest leaf was measured for 25 other shoots, and in large populations shoots were sampled as described above. At the second visit, the number of fruits on the marked flowering shoots was counted. From the fruit setting populations, five seed capsules were collected randomly, and the seeds were later dissolved in a solution of water and detergent to remove surface tension. From this seed solution, 10 subsamples of 50 μl were taken, and the mature seeds were counted under a microscope (5 × magnification). To calculate the total number of seeds collected from the site, the mean number of seeds in the subsamples was multiplied by the total volume of the seed solution. The seed production per capsule was then calculated by dividing the total number of seeds by the number of capsules collected from the site.

To estimate light inflow, the canopy cover was photographed at up to five locations in each study site in five directions: upwards and at 45 degrees tilt at north, west, south and east. The percentage canopy cover in the photos was analysed using the software ImageJ (Rasband 2013), and the parameter 'light inflow' was computed as 100 − (mean value of percentage canopy cover).

A mean value of cover for each species in the field layer was calculated for each site based on five randomly placed 40 × 40 cm plots. In subsequent statistical analysis, the cover of the dominating ericaceous shrub *Vaccinium myrtillus* and graminoid species was grouped together. The following graminoids were identified: *Agrostis capillaris* L., *Agrostis vinealis* Schreb., *Calamagrostis arundinacea* (L.) Roth., *Carex digitata* L., *Carex* spp., *Carex vesicaria* L., *Dactylis glomerata* L., *Deschampsia cespitosa* (L.) P. Beauv., *Deschampsia flexuosa* (L.) Trin., *Festuca ovina* L., *Luzula pilosa* (L.) Willd., *Luzula* spp., *Melica nutans* L. and *Poa nemoralis* L.

Increment cores were taken at breast height from the three thickest trees within a 5-metre radius of the *C. umbellata* population, using an increment borer. The age of the oldest tree was included in the statistical analysis to account for minimum forest cover continuity.

Soil samples were collected at three locations in each study site, at approximately 10 cm depth, and pooled to a total of approximately 0.4 dm^3. The samples were kept frozen to halt microbial activity and avoid evaporation of gaseous nitrogen. Amounts of ammonium nitrogen (mg/100 g dry mass) and nitrate nitrogen (mg/100 g dry mass) were analysed by an accredited laboratory (Eurofins, Kristianstad, Sweden, http://eurofins.se) and summarized to total soil nitrogen (mg/100 g dry mass).

Soil texture samples (not the same samples as above) were collected at three locations within each site, at approximately 10 cm depth, and analysed by sieving and weighing the different grain sizes (coarse, medium and fine sand, silt and clay; according to ISO 14688-1). The proportion of coarse grain size was calculated by adding together the weights of medium and coarse sand, and dividing the value with the total weight of the soil sample. Soil samples that consisted of mainly organic material (n = 13) were not sieved and were excluded from further analysis.

Data analyses

Before analysing the effects of the environmental conditions on *C. umbellata* populations, the data was explored for collinearity among the environmental variables (light inflow, cover of competitive species, soil nitrogen, soil texture and continuity of forest cover). Analyses showed no pair-wise correlations (Pearson's correlation coefficient < 0.7), and all environmental variables were hence used as explanatory variables in generalized linear models (GLM). The effect of soil texture was tested separately due to a lower sample size. Population size and seed production per capsule were used as response variables in GLM with a negative binomial distribution (link = log; because of overdispersion). Flowering frequency and fruit set were used as response variables in GLM with a quasibinomial distribution (link = logit; because of overdispersion). Leaf length was used as response variable in a GLM with a Gaussian distribution (link = log). The models were evaluated using a likelihood ratio test by stepwise omitting the least significant explanatory variable and testing the simplified model against the full model. Hence, explanatory variables were only included if they significantly improved the fit of the model.

To analyse the effect of population size on fruit set, we used a GLM with a quasibinomial distribution (link = logit; because of overdispersion). To analyse the effect of population size on seed production per capsule, we used a GLM with a negative binomial distribution (link = log; because of overdispersion). All analyses were performed in R 3.0.2 (R Development Core Team 2013).

Results

Population size ranged between one and 1,776 shoots at the 34 extant sites (Fig. 3a). Population density (in populations with > 10 shoots) ranged between 0.6 and 98 shoots/m^2. When aggregations of shoots occurred, densities in the densest part ranged between 11.1 and 217.9 shoots/m^2. Population size decreased with increasing cover of competitive species (Table 2, Fig. 3b). There were no relationships between population size and light inflow, soil nitrogen, continuity of forest cover or soil texture ($P > 0.05$).

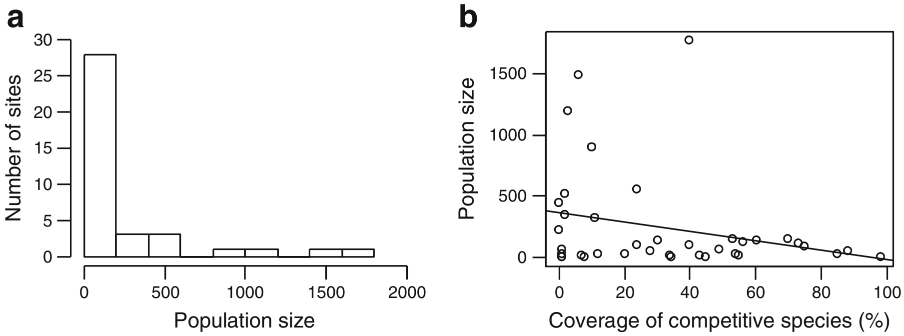

Fig. 3 **a** Distribution of population size (number of ramets) and **b** relationship between population size in *Chimaphila umbellata* and cover of competitive species (*Vaccinium myrtillus* and graminoids) at study sites in Sweden.

In the 23 flowering populations, flowering frequency ranged between 0.18 % and 38 %. Flowering frequency increased with increasing light inflow (Table 3, Fig. 4a). Flowering frequency was also affected by continuity of forest cover (Table 3), but there were no relationships between flowering frequency and cover of competitive species, soil nitrogen or soil texture ($P > 0.05$).

In the 18 fruit producing populations, fruit set ranged between 3.7 % and 100 %. It was negatively related to the cover of competitive species (Table 3, Fig. 4b), but there were no relationships between fruit set and light inflow, soil nitrogen, continuity of forest cover or soil texture ($P > 0.05$).

Seed production ranged between 1,600 and 18,960 seeds per capsule. Numbers of seeds per capsule decreased with increasing soil nitrogen content (Table 2, Fig. 4c). There were no relationships between seed production per capsule and light inflow, cover of competitive species, continuity of forest cover or soil texture ($P > 0.05$).

There were no relationships between leaf length and light inflow, cover of competitive species, soil nitrogen, continuity of forest cover or soil texture ($P > 0.05$).

Fruit set and seed production per capsule increased with increasing population size (Table 2, Table 3, Fig. 5). The significance of these relationships remained unchanged or was strengthened when only populations with a flowering frequency > 1 % were included in the analysis (Table 2, Table 3).

Discussion

There were several significant relationships between *C. umbellata* population structure and environmental factors, which we suggest indicate causes of the current decline of this endangered species. Increased competition from *Vaccinium* shrubs, particularly *V. myrtillus*, and graminoids, species that are favoured by eutrophication and cessation of forest grazing (Manninen et al.

Table 2 Effects of environmental conditions on population size and seed production per capsule, and the effect of population size on seed production per capsule, in *Chimaphila umbellata*. Results are based on GLM with a negative binomial distribution.

		Estimate	*SE*	*z* value	*Pr*(>|*z*|)
Population size	Intercept	6.11			
	~ Cover of competitive species	−2.43	0.92	−2.65	0.008
Seed production/capsule	Intercept	9.06			
	~ Soil nitrogen	−0.14	0.06	−2.56	0.010
Seed production/capsule	Intercept	8.44			
	~ Population size[a]	0.0006	0.0003	2.04	0.041
Seed production/capsule	Intercept	8.47			
	~ Population size[b]	0.0008	0.0003	2.87	0.004

[a] Including all flowering populations

[b] Including populations with a flowering frequency > 1 %

Table 3 The effects of environmental conditions on flowering frequency and fruit set, and the effect of population size on fruit set, in *Chimaphila umbellata*. Results are based on GLM with a quasibinomial distribution.

		Estimate	*SE*	*t* value	*Pr*(>|*t*|)
Flowering frequency	Intercept	−3.07			
	~ Light inflow	5.73	1.25	4.57	< 0.001
	~ Tree age	−0.02	0.007	−2.31	0.028
Fruit set	Intercept	1.36			
	~ Cover of competitive species	−2.88	1.95	−2.75	0.012
Fruit set	Intercept	−0.23			
	~ Population size[a]	0.002	0.0007	2.32	0.031
Fruit set	Intercept	−0.30			
	~ Population size[b]	0.002	0.0008	2.34	0.031

[a] Including all flowering populations

[b] Including populations with a flowering frequency > 1 %

2009), has been suggested as a cause of decline in *C. umbellata*, together with increasingly shaded conditions in forest habitats due to modern forestry practices (Rydberg and Wanntorp 2001; Maad et al. 2009). Our results support these suggestions. Cover of *V. myrtillus* and graminoid species was negatively associated with population size, indicating that *C. umbellata* may be competitively inferior to these species. However, since population dynamics were not investigated, it is not possible to identify which vital rates that underlie the observed effect on population size. Furthermore, increased productivity at sites may favour *V. myrtillus* and graminoids and at the same time disfavour *C. umbellata*, thus resulting in a spurious association between these species.

Recruitment of plants can be limited by both seed and microsite availability (Eriksson and Ehrlén 1992). A sowing experiment by Johansson and Eriksson (2013)

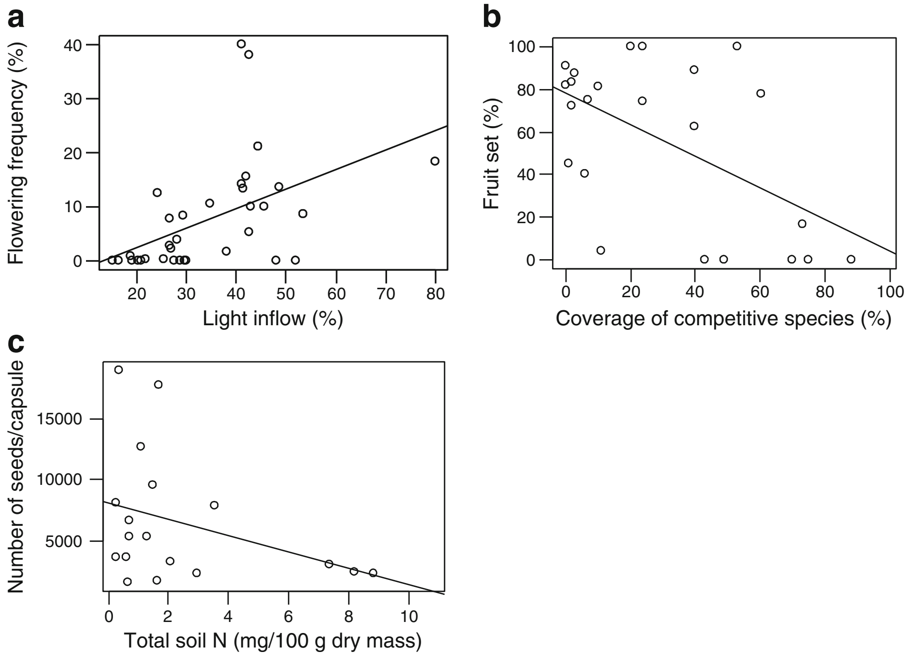

Fig. 4 Relationship between **a** flowering frequency and light inflow, **b** fruit set and cover of competitive species (*Vaccinium myrtillus* and graminoids) and, **c** seed production per capsule and soil nitrogen, in *Chimaphila umbellata* at study sites in Sweden.

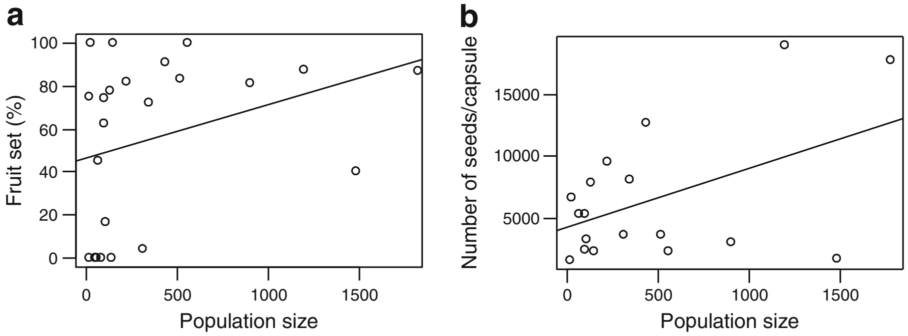

Fig. 5 Relationship between population size and **a** fruit set **b** seed production per capsule in *Chimaphila umbellata* at study sites in Sweden.

showed that microsite availability was the main limitation in *C. umbellata*, as the fraction of germinated seeds was higher at sites where adults were present (18 %) than at sites where adults were absent (8.7 %). Furthermore, increased levels of (phosphorous) soil nutrients had a negative effect on seedling size, and the authors suggest that also the continued juvenile development might be affected. Johansson and Eriksson (2013) hypothesized that the observed decline in *C. umbellata* might be caused by a reduction in microsites that meets the requirements of the species, for example competition from other species may prevent contact with suitable fungi, in turn hampering recruitment from seeds. Also clonal recruitment may be hindered if the field vegetation is too extensive, especially if perennial grasses are abundant, as they are effective competitors due to their extensive tillering and high root:shoot ratios (Wilson 1998). Furthermore, cover of *V. myrtillus* and graminoid species was negatively associated with fruit set indicating competition, or that other plants may prevent *C. umbellata* from detection by pollinators.

Population size was not associated with variation in light availability whereas flowering frequency decreased with increased shading. These results suggest that *C. umbellata* is able to propagate clonally in habitats with darker conditions, while sexual reproduction occurs to a lesser extent in such environments. The lack of flowering under low-light conditions is a common characteristic of shade-tolerant woodland species (Grime 2001) and has been reported for other clonal forest species. For example, Lezberg et al. (2001) demonstrated very limited flowering and seed production in the herb *Maianthemum dilatatum* (Alph. Wood) A. Nelson & J.F. Macbr. growing in the low-light conditions of young, dense stands when compared to populations growing in mature stands. Also, the clonal structure and reproductive strategy of *Uvularia perfoliata* L. differed in sites with open and closed canopies (Kudoh et al. 1999), where populations in gap habitats consisted of several or many genets, indicating an on-going recruitment from seeds, while populations in closed habitats more often consisted of a single genet. Kudoh et al. (1999) suggested a 'waiting strategy' in populations under closed canopies, i.e. mainly clonal reproduction until light conditions become favourable enough to initiate sexual reproduction.

There is currently no data on longevity in *C. umbellata*, but the longevity of genets in clonal plants can be substantial, with a range of genet age in clonal shrubs from approximately 50 years to many thousands years (de Witte and Stöcklin 2010). Furthermore, Ozinga et al. (2007) showed that the local aboveground persistence was extended when the clonal connections are long-lasting (> 1 year), which they are in *C. umbellata*, and woody plants have been found to have longer life spans than non-woody plants (Ehrlén and Lehtilä 2002). Life-cycle characteristics like clonality and (the likely) longevity of genets in *C. umbellata* may hence buffer population decline from habitat deterioration and a limited recruitment from seeds, and reduce the risk of local extinction. Some of the populations of the species may therefore exist as remnant populations (Eriksson 1996), i.e. they persist despite a population growth rate (λ) below 1 because of population inertia.

The possible development of remnant populations in *C. umbellata* may contribute to an extinction debt in the species, i.e. a time lag in the response to unfavourable conditions (Tilman et al. 1994; Hylander and Ehrlén 2013). There are few empirical studies demonstrating extinction debts in species, mainly due to the lack of long-term data of species losses or comparisons of similar habitats with varying land use histories (Vellend et al. 2006). One of these studies demonstrated that extinction debt persisted more than a century after forest fragmentation in slow forest species, i.e. species with low rates of population extinction and colonization (Vellend et al. 2006).

Plants growing in shaded understorey conditions of closed-canopy stands can allocate resources to leaf growth to enhance light capture (Grime 2001). However, we found no support for increased leaf length in *C. umbellata* under low light conditions. This result is similar to Lezberg et al. (2001) who studied the leaf area of *M. dilatatum* in forests with various structure and light conditions. They suggested that the lack of response might be attributed to the physiological adaptations of the species to tolerate low-light environments and that the shaded conditions were not extreme enough to initiate allocation of resources to leaves. This might apply also for this study on *C. umbellata*.

Both fruit set and seed production per capsule increased with increasing population size, suggesting an Allee effect. This may be due to pollinators being attracted to larger populations, but also reflect low genetic diversity of small populations, or simply other aspects of poor conditions at sites inhabited by small populations. Additional studies with the focus on pollination are needed in order to clarify the underlying cause of the effect of population size. Also studies including the genetic diversity of the populations would be valuable, since this is not necessarily related to ramet population size in clonal species.

Although we did not find any relationship to forest cover continuity per se, forest cover continuity is still probably an important factor for understanding the long-term development of *C. umbellata* populations. A study by Halpern and Spies (1995) found both higher persistence and greater cover of *C. umbellata* in old-growth forests (> 210 years) compared to mature and younger stands. In addition, they showed that the species was sensitive to disturbance by fire. Although one should be cautious when comparing North American and European populations of *C. umbellata*, these findings indicate that re-establishment and growth of *C. umbellata* is slow (Halpern and Spies 1995). An insufficient range in the age material could explain the limited effect of continuity of forest cover in this study – the maximum tree age recorded was 160 years. The extensive forest exploitation in the study region in the previous centuries might be the reason why no old-growth forests (> 200 years) were included in the study. Another possible reason for the lack of effect of forest cover continuity may be that we were not able to examine forest conditions and management before establishment of the oldest trees occurring at the sites.

Conclusion

Chimaphila umbellata population size decreased with increased competition from *V. myrtillus*, and graminoids and the sexual reproduction was hampered under shaded conditions, with higher abundance of *V. myrtillus* and graminoids, and increased soil nitrogen. The possible development of remnant populations, where longevity and clonal recruitment buffers the effects of unfavourable environmental conditions, might contribute to an extinction debt in the species. These results indicate the need of targeted management to restore forest habitat quality, including moderate disturbance regimes to increase light inflow and reduce competition in the field layer. Furthermore, given the general effects of euthrophication, actions for reduced large-scale emissions of nutrients are important for long-term preservation of the species.

We still know little about how *C. umbellata* associates with mycorrhizal fungi, while soil nutrient increase and clearcut logging has been shown to change the species composition of the mycorrhizal community. Additional studies, with emphasis on demography of *C. umbellata* and the identification of limiting life history stages, are needed to clarify the impacts of environmental conditions on population vital rates. Also, the assessment of potential remnant populations and extinction debt in the species is of critical importance. This approach would give a fuller understanding of extinction risks and identify management actions that would most effectively maintain viable populations of *Chimaphila umbellata*.

Acknowledgments We are grateful to V. Johansson, E. Meineri and H. Grudd for their help in conducting this study, and to two anonymous reviewers for comments on the manuscript. Thanks also to the landowners and the County Administrative Boards in Stockholm and Uppsala for permissions to conduct bores at the study sites, and to U. Johansson, A. Erixon and Å. Strid who provided information regarding *C. umbellata* sites.

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