

Performance of the endemic alpine herb *Primula scandinavica* in a changing European mountain landscape

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This paper reports on the performance of the red-listed *Primula scandinavica*, endemic to Scandinavia. The study took place in Jotunheimen, Norway. We evaluated occurrence, density and sexual reproduction variables (number of fertile individuals and number of seed capsules). Habitats were registered as land-cover categories (historical and current; broad habitat types) and habitat patch classes (semi-natural and natural; fine-grained habitat types). Spatial overlay analyses and maximum likelihood tests of generalized linear mixed models (GLMMs) were performed to assess the habitat quality of the land-cover categories and the habitat patch classes. In most (96%) of the observed occurrences the species was located at a site that had open vegetation 40 years ago but is now becoming forested or covered by shrubs. The highest densities of *P. scandinavica* were found in “heathland” and “grassland in transition into woodland”, while the potential for sexual reproduction was highest in “grassland” and lowest in “grassland in transition into woodland”. The results indicate that many of the populations in the study area are remnants and that the habitats of highest quality are semi-natural habitat patches. The changed land use practices in mountain areas have resulted and will result in fewer and smaller populations. However, as also climatic conditions will change it is not straightforward to predict the future performance of *P. scandinavica*.

Introduction

The practice of summer farming or seasonal use of vegetation has been common in most mountain regions. Summer farming is a transhumance practice in which livestock are moved on a seasonal basis from permanent farm settlements to climatically harsher environments when pasture

is available there (Bunce *et al.* 2004). These long-used farming practices have given rise to a diversity of semi-natural habitats and mountain agricultural landscapes (Dodgshon & Olsson 2007). The semi-natural habitats consist of plant species that occur naturally in the area. However, maintenance of the species composition requires disturbances, which in most cases are caused by

human activity. These semi-natural habitats are found alongside natural habitats and this results in an ecological mosaic of high landscape diversity (Olsson *et al.* 2004, 2011). Additionally, the semi-natural habitats have high α -diversity and they offer refuges for plant species that are threatened elsewhere (Olsson *et al.* 2004).

Over the last century, traditional land-use practices, such as livestock grazing in semi-natural vegetation, successively diminished throughout Europe (Olsson 2004, Halada *et al.* 2011). Abandonment of semi-natural grasslands has led to the degradation and fragmentation of semi-natural habitats (Emanuelsson 2009). This has left many grassland species that grow in semi-natural habitats under threat (Stehlik *et al.* 2007, Prévosto *et al.* 2011). Approximately 40% of the vascular plants in the Norwegian Red List grow in alpine environments and are now threatened because of changes in farming practice (Austrheim *et al.* 2010). One of those species, *Primula scandinavica*, which is also one of the few plants endemic to Scandinavia (Lid & Lid 2005), is red-listed both in Norway (Kålås *et al.* 2010) and in Sweden (Gärdenfors 2010).

Most species that are associated with semi-natural habitats are also found in natural habitats. Species survival is therefore linked to three factors; present land-use, historical land-use and the presence of suitable, natural habitats. Consequently, it is important to examine performance not only in semi-natural habitats (as related to both historical and current land-use) but also in natural habitats. Some studies have addressed the consequences of historical land-use (Mildén *et al.* 2007, Lindborg & Ehrlén 2002, Prince *et al.* 2012) but none have yet included investigations of the quality of natural habitats.

One way to rapidly assess habitat quality is to perform a one-time census (Adriaens *et al.* 2009) and assess plant performance in different habitats (Mortelliti *et al.* 2010). Here, we build upon the definition of habitat quality by Hall *et al.* (1997) as the ability of a habitat to maintain persistent populations. However, that definition does not specify a period over which the populations should be maintained and, since our results are based on one-time censuses, we categorize habitat quality according to plant densities and measurements of the potential for sexual reproduction.

The aim of this study was to assess the performance of *P. scandinavica* in different habitats in Jotunheimen, southern central Norway. The following questions were asked: (1) What is the relationship between current and historical land-use practices and the spatial distribution of *P. scandinavica*? (2) Does the density of *P. scandinavica* differ according to land-use practice and between natural and semi-natural habitat patches? (3) Does the potential for sexual reproduction differ according to land-use practice and between natural and semi-natural habitat patches?

Material and methods

Study area

Our study was carried out in eastern Jotunheimen in southcentral Norway (61°30'–61°39'N, 8°51'–9°08'E; 870–1370 m a.s.l.), where there is a long tradition of summer farming which is still practiced although it is rapidly diminishing (Olsson 2004). The climate is continental, with a mean annual temperature of -0.2 °C and a mean annual precipitation rate of 490 mm (data provided by Norwegian Meteorological Institute). A feature that now characterises this landscape is that previously open habitats are undergoing various stages of transition into forest (Wehn 2009, Wehn *et al.* 2011, 2012).

Study species

Primula scandinavica is a small (5–15 cm), long-lived rosette-forming herb that is found in open alpine vegetation and agricultural landscapes in mountainous areas (Lid & Lid 2005, Kålås *et al.* 2010, Gärdenfors 2010) in a certain type of habitat (Table 1).

Data collection

We inventoried 13 study sites in June, the month of flowering, in 2004 and 2007, and recorded the geographical positions of occurrences of *Primula scandinavica*.

The performance variables that were registered were (1) density and (2) potential for sexual reproduction, which we measured by counting the number of fertile individuals and the number of seed capsules. Statistics taken from Aarnes (2003) showed that seeds inside seed capsules of *P. scandinavica* are usually fertile (mean percentage of fertile seeds per seed capsule = 92) and so, in order to measure the number of fertile individuals, we simply counted how many individuals had seed capsules. Fertile individuals may have different numbers of seed capsules, and we observed between one and eight capsules per fertile individual. Aarnes (2003) found a constant number of seeds in the seed capsules even if the number of flowers per individual varied. We therefore assumed that the number of seeds was positively related to the number of seed capsules.

An area defined according to one kind of land use may include several habitat patches. In order to investigate both land-cover (broad vegetation types that indicate land-use) and habitat patches (fine-grained habitat classes that are either natural or semi-natural vegetation; see Table 2), performance was investigated on two scales: plots of 100 m² and squares of 0.25 m². Density was registered for 242 plots (range 1–285) and 225 squares (range 1–50). The number of fertile individuals and the number of seed capsules were registered in the squares only (range 0–4 and 0–17, respectively). The plots and squares were inventoried in June and the squares were checked again at the end of July, when the flowering season of *P. scandinavica* was over in the study area.

Using GIS and field verification, each of the plots and squares was classified into current and historical land-cover categories (in Wehn 2009; see also Table 2). The squares were also classi-

fied into habitat patch classes by field assessment (Table 2).

Analyses

The observed occurrences of the specimens (on both scales) were resampled to a resolution of 10 m × 10 m using ArcMap 10.0 (1999–2010 ESRI) and plotted on a single map to enable spatial overlay analyses with land-cover maps. The spatial overlay analyses enabled us to explore how the current and the historical land-cover had influenced the occurrence of *P. scandinavica* today. When assessing the habitat quality in current and historical land-cover and in natural and semi-natural habitat patches, we developed and compared generalized linear mixed models (GLMM's) by applying maximum likelihood tests using R 2.14.2 (R development Core team), package *lme4* (Bates & Sarkar 2006). The plots and squares (the two study units) were analysed separately. The first modelling step was to assess which GLMM approach should be achieved. To account for possible spatial autocorrelation, study unit was included as a random variable and to account for possible correlations within a study site, also study site was included as a random variable. Models including each of these random variables were tested against null models of no relation between the response and explanatory variables (a model that contained only the intercept term). If both were significant, models with both random variables were compared with the models containing only one random variable, according to Field *et al.* (2012: 879–881). GLMMs that included study unit (plot) nested in study site were assessed as the best approach at 100 m² scale and GLMMs that included only

Table 1. Potentially important habitat properties for the life history of *Primula scandinavica*.

Life history components	Potential habitat properties
Germination	patches of bare soil, access to light and soil moisture
Survival and growth	light, soil moisture, low inter- and intraspecific competition, low or absent herbivory on <i>P. Scandinavica</i>
Seed production	pollinators, low or absent seed-predation
Seed dispersal	dispersal agents
Vegetative regeneration	undisturbed bottom and field layers

Table 2. Habitats in which *Primula scandinavica* was observed and which were used as fixed factors in the modelling procedures. Current and historical (1960s) land-cover categories were registered in 100 m² plots and 0.25 m² squares. Habitat patch categories were registered in 0.25 m² squares.

Current land-cover	Historical land-cover	Semi-natural habitat patch	Natural habitat patch
grassland ¹	grassland ¹	hay meadow ²	scree
grassland ¹ in transition ³	heathland ¹	grazed heath ⁴	snowbed
heathland ¹	heathland in transition ³	pasture ²	snow-melt brooklet ⁵
heathland in transition ³	forest ¹	scrubby pasture	stream verge
forest ¹		ditch	river verge
new pasture ⁶		under power-line ⁷	
		road verge ⁸	

¹) Land-use not defined.

²) Not ploughed, not re-sown, not fertilized, established > 13 years before this study.

³) Into woodland.

⁴) By livestock.

⁵) Temporary habitat.

⁶) Not ploughed, not re-sown, not fertilized, recently established (two years ago) by logging.

⁷) One square registered; removed from the analyses.

⁸) Included no fertile individuals; all squares removed when analysing the potential for sexual reproduction.

study unit (square) as a random variable were assessed as the best approach at 0.25 m² scale.

Then we performed a stepwise model selection procedure in order to establish whether there were any interaction effects between the habitat categories (historical land-cover, current land-cover and habitat patch), density and the number of fertile individuals on the number of seed capsules.

Table 3. Shifts from historical (H; 1960s) to current (P) land-cover in study units where *Primula scandinavica* was observed during the study in eastern Jotunheimen, Norway. n_{Hi} = number of registered plots categorised as historical land-cover class i . n_{Pj}/n_{Hi} = the proportion of registered plots categorised as current land-cover class j in plots categorised as historical land-cover class i .

Historical land-cover category i (n_{Hi})	Shifts to current land-cover category j (n_{Pj}/n_{Hi})
heathland (180)	heathland in transition (0.60) heathland (0.14) forest (0.13) new pasture (0.11) grassland (0.2)
grassland (110)	grassland (0.62) grassland in transition (0.36) forest (0.2)
forest (8)	forest (0.50) new pasture (0.50)
heathland in transition (4)	grassland (0.50) heathland (0.50)

Finally, based on the above analyses, we grouped the habitats into categories and ranked them according to their quality for *P. scandinavica*. Compared with potential for sexual reproduction, density is a weak indicator of habitat quality (discussed in Mortelliti *et al.* 2010). Therefore, if results were contrasting, number of fertile individuals and seed capsules were awarded greater significance than density.

Results

We found *P. scandinavica* in all categories of land-cover from open vegetation to forest. Most (57%) of the specimens were seen in heathland that was undergoing transition into woodland. However, overlay analyses showed that almost all specimens were growing in areas designated as grassland or heathland in the historical land-cover map (Table 3).

The density of *P. scandinavica* in 100 m² plots differed significantly between the categories of current land-cover (Table 4a and Fig. 1a) but not between the categories of historical land-cover. The highest densities in the 100 m² plots were found in heathlands and grasslands that were undergoing transition to woodland. Neither historical nor current land-cover influenced the density in the 0.25 m² squares (Table 4b). However,

after categorizing habitats into more fine-grained classes we found a significantly higher number of individuals in the semi-natural habitat patches than in the natural habitat patches. Overall, there were significant differences in density between the 11 habitat patches (Table 4b and Fig. 2a). The highest density was found in road verges followed by grazed heath and semi-natural hay meadow. We found no differences among the five natural habitat patches but there was variation in density among the six semi-natural habitat patches.

While the current land-cover influenced the number of fertile individuals (Table 4b and Fig. 1b) and the number of seed capsules (Fig. 1c), historical land-cover did not. Both of the measurements of the potential for sexual reproduction were highest in grassland and lowest in grassland that was undergoing transi-

tion into woodland. Although there were no overall significant differences in the number of fertile individuals among the ten habitat patch categories, the six semi-natural habitat patches differed (Fig. 2b) when splitting the dataset into semi-natural and natural habitat patches. There was an overall difference in the number of seed capsules among the habitat-patch categories (Fig. 2c). When the dataset was divided into natural and semi-natural habitat patches, significant differences in the number of seed capsules were found only among semi-natural habitat patches. The number of fertile individuals was lowest in road verges and scrubby pasture and was highest in grazed heath, ditch and hay meadow — all of which are semi-natural habitat patches (Fig. 2b). The same was observed when examining the number of seed capsules. However, there was

Table 4. Results of maximum likelihood tests of generalized linear mixed models (GLMMs). The models in **a** are based on study units of size 100 m² (plots) and the models in **b** is based on study units of size 0.25 m² (squares). GLMMs in **a** included plot and study site as random variables and GLMMs in **b** included square as a random variable (see Material and methods: Analyses). *p* values set in boldface indicate significant results.

Explanatory variables	Response variables								
	Density			Number of fertile individuals			Number of seed capsules		
	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>
a: Land-cover									
current	17.06	5	0.004						
historical	4.86	2	0.088						
b: Land-cover									
current	5.76	4	0.218	12.62	4	0.013	10.89	4	0.028
historical	4.55	3	0.208	5.80	3	0.122	6.25	3	0.100
Habitat patch									
overall	39.68	10	< 0.001	15.44	9	0.078	21.11	9	0.012
semi-natural vs. natural	11.80	1	< 0.001	1.65	1	0.199	2.46	1	0.117
among semi-natural	23.77	5	< 0.001	15.16	5	0.010	21.27	5	< 0.001
among natural	0.37	4	0.985	0.35	3	0.951	0.19	3	0.979
Density				5.93	1	0.015	4.77	1	0.029
Number of fertile individuals							162.05	1	< 0.001
Current land-cover + number of fertile individuals ¹							0.78	1	0.377
Habitat patch + number of fertile individuals ¹							24.45	9	0.004
Density + number of fertile individuals ¹							0.09	1	0.759
Current land-cover/number of fertile individuals ¹							1.77	2	0.412
Habitat patch/number of fertile individuals ²							8.01	9	0.533
Density/number of fertile individuals ¹							12.28	2	0.002

¹) Compared with the model that included the effect of number of fertile individuals.

²) Compared with the model that included the summed effect of number of fertile individuals and habitat patches.

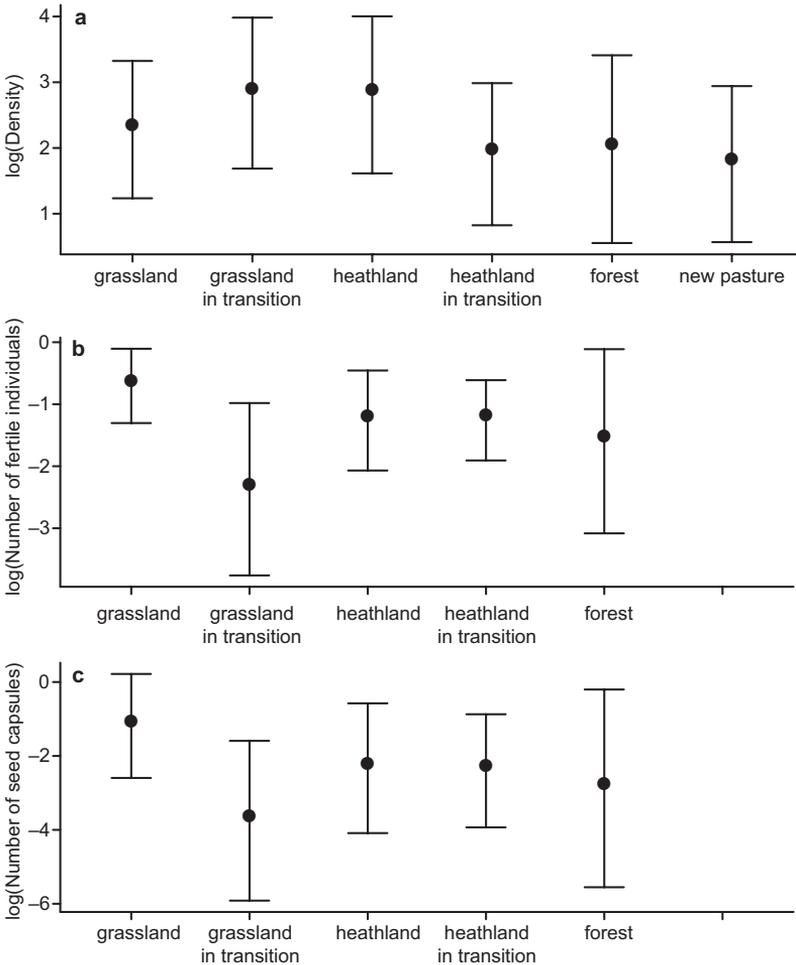


Fig. 1. Estimates and 95% confidence intervals of generalized linear mixed effect models describing significant differences between land-cover categories in (a) the density of *Primula scandinavica* in 100 m² plots [random variables: study unit (variance = 1.1023, SD = 1.0499) and study site (variance = 1.0658, SD = 1.0324)], (b) the number of fertile individuals in 0.25 m² squares [random variable: study unit (variance = 0.72375, SD = 0.85073)], and (c) the number of seed capsules in 0.25 m² squares [random variable: study unit (variance = 7.5314, SD = 2.7443)].

one difference; in pastures the number of fertile individuals was relatively high while the number of seed capsules was relatively low (Fig. 2c).

The number of fertile individuals was the most significant factor for the number of seed capsules in the 0.25 m² squares (χ^2 values; Table 4b), but both density and habitat patch category affected the relationship between the number of fertile individuals and the number of seed capsules. The ratio of seed capsules to fertile individuals increased more sharply in squares of low density than in those of high density (Fig. 3a). In pastures, there was no significant relationship between the number of fertile individuals and the number of seed capsules; in temporary snowmelt brooklets the ratio decreased according to the number of fertile individuals, and in other habitat patches the ratio increased (Fig. 3b).

We found that habitat patch categories explained more of the variance in density and the potential for sexual reproduction than the land-cover categories (by comparing χ^2 values; Table 4b). Fine-grained patterns influenced performance more than broader ones. The habitat patches judged to be of the highest quality were semi-natural hay meadow and grazed heath, while the habitat patches judged to be of low quality were scrubby pasture, scree, river verge and areas under power-lines (Table 5).

Discussion

Small-scale, semi-natural habitat patches provide the best habitats for *P. scandinavica* (Table 5). There was a significant decrease of semi-natural habitats in the mountains — an ongoing change

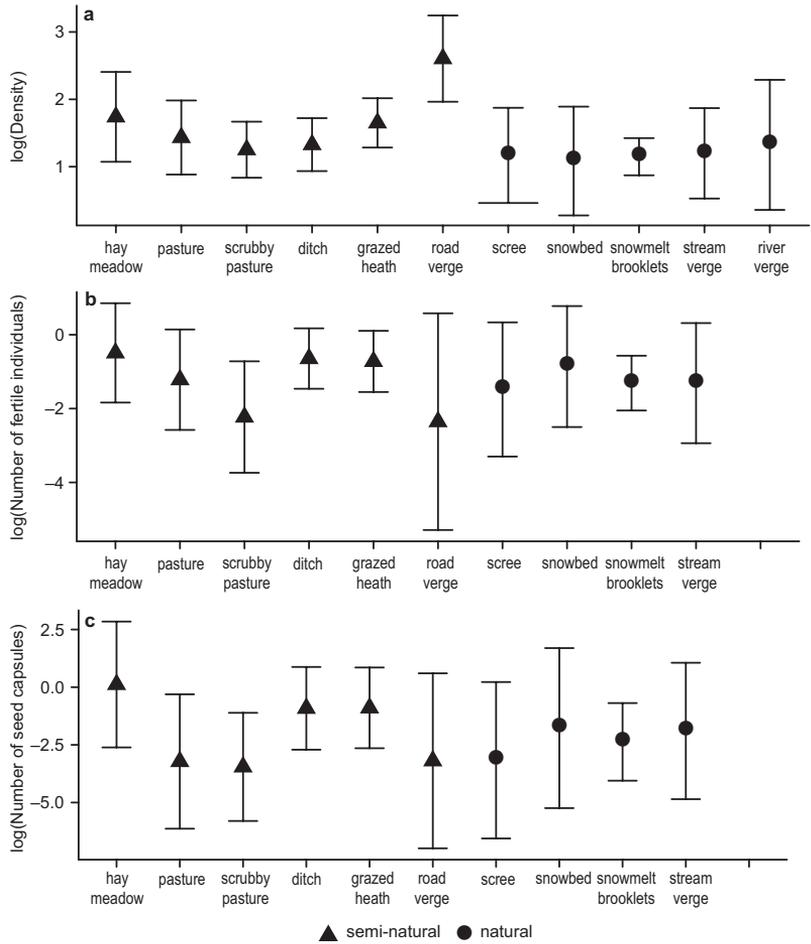


Fig. 2. Estimates and 95% confidence intervals of generalized linear mixed effect models describing significant differences between habitat patch categories in (a) the density of *Primula scandinavica* in 0.25 m² squares [random variable: study unit (variance = 0.32252, SD = 0.56791)], (b) the number of fertile individuals in 0.25 m² squares [random variable: study unit (variance = 0.6279, SD = 0.7924)], and (c) the number of seed capsules in 0.25 m² squares [random variable: study unit (variance = 6.0413, SD = 2.4579)].

in landscape that has already been documented for Scandinavian (Bryn & Hamsing 2012, Wehn *et al.* 2012) and other European mountain regions (Tasser & Tappeiner 2002, Fonderflick *et al.* 2010). *Primula scandinavica* has a scattered distribution in this mountainous region, but most (96%) of the today’s specimens were found in vegetation that had been open 40 years earlier.

Today, many of these areas are undergoing transition into forest. This means that the current distribution stems from earlier types of land-cover that resulted from traditional land-use practices. This suggests that the current distribution of *P. scandinavica* in the Jotunheimen study area may consist of remnant populations.

Remnant populations may continue to sur-

Table 5. Habitat patches grouped according to performance using the results presented in Fig. 2. Performance is a measure of habitat quality; the habitat quality increases from left to right in the table.

Low density, low sexual reproduction*	High density, low sexual reproduction*	Low density, high sexual reproduction*	High density, high sexual reproduction*
scrubby pasture scree river verge under power-line	pasture road verge	ditch snowbed stream verge snow-melt brooklets	hay meadow grazed heath

* Potential for sexual reproduction measured by the number of fertile individuals and the number of seed capsules.

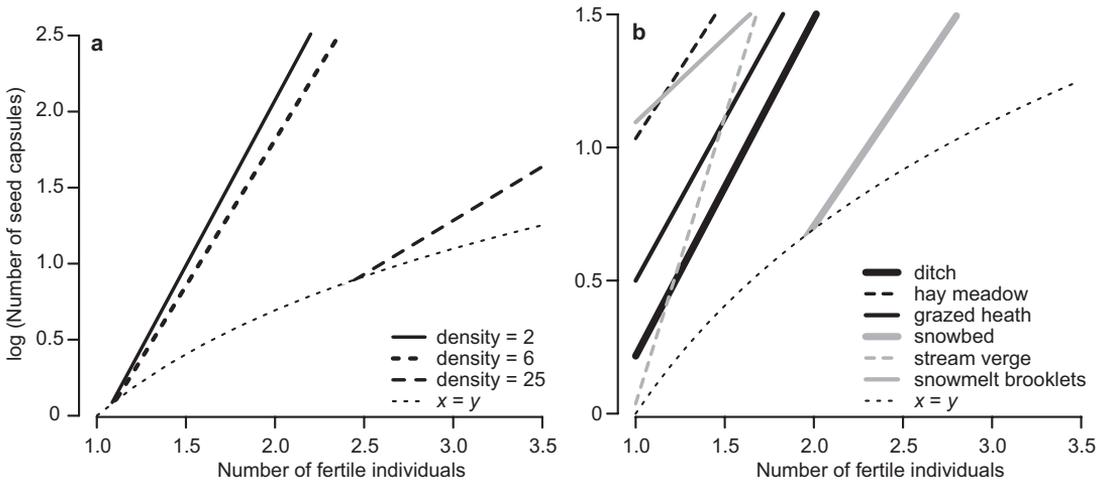


Fig. 3. Combined effects on the number of seed capsules produced by *Primula scandinavica* individuals in 0.25 m² squares, of (a) the number of fertile individuals and density, and (b) the number of fertile individuals and habitat patches. In b only those habitat patches in which there was a significant relationship between the number of fertile individuals and the number of seed capsules were included in the figure.

vive even when conditions are deteriorating (Eriksson 1996). However, if there are only remnant populations, the future risk of extinction is high because of extinction debt. As a result of habitat degradation extinctions might occur, however, with a substantial delay (Tilman *et al.* 1994, Kuussaari *et al.* 2009). Extinction may be delayed by as much as 40 years in semi-natural grasslands (Lindborg & Eriksson 2004, Krauss *et al.* 2010). Our study found high densities of *P. scandinavica* in grassland that was undergoing transition into woodland. Lindborg and Ehrlén (2002) found that shortly after grazing had been discontinued, the population of the perennial herb *Primula farinosa* underwent a period of increased growth rate. However, when they compared historical and current distributions, they found a high extinction rate in habitats that had been abandoned a long time ago (> 70 years; Lindborg & Ehrlén 2002). The increased density of *P. scandinavica* that we found in encroached grasslands may therefore be followed later by a population decrease due to greater interspecific competition.

The potential for sexual reproduction did not show the same tendency as the measurements of density alone. Our study suggests that along the gradient from open to tree-colonised vegetation, *P. scandinavica* shifts its regenerative strategy from one involving a combination of seeds and

clonal regeneration to one dominated by vegetative reproduction. Although the density was highest in grasslands that were undergoing transition into woodland, this land-cover category also yielded the lowest values for both of the variables for the potential for sexual reproduction. This means that the populations in tree-colonised areas showed a lower performance than those in open vegetation. It is advantageous to have multiple regenerative strategies in varying environments (Grime 2001). As emergence rates of fen species are shown to be negatively affected by abandonment of land-use practices (Stammel *et al.* 2006), populations may be able to persist by using vegetative reproduction (Eriksson 1996, Grime 2001). *Primula scandinavica* seeds require patches of bare soil in order to germinate (Aarnes 2003), which means that the best strategy for its survival in overgrown vegetation is that of vegetative regeneration.

Neither the frequency or distribution pattern of natural habitats in the landscape, nor dispersal agents have been studied until now and we need information about these in order to predict the future development of *P. scandinavica*. However, our findings show that it performs better in semi-natural habitats than in natural habitats (Fig. 2 and Table 5) although the differences were small. We found generally low density and poor potential for sexual reproduction in *P. scan-*

scandinavica in natural habitat patches. If seed dispersal among habitats becomes less viable as the distance between habitats increases, then population development will be at risk. In addition, in small populations there is a high risk of extinction due to demographic stochasticity (Matthies *et al.* 2004) and that risk may grow with climate change. In Scandinavia, climate change is expected to result in warmer and wetter conditions in the mountains (IPCC 2013). This could be beneficial for seed germination and seedling establishment and thus perhaps weigh against the reduction in suitable, semi-natural habitats. Sala *et al.* (2000) contended that the greatest factors influencing global biodiversity were changing land-use patterns. However, the effects of interaction between climate change and land-use changes in mountainous regions are not known.

Concluding remarks

This study attests that some semi-natural habitat patches are of better quality for *P. scandinavica* than natural habitat patches. Further, a large proportion of the populations in the Norwegian mountain Jotunheimen are remnant populations that were established when the landscape had more semi-natural habitats. There are a number of risk factors whose consequences remain unknown for the populations of *P. scandinavica* in the Scandinavian mountains.

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