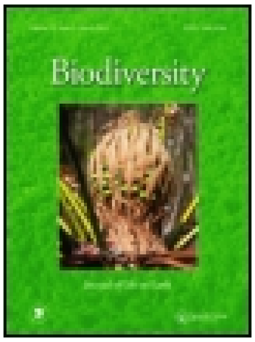

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The distribution of the endemic plant *Primula scandinavica*, at local and national scales, in changing mountainous environments

Sølvi Wehn* and Line Johansen

Norwegian Institute for Bioeconomy Research (NIBIO), Stjørdal, Norway

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Primula scandinavica is endemic to Norway and Sweden and populations are in decline due to changes in land use. Future climate change might have an additive effect on its distribution. To predict the future distribution of *P. scandinavica*, its potential suitable habitats with regard to land use and climate need to be investigated. We have generated species distribution models (SDMs) both for local (Eastern Jotunheimen) and national (Norway) scales and projected future distribution based on predicted climate and land use change. The best SDM at a national scale includes climate (temperature, precipitation, number of snow days) and elevation. The future potential distribution is projected to expand in the mountainous areas in the south and move north. At a local scale, the best SDM includes historic and present land use and livestock grazing pressure. Future distribution in the studied mountainous area is projected to decrease with continued abandonment of grazing.

Keywords: Maxent; land use; livestock grazing; climate; global warming; alpine

Introduction

Global warming is expected to change vascular plant species richness on mountains (Gottfried et al. 2012; Pauli et al. 2012) and the changes are predicted to cause many European plant species to become threatened (Thuiller et al. 2005). In addition, change in land cover is one of the strongest drivers of biodiversity change due to both climate and socio-economic changes (Sala et al. 2000). Heterogeneous spatial distribution of natural resources and centuries of human influence have caused mountain landscapes to become mosaics of different habitat types. Agriculture in remote European mountain areas has, however, decreased and traditional land use practices, such as livestock summer grazing, have diminished in the last century (Halada et al. 2011; Olsson 2004). Forest and scrub have therefore expanded into previously open habitats (Chauchard, Carcaillet, and Guibal 2007; Tasser et al. 2007; Wehn 2009; Wehn, Olsson, and Hanssen 2012; Wehn, Pedersen, and Hanssen 2011). Global warming might accelerate the effect of encroachment as tree species might be able to establish at higher elevations as well as producing more seeds (Kullman 2010). Abandonment of semi-natural grassland has reduced and altered semi-natural habitats (Emanuelsson 2009). To define the best management actions, knowledge on species distributions and which predictors influence their distribution has to be developed.

There is a hierarchy of drivers for the distribution of species in alpine areas (Carlson et al. 2013). Therefore, to detect all requirements of a species, several scales have to be examined. At a broad scale, coarse-grained bioclimatic variables have extensively been used to predict the overall ranges of plant species (Chitale et al. 2012; Gaikwad, Wilson, and Ranganathan 2011; Illoldi-Rangel et al. 2012). Fewer studies (but see Edvardsen, Bakkestuen, and Halvorsen 2011) have been performed at finer scales. Further, there is a lack of studies that have addressed possible combined effects of land use and climate at different scales on the ecological requirements of plants that are considered at risk of extinction, as Razgour, Hanmer, and Jones (2011) did for animals.

Norwegian semi-natural habitats have, as in other European countries, decreased due to forest expansion (Lundberg 2011; Vandvik and Birks 2004; Wehn 2009; Wehn, Olsson, and Hanssen 2012; Wehn, Pedersen, and Hanssen 2011). Approximately 40% of the species associated with alpine environments in the Norwegian National Red List are threatened because of changing land use in the alpine region (Austrheim et al. 2010). *Primula scandinavica* is one of the few endemic vascular plants in Scandinavia (Lid and Lid 2005) and listed in both the Swedish Red List (Gärdenfors 2005) and the Norwegian Red List (Kålås et al. 2010). The main threat is defined to be land use change. However, climate change is also assumed to have a potential negative effect (Gärdenfors 2005; Kålås et al. 2010).

The overriding objective of this study is to model ecological niches (considering land use and climate) of

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*Corresponding author. Email: solvi.wehn@nibio.no

P. scandinavica at two scales, local and national, and project the effects of predicted climate and land use change on the distribution of suitable habitats for *P. scandinavica.* The questions addressed are:

1. Which available land use and climatic variables are best able to model suitable habitats for *P. scandinavica*?
2. How might future environmental change influence the distribution of suitable habitats for *P. scandinavica*?

Material and methods

Study species

P. scandinavica (Figure 1) is a small (5–15 cm) long-lived herb whose habitat is open vegetation on calcareous bedrock, mainly in the mountains but also in coastal areas in northern Scandinavia (Lid and Lid 2005). In the mountainous areas, the species grows in open alpine vegetation and agricultural landscapes. Suitable habitats for the species are grassland, heathland, road verge, ditch, scree, snow bed and stream and river banks (Lid and Lid 2005; Wehn and Olsson 2015). Low-intensive livestock farming has a positive impact and forest a negative impact on *P. scandinavica* performance (Gärdenfors 2005; Kålås et al. 2010; Wehn and Olsson 2015). *P. scandinavica* is a perennial herb with clonal growth and it is assumed that its distribution might include remnant populations (Wehn and Olsson 2015). The species' distribution could therefore, be explained not only from present, but also from historical land use (Heubes et al. 2011). Climate (temperature, precipitation, snow-cover duration) and elevation are considered to be the main causes of regional shifts in vegetation in Norway (Bakkestuen, Erikstad, and Halvorsen 2008). We, therefore, assume these variables as essential also for the regional distribution of *P. scandinavica.*

Figure 1. *Primula scandinavica.*

Study areas

The national-scale study area is Norway and local-scale study area is the mountain area Eastern Jotunheimen in south central Norway. The extent for the national scale analyses includes the entire mainland and the islands along the coast of Norway (58°N–71°N, 5°E–31°E, 0–2469 m a.s.l.). The extent for the local scale analyses includes 13 circular areas in Eastern Jotunheimen mountain region (68°18' N–68°47' N, 48°25' E–50°56' E, 870–1370 m a.s.l.; Wehn 2009; Wehn, Pedersen, and Hanssen 2011). Eastern Jotunheimen includes landscape elements shaped through centuries of traditional low-intensity land use where *P. scandinavica* is widely distributed.

Data collection

Data were georeferenced, resampled to 1 km^2 resolution at national scale and 100 m^2 at local scale, recalculated and spatially joined using ArcMap 10.1 (ESRI). When modelling species distributions the quality of the models relies on relevant environmental variables. We searched databases and data sets which provided information on assumed relevant climatic and land use variables and then included the available environmental data in our modelling procedures. As it is known that the species depends upon calcareous bedrock (Lid and Lid 2005), we searched for maps describing the bedrock. Maps on the scale 1:50.000 are available (provided by the Geological Survey of Norway); however, field verifications showed these maps to be too coarse for the local-scale study and a nationally consistent map is not yet available. Hence, bedrock was not included in the modelling.

Norway (national scale)

Data on geographical positions of *P. scandinavica* observations in Norway are available from the Species Map Service 1.6 (provided by the Norwegian Biodiversity Information Centre). From this database, we extracted data on observations after 1990 with an accuracy <100 m and assigned these into 279 plots of 1 km^2 using ArcMap 10.1 (ESRI) (Table 1(a)).

Table 1. Data used for modelling climatic and land use niches of *P. scandinavica* (a) at the national scale, resolution 1 × 1 km^2, and (b) at local scale, resolution 10 × 10 m^2. [1]Data were grouped at the national scale modelling approach.

Proxies of	Data	Database/Reference
(a)		
Occurrence	Post 1990: *P. scandinavica* observations (coordinate accuracy < 100 m)	Species Map Service 1.6.
Elevation	DEM^a (m a.s.l.)	Digital elevation model (resolution: 1 km^2)
Climate[1]	1961–1990: Annual mean temperature (°C) Annual precipitation (mm) Number of (#) snow days	Norwegian Water Resources and Energy Directorate; Beldring et al. 2003
Grazing pressure	Number of (#) livestock	Grazing map: Norwegian Institute of Bioeconomy Research (NIBIO)
Land use[1]	Portion covered by (%) pasture Portion covered by (%) forest	Land resource map (AR50)
Future climate[1]	2071–2100: Precipitation Temperature Number of snow-days	NVE; Engen-Skaugen, Haugen, and Hanssen-Bauer 2008; Beldring et al. 2008; Engen-Skaugen 2007
(b)		
Occurrence	*P. scandinavica* observations (accuracy < 20 m)	
Elevation	DEM^b (m a.s.l.)	Digital elevation model (resolution: 100 m^2)
Climate	Slope Solar radiation Water flow accumulation Curvature	Derived from DEM^b: ArcMap version 10.1
Grazing pressure	Potential grazing pressure by livestock (kg/km2 year)	Wehn 2009
Land use	Present (2002) and historic (prior to 1960s) land cover: Arable field Grassland Grassland in transition to woodland Recently established (two years ago) pasture by logging Heathland Heathland in transition to woodland Coniferous forest Deciduous forest Mixed forest Mire Scree Lake/river	Wehn 2009; Wehn, Pedersen, and Hanssen 2011; Wehn, Olsson, and Hanssen 2012

Climatic and land use data at national scale collected (Table 1a) were elevation (m a.s.l.; provided by DEM^a), average annual mean temperature (°C; provided by NVE), average annual precipitation (mm; provided by NVE), average yearly number of snow-cover days (number of snow-days; provided by NVE), number of outfield grazing domestic animals (cattle, goats and sheep in 2014; provided by NIBIO), % pasture (proportion covered by enclosed pasture; provided by AR50) and % forest (proportion covered by forest; provided by AR50). The % forest and pasture in each 1 km^2 cell of the map were calculated based on data provided from land resource maps (AR50; scale: 1:50 000; Table 1(a)). In AR50, forest is defined as areas with at least six trees (height: 3–5 m) per 1000 m^2. Pastures are grasslands that are used for grazing, cannot be harvested with large machinery and at least 50% of the field layer consists of grazing-tolerant grass and herb species (Ahlstrøm, Bjørkelo, and Frydenlund 2014). The collected data on these environmental variables were assigned into all 1 km^2 plots of the national study area.

Eastern Jotunheimen (local scale)

During 2003–2005 and 2007, surveys of *P. scandinavica* individuals were performed in three valleys in Eastern Jotunheimen. Thirteen summer farm sites were selected as starting points from where the surveys started. These were selected because local-scale maps of present (2002) and historic (1960s) land use categories are available (Wehn 2009). All land use categories in the surroundings of these summer farms (which represented all land use categories in the valleys) were thoroughly surveyed for *P. scandinavica*. Geographical coordinates (error < 20 m) of specimens were registered in June. The survey data were assigned into occurrences in 285 plots of 100 m^2 (Table 1(b)).

No climatic data at the local-scale resolution were available but topographic variables can be used as indications of local climate variability over complex topographies (Fu and Rich 2002). Climatic and land use data at local scale collected (Table 1(b)) were elevation (m a.s.l.; provided by DEM^b), slope, solar radiation, water flow accumulation and curvature (derived from DEM^b), grazing pressure (estimated sum of potential grazing pressure of cattle, sheep and goats; Wehn 2009) and present and historic land use classes (Wehn 2009; Wehn, Pedersen, and Hanssen 2011; Wehn, Olsson, and Hanssen 2012). The collected data on these environmental variables were assigned into all 100 m^2 plots of the local study area.

Modelling present distribution

To model environmental niches using species distribution models (SDMs), maximum entropy distribution modelling (Maxent; Phillips, Anderson, and Schapire 2006; Elith et al. 2011) was performed using Maxent version 3.3.3 k. Area under the receiver operating characteristic curves (AUC) derived from receiver operating characteristic (ROC) analyses describes the performance of the models (Phillips, Anderson, and Schapire 2006) and is used to measure whether a SDM performs better than random (AUC = 0.5; Araújo et al. 2005). The default setting of the regularisation procedure in Maxent has been shown to perform well for a wide range of species (Phillips and Dudík 2008) and was therefore used to model species distribution. When predicting future distribution models finer details are better to be ignored (Elith, Kearney, and Phillips 2010). Therefore, also more general models were fitted allowing only hinge features with beta multiplier of 2.5 in the parametrisation process. In both procedures a 10-fold cross-validation run type was used. The datasets were split into 10 mutually disjoint folds. Each of the folds was used as a test set while the others were used as training sets.

In order to minimise complexity and include as few environmental variables as possible, a stepwise forward selection procedure was performed. In the first step, each environmental variable was included separately to produce simple SDMs (SDM$_1$). Then, mean values and 95% confidence intervals (CIs) of the AUCs produced

Table 2. The stepwise forward selection process investigating which environmental variables to include in a national (Norway) species distribution model (SDM) of Primula scandinavica. AUC = mean area under the curve. CI = 95% confidence interval of AUCs. Step 1) SDMs including each of the environmental variables. Step 2) SDMs including the environmental variable (AUC and CI in bold) in the best model from step 1) + one of the grouped environmental variables that performed models with AUC > 0.6. Step 3) SDMs including the environmental variable (AUC and CI in bold) in the best model from step 2) + one the grouped environmental variables that together with the best model from step 1) performed significant better models (higher and not overlapping confidence intervals). The final model (environmental variables in bold and AUC and CI in bold and cursive) was the model that did not significantly improve when adding more environmental variables. Program used: Maxent version 3.3.3 k; a) using the default settings and auto features but a 10-fold cross validation, b) using the default settings but only hinge features and a 10-fold cross validation. Land use and climate were variables including several environmental variables (in cursive).

	Step 1)		Step 2)		Step 3)	
Environmental variable	AUC	CI	AUC	CI	AUC	CI
(a)						
Elevation	0.73	0.700–0.764	***0.83***	***0.818–0.850***		
Temperature	0.64	0.620–0.658				
Precipitation	0.66	0.622–0.696				
# snow-days	0.62	0.594–0.638				
Climate	**0.76**	**0.733–0.783**				
Grazing pressure	0.66	0.599–0.711	0.81	0.790–0.824	0.85	0.832–0.862
% pasture	0.62	0.596–0.646				
% forest	0.59	0.563–0.615				
Land use	0.69	0.668–0.708	0.79	0.762–0.816		
(b)						
Elevation	0.73	0.700–0.760	***0.82***	***0.798–0.836***		
Temperature	0.62	0.589–0.645				
Precipitation	0.63	0.603–0.647				
# snow days	0.61	0.586–0.636				
Climate	**0.74**	**0.722–0.764**				
Grazing pressure	0.62	0.574–0.672	0.78	0.759–0.797		
% pasture	0.62	0.598–0.648				
% forest	0.60	0.569–0.623				
Land use	0.69	0.664–0.706	0.78	0.754–0.800		

were calculated to fit each model. The environmental variable included in the model with the highest mean AUC was selected, and more complex models (SDM_{+1}) including this variable in addition to each of the other environmental variables were then calculated. Only environmental variables in a SDM_1 with $AUC > 0.6$ were included in step 2. If the range of the CI of a SDM_{+1} was within the range of the CI of the SDM_1, we assumed that this SDM_{+1} was not different/better compared to the SDM_1. We also visually interpreted the jackknife test of variable importance included in the Maxent program. The results of the two methods were consistent. The environmental variable added in the SDM_{+1} that did not improve AUC was left out of more complex models. This procedure was performed until no more environmental variables were left to include. Data used for modelling at national and local scale were not identical (Table 1). In order to make a comparison between the results from the local and national modelling climatic and land use variables at national scale were

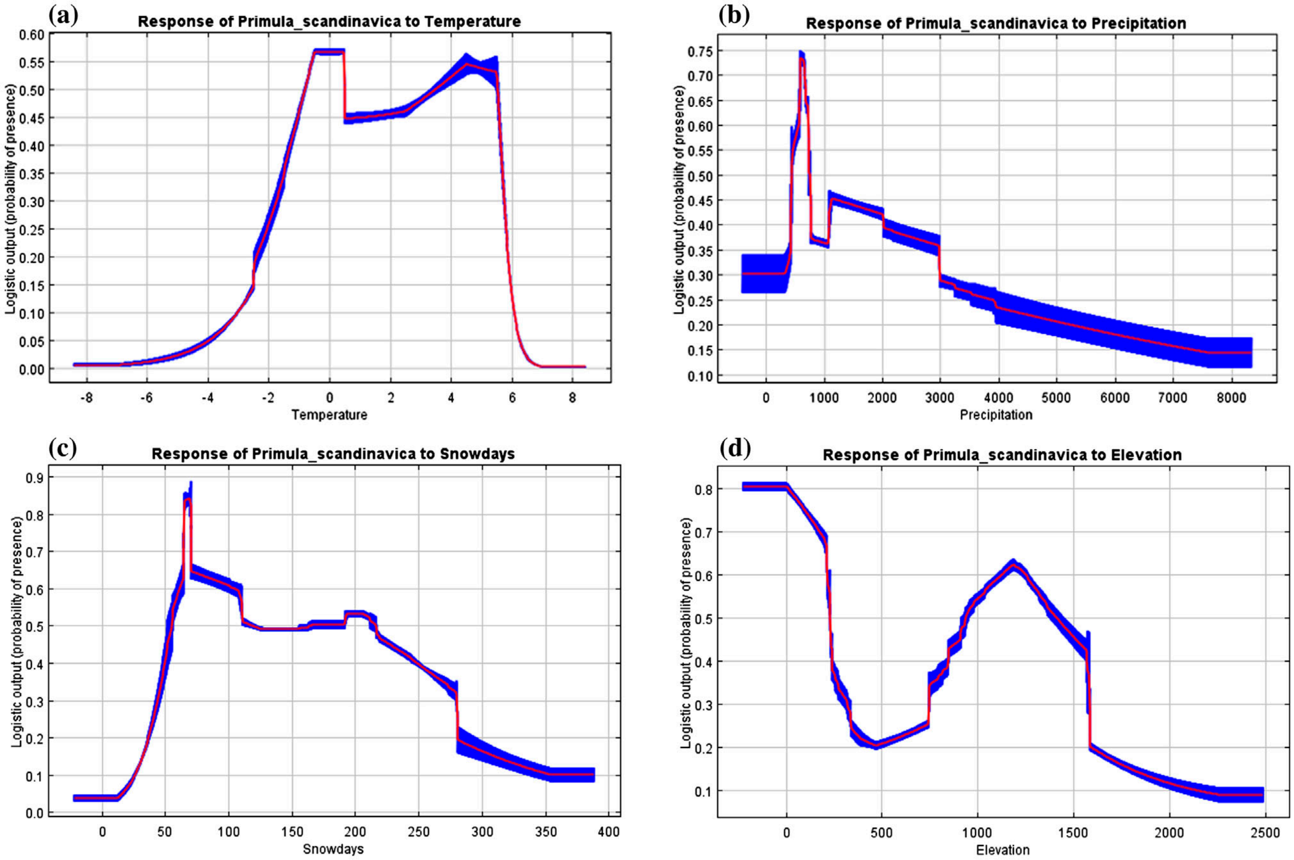

Figure 2. Response curves (logistic Maxent prediction) of the environmental variables (a) annual mean temperature (°C), (b) annual precipitation (mm), (c) number of snow days and (d) elevation (m a.s.l.)) included in the model of the species distribution of *P. scandinavica* at a national scale (resolution 1 km^2). Dependencies due to the other variables are included. Red: mean response of 10 replicate Maxent runs. Blue: mean ± one standard deviation.

Table 3. Pairwise Pearson correlation coefficients (r) of environmental variables at a national scale (Norway). Bold: highly correlated ($r > 0.7$).

	Elevation	Temperature	Precipitation	# snow days	Grazing pressure	% pasture
Elevation						
Temperature	−0.63					
Precipitation	0.28	0.17				
# snow days	**0.73**	**−0.89**	0.14			
Grazing pressure	0.17	−0.06	0.11	0.11		
% pasture	−0.15	0.26	0.01	−0.30	−0.03	
% forest	−0.45	0.43	−0.25	−0.51	−0.07	0.06

grouped; climate: temperature, precipitation and number of snow days; land use: % forest and % pasture. The groups were used as proxies in the national-scale modelling approach.

Pairwise Pearson correlations (r) were calculated for the environmental variables in order to interpret the final models.

Predicting future distribution

The Norwegian Water Resources and Energy Directorate has produced scenarios of climatic variables including estimates of average annual mean temperature, average annual precipitation, and average number of snow days for the period 2071–2100 (Beldring et al. 2008; Engen-Skaugen 2007; Engen-Skaugen, Haugen, and Hanssen-Bauer 2008). If these climatic variables were included in the final SDM (including only hinge features) at the national scale, they were used to project the probability of presence of *P. scandinavica* in the future. A land use type at high risk of abandonment is outfield grazing by domestic animals in rural alpine areas (Olsson et al. 2011). If grazing pressure was included in the best SDM (including only hinge features), we projected the probability of presence under a scenario of no outfield grazing by domestic animals.

At both national and local scale, we calculated the proportion of the currently occupied localities that in the future would be in habitats with a projected probability above 0.1.

Results

At the national scale, climate (temperature, precipitation and number of snow-days) and elevation are the two environmental variables that produce the best SDM using the auto features command in Maxent (Table 2a). When including all the variables in the final national model, response curves (Figure 2) show that the probability of presence of *P. scandinavica* is high when mean annual temperature range from −2 to 6 °C, decreases if precipitation increases but is low if annual precipitation is below 500 mm and high if yearly number of snow days range from 50 to 250. Along the elevation gradient the probability of presence of *P. scandinavica* is highest at both low elevation (near seashore) and at mountainous elevations around 1200 m a.s.l. Elevation correlated with number of snow-days ($r = 0.73$; Table 3) and temperature ($r = -0.63$; Table 3). The same output was computed when including only hinge features in the Maxent model (Table 2(b)).

The future potential distribution is estimated to expand in the mountainous areas in south and move north (Figure 3). However, only 86% of the currently occupied localities will be in habitats with a probability above 0.1 for *P. scandinavica* presences in the future.

At the local scale both when modelling more complex as well as smoothed responses of the environmental variables, historic and present land use and grazing pressure by livestock, produce the best SDMs (Table 4). The probability of presence of *P. scandinavica* is highest at medium–high grazing pressures and in semi-natural land

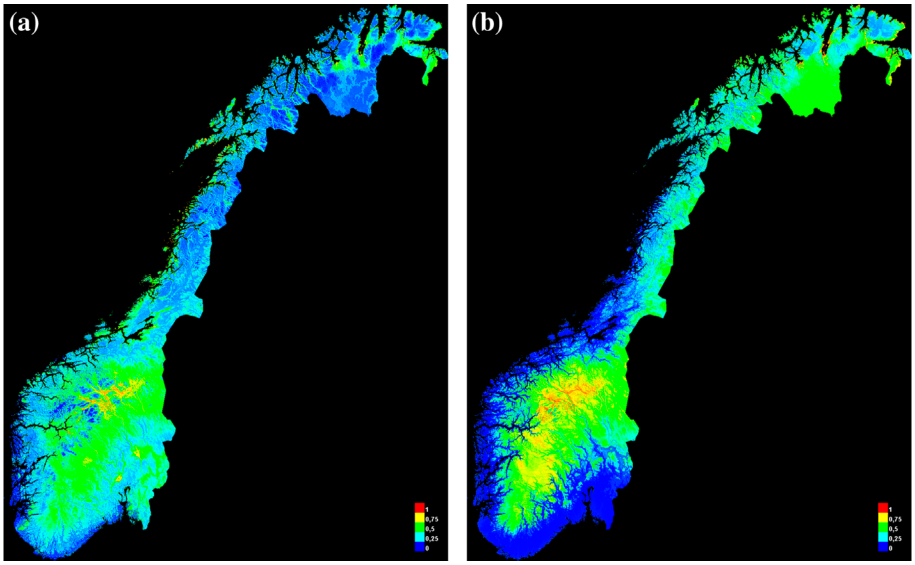

Figure 3. Species distribution model (SDM) of *P. scandinavica* based on Maxent models including mean annual temperature (°C), annual precipitation, number of snow days and elevation (m a.s.l.). (a) Predicted present and (b) projected future SDM at national scale (resolution 1 km^2).

use categories: grasslands (2), grasslands in transition to woodland (3) and recently established pastures (4) in areas that historically were open grassland (2) or heathland (5; Figure 4). Simple models including only present land use, historic land use or grazing pressure are not significantly different (Table 4), and present and historic land use are highly correlated ($r = 0.87$; Table 5). Our future projection shows a substantial decrease in the probability of presence in the study area if no outfield grazing by livestock takes place (Figure 5). We predict that at the local scale, 58% of the currently occupied localities will be in habitats with a probability above 0.1 for *P. scandinavica* presences in the future.

Discussion

Alpine-plant species diversity is driven by multiple and interacting determinants, both locally and regionally (Wehn, Lundemo, and Holten 2014). Gradients of key abiotic drivers of alpine-plant species distributions are considered multi-scalar; for example, mesoscale gradients define the lower limits of the alpine zone while micro-scale gradients define micro refuges (Carlson et al. 2013). Based on the present available data, climate and elevation are the selected environmental variables that are most relevant in modelling the distribution of *P. scandinavica* at a national scale (macro-scale) for Norway. Elevation is suggested to be the main driver of species persistence in mountains (Randin et al. 2009). It is therefore recommended to be included together with climatic variables as predictors in SDM for mountain-plant species (Oke and Thompson 2015). Elevation is associated with environmental changes in atmospheric pressure, temperature, solar radiation and UV-B radiation, which might influence plant performance (Körner 2007). As is the case for several plant species typical of mountainous areas in southern Norway, *P. scandinavica* is present both near the seashore in northern Norway and in mountainous areas in south-central Norway. This is due to their similar climatic conditions (Moen 1999). At the national scale, suitable areas, given predicted future climate, will increase compared to the present suitable

Table 4. The stepwise forward selection process investigating which environmental variables to include in a local (Eastern Jotunheimen) species distribution model (SDM) of Primula scandinavica. AUC = mean area under the curve. CI = 95% confidence interval of AUCs. Step 1) SDMs including each of the environmental variables. Step 2) SDMs including the environmental variable (AUC and CI in bold) in the best model from step 1) + one of the environmental variables that performed models with AUC > 0.6. 3) SDMs including the environmental variables (AUC and CI in bold) in the best model from step 2) + one of the environmental variables that performed models with AUC > 0.6 in step 2. The final model (environmental variables in bold and AUC and CI in bold and cursive) was the model that did not significantly improve when adding more environmental variables. Program used: Maxent version 3.3.3 k; a) using the default settings and auto features but a 10-fold cross validation, b) using the default settings but only hinge features and a 10-fold cross validation.

	Step 1)		**Step 2)**		**Step 3)**	
Environmental variable	**AUC**	**CI**	**AUC**	**CI**	**AUC**	**CI**
(a)						
Elevation	0.74	0.714–0.758	0.87	0.832–0.865	0.91	0.896–0.916
Slope	0.64	0.629–0.654	0.82	0.803–0.837		
Solar radiation	0.71	0.677–0.746	0.85	0.827–0.867	0.90	0.878–0.916
Flow accumulation	0.51	0.472–0.549				
Curvature	0.56	0.544–0.572				
Grazing pressure	0.80	0.775–0.828	**0.89**	**0.874–0.902**		
Present land use	*0.78*	0.765–0.803	0.86	0.843–0.871	***0.92***	***0.910–0.925***
Historic land use	**0.80**	**0.778–0.803**				
(b)						
Elevation	0.72	0.700–0.740	0.86	0.845–0.877	0.88	0.861–0.890
Slope	0.61	0.589–0.631	0.82	0.804–0.836		
Solar radiation	0.65	0.633–0.667	0.84	0.815–0.864		
Flow accumulation	0.50	0.483–0.517				
Curvature	0.56	0.546–0.574				
Grazing pressure	0.77	0.745–0.795	**0.875**	**0.861–0.890**		
Present land use	0.79	0.772–0.808	0.851	*0.836–0.867*	***0.90***	***0.895–0.915***
Historic land use	**0.80**	**0.777–0.816**				

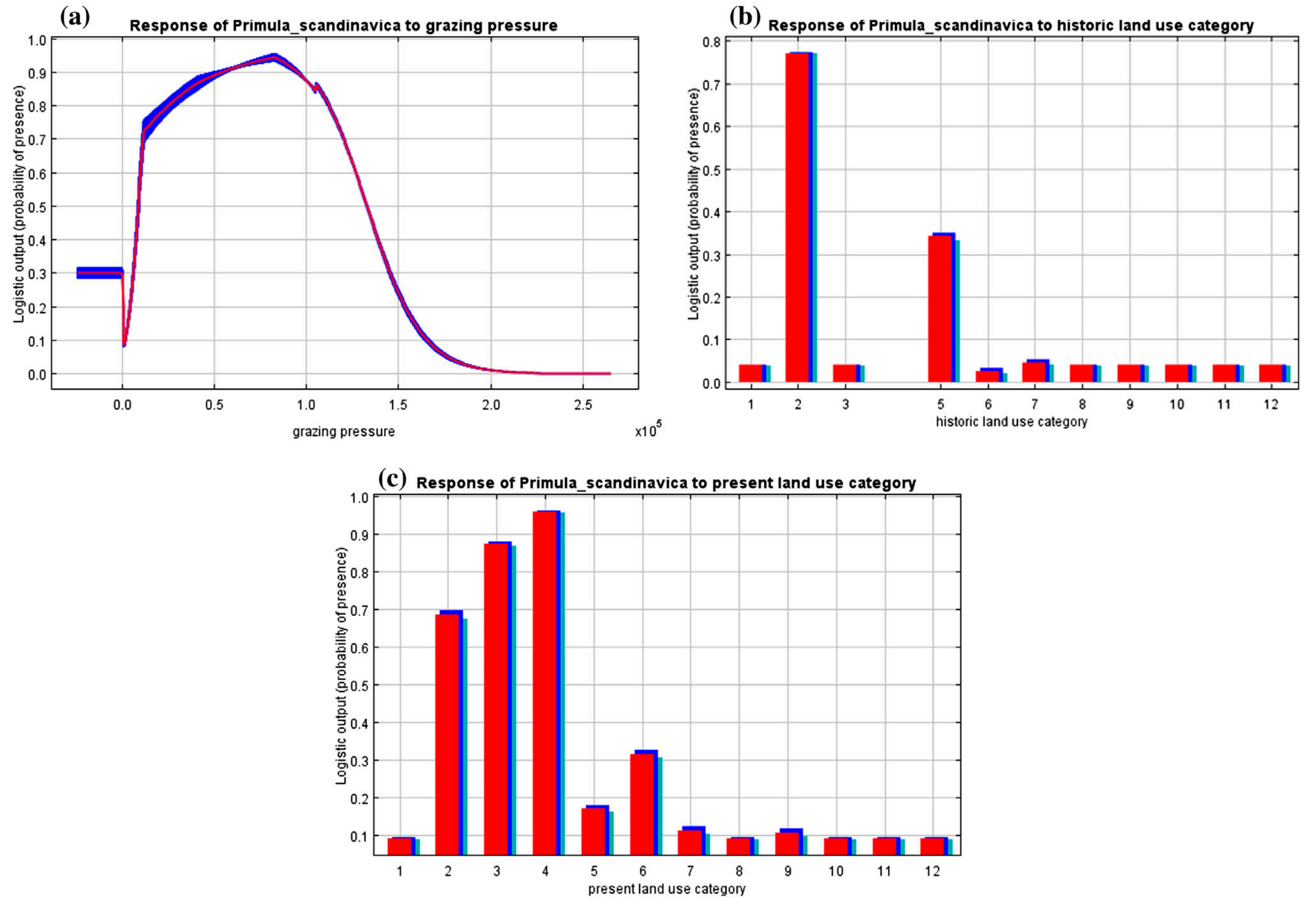

Figure 4. Response curves (logistic Maxent prediction) of the environmental variables (a) potential grazing pressure (kg km^{-2} year) and (b) historic and (c) present land use included in the species distribution model of *P. scandinavica* at a local scale (resolution 100 m^2). Land use categories: 1: Arable field, 2: Grassland, 3: Grassland in transition to woodland, 4: Recently established (two years ago) pasture by logging, 5: Heathland, 6: Heathland in transition to woodland, 7: Coniferous forest, 8: Deciduous forest, 9: Mixed forest, 10: Mire, 11: Scree, 12: Lake/river bank. Dependencies due to the other variables are included. Red: mean response of 10 replicate Maxent runs. Blue (two shades for categorical variables): mean ± one standard deviation.

Table 5. Pairwise Pearson correlation coefficients (r) of environmental variables at a local scale (Eastern Jotunheimen). Bold: highly correlated ($r > 0.7$).

	Elevation	Slope	Radiation	Accumulation	Curvature	Grazing pressure	Historic land use
Slope	0.41						
Radiation	0.34	−0.02					
Accumulation	−0.03	−0.06	−0.01				
Curvature	0.02	0.01	0.00	−0.02			
Grazing pressure	−0.10	−0.03	0.02	−0.01	0.00		
Historic land use	−0.20	−0.22	−0.11	0.04	0.00	−0.24	
Present land use	−0.24	−0.18	−0.18	0.03	0.00	−0.27	**0.87**

areas. We do not know if *P. scandinavica* will migrate to new climatically suitable areas, but other alpine species have been reported to migrate as a consequence of changed temperatures (Gottfried et al. 2012; Pauli et al. 2012). The suitability of the ‘new’ areas and the potential for *P. scandinavica* to migrate and establish

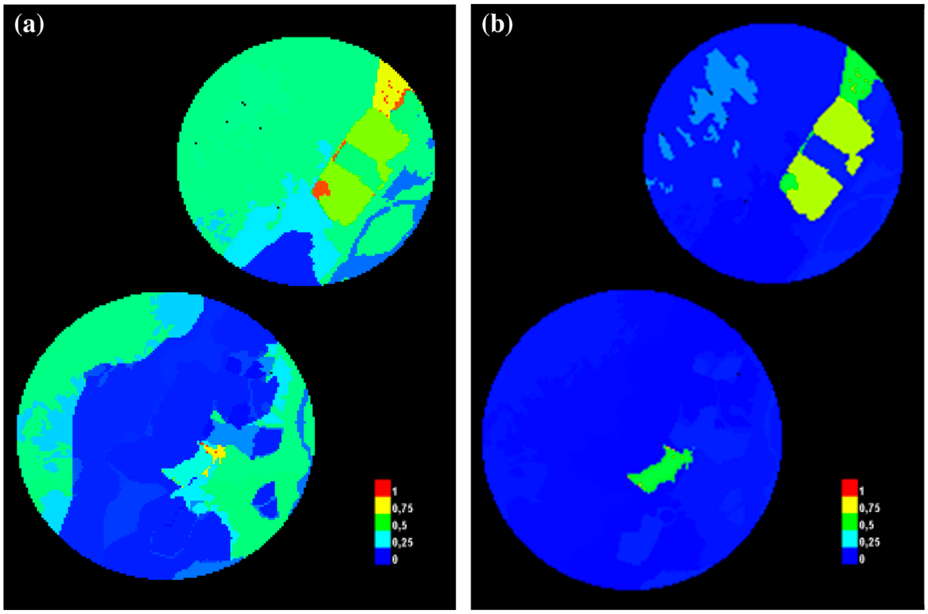

Figure 5. Species distribution model (SDM) of *P. scandinavica* based on Maxent models including grazing pressure (kg km^{-2} year) and historic and present land use. (a) Predicted present and (b) projected future SDM at local scale (resolution 100 m^2).

will largely depend on the alkaline content of the substrate and soil. Since bedrock is not included as a predictor in our modelling procedure, the final models may possibly overestimate the distribution of suitable areas.

At the local scale, *P. scandinavica* is most likely to be present in semi-natural habitats where livestock grazing pressure is at medium levels. The modelled response curves indicate that abandonment of the habitats and cessation of domestic grazing will reduce the suitability of the areas. Earlier studies have shown that changes in grazing pressure by domestic animals in mountainous areas in Norway have caused radical vegetation shifts from open semi-natural vegetation to more forested and scrubby areas (Lundberg 2011; Vandvik and Birks 2004; Wehn 2009; Wehn, Olsson, and Hanssen 2012; Wehn, Pedersen, and Hanssen 2011). Livestock grazing supresses taller plant species (Wehn 2009) and thus allows more light for *P. scandinavica* to persist. Furthermore, livestock trampling creates patches of bare soil (poaching) that are required for seeds to germinate (Aarnes 2003). This means that abandonment of livestock grazing will not only directly affect suitable habitats, but it will also indirectly influence their suitability through changing the land use category. Areas of land use categorised as suitable will become fragmented and degraded if no livestock grazing takes place in the climatically suitable mountainous areas.

The performance of *P. scandinavica* is known to be highly influenced by historic land use (Wehn and Olsson 2015). The species has clonal growth, and clonal propagation can increase its capacity to develop remnant populations and delay local extinction (Johansson, Cousins, and Eriksson 2011; Lindborg and Ehrlen 2002). Therefore, the consequence of changed land use on *P. scandinavica* distribution may not be visible for a long time (Wehn and Olsson 2015). In a study by Lehsten et al. (2015), land use change was regarded as the major driver of changing habitat, especially grasslands which will consequently reduce biodiversity (Newbold et al. 2015). Other studies have shown the importance of climate change (Hickler et al. 2012). In Europe, grasslands are expected to change mostly due to land use with only a minor effect from climate change (Lehsten et al. 2015). Habitats change faster in response to global change than species extinctions occur (Pereira et al. 2010), therefore the focus on mitigation actions should be on land use changes (Lehsten et al. 2015) and, in particular, the abandonment of livestock grazing in *P. scandinavica* habitats, especially in the projected climatically suitable areas where the species already exists.

Conclusions

Climate change is predicted to change the distribution of suitable habitats for *P. scandinavica* at national scale. Area of suitable climates in Norway will increase, but abandonment of grazing will reduce the distribution of suitable habitats. Land use change is one of the largest threats for the species at a local scale. Management actions to conserve the species need to focus on land use practices in climatically suitable areas.

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References

Aarnes, E. T. 2003. *The Influence of Disturbance on Primula Scandinavica.* Master thesis, Department of Biology. Norwegian University of Science and Technology NTNU, Trondheim.

Ahlstrøm, A. P., K. Bjørkelo, and J. Frydenlund. 2014. *AR50 Klassifikasjonssystem*. Skog og landskap report 06/2014. Ås, Norway: Norwegian Forest and Landscape Institute.

AR50. "Norwegian Forest and Landscape Institute." Accessed October 2012 http://www.skogoglandskap.no/kart/arealressurskart

Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. "Validation of Species–Climate Impact Models under Climate Change." *Global Change Biology* 11 (9): 1504–1513.

Austrheim, G., K. A. Bråthen, R. A. Ims, A. Mysterud, and F. Ødegaard. 2010. "Alpine Environments." In *Environmental Conditions and Impacts for Red List Species*, edited byJ. A. Kålås, S. Henriksen, S. Skjelseth and Å. Viken, 107–119. Trondheim, Norway: Norwegian Biodiversity Information Centre.

Bakkestuen, V., L. Erikstad, and R. Halvorsen. 2008. "Step-Less Models for Regional Environmental Variation in Norway." *Journal of Biogeography* 35 (10): 1906–1922.

Beldring, S., K. Engeland, L. A. Roald, N. R. Sælthun, and A. Voksø. 2003. "Estimation of Parameters in a Distributed Precipitation-Runoff Model for Norway." *Hydrology and Earth-System Sciences* 7: 304–316.

Beldring, S., T. Engen-Skaugen, E. J. Førland, and L. A. Roald. 2008. "Climate Change Impacts on Hydrological Processes in Norway Based on Two Methods for Transferring Regional Climate Model Results to Meteorological Station Sites." *Tellus a* 60 (3): 439–450.

Carlson, B. Z., C. F. Randin, I. Boulangeat, S. Lavergne, W. Thuiller, and P. Choler. 2013. "Working toward Integrated Models of Alpine Plant Distribution." *Alpine Botany* 123: 41–53.

Chauchard, S., C. Carcaillet, and F. Guibal. 2007. "Patterns of Land-Use Abandonment Control Tree-Recruitment and Forest Dynamics in Mediterranean Mountains." *Ecosystems* 10 (6): 936–948.

Chitale, V. S., P. Tripathi, M. D. Behera, S. K. Behera, and R. Tuli. 2012. "On the Relationships among Diversity, Productivity and Climate from an Indian Tropical Ecosystem: A Preliminary Investigation." *Biodiversity and Conservation* 21: 1177–1197.

DEM^{a} – Digital elevation model. "WordClim." Accessed October 2012. http://www.worldclim.org/bioclim.htm.

DEM^{b} – Digital elevation model. "Norge Digital." Accessed October 2012

Edvardsen, A., V. Bakkestuen, and R. Halvorsen. 2011. "A Fine-Grained Spatial Prediction Model for the Red-Listed Vascular Plant Scorzonera Humilis." *Nordic Journal of Botany* 29 (4): 495–504.

Elith, J., M. Kearney, and S. Phillips. 2010. "The Art of Modelling Range-Shifting Species." *Methods in Ecology and Evolution* 1 (4): 330–342.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, C. Yates, and J. 2011. "A Statistical Explanation of MaxEnt for Ecologists." *Diversity and Distributions* 17 (1): 43–57.

Emanuelsson, U. 2009. *The Rural Landscapes of Europe: How Man Has Shaped European Nature*. Stockholm, Sweden: Formas Swedish Research Council for Environment, Agriculture Science and Spatial Planning.

Engen-Skaugen, T. 2007. "Refinement of Dynamically Downscaled Precipitation and Temperature Scenarios." *Climate Change* 84: 365–382.

Engen-Skaugen, T., J. E. Haugen, and I. Hanssen-Bauer. 2008. *Dynamically Downscaled Climate Scenarios Available at the Norwegian Meteorological Institute per December 2008.* Met.no report 24/2008. Oslo, Norway: Norwegian Meteorological Institute.

Fu, P., and P. M. Rich. 2002. "A Geometric Solar Radiation Model with Applications in Agriculture and Forestry." *Computers and Electronics in Agriculture* 37 (1–3): 25–35.

Gaikwad, J., P. D. Wilson, and S. Ranganathan. 2011. "Ecological Niche Modeling of Customary Medicinal Plant Species Used by Australian Aborigines to Identify Species-Rich and Culturally Valuable Areas for Conservation." *Ecological Modelling* 222: 3437–3443.

Gärdenfors, U., ed. 2005. *Rödlistade Arter I Sverige 2005 - the 2005 Red List of Swedish Species*. Uppsala: Artdatabanken.

Gottfried, M., H. Pauli, A. Futschik, M. Akhalkasti, P. Barancok, J. L. B. Alonso, G. Coldea, et al. 2012. "Continent-Wide Response of Mountain Vegetation to Climate Change." *Nature Climate Change* 2: 111–115.

Halada, L., D. Evans, C. Romano, and J. E. Petersen. 2011. "Which Habitats of European Importance Depend on Agricultural Practices?" *Biodiversity and Conservation* 20: 2365–2378.

Heubes, J., V. Retzer, S. Schmidtlein, and C. Beierkuhnlein. 2011. "Historical Land Use Explains Current Distribution of Calcareous Grassland Species." *Folia Geobotanica* 46 (1): 1–16.

Hickler, T., K. Vohland, J. Feehan, P. A. Miller, B. Smith, L. Costa, T. Giesecke, et al. 2012. "Projecting the Future Distribution of European Potential Natural Vegetation Zones with a Generalized, Tree Species-Based Dynamic Vegetation Model." *Global Ecology and Biogeography* 21: 50–63.

Illoldi-Rangel, P., M. Ciarleglio, L. Sheinvar, M. Linaje, V. Sanchez-Cordero, and S. Sarkar. 2012. "*Opuntia* in Mexico: Identifying Priority Areas for Conserving Biodiversity in a Multi-Use Landscape." *PloS One* 7(5): 1–16.

Johansson, V. A., S. A. Cousins, and O. Eriksson. 2011. “Remnant Populations and Plant Functional Traits in Abandoned Semi-Natural Grasslands.” *Folia Geobotanica* 46 (2–3): 165–179.

Kålås, J. A., Å. Viken, S. Henriksen, and S. Skjelseth, eds. 2010. *The 2010 Norwegian Red List for Species*. Trondheim: Norwegian Biodiversity Information Centre.

Körner, C. 2007. “The Use of ‘Altitude’ in Ecological Research.” *Trends in Ecology & Evolution* 22 (11): 569–574.

Kullman, L. 2010. “A Richer, Greener and Smaller Alpine World: Review and Projection of Warming-Induced Plant Cover Change in the Swedish Scandes.” *Ambio* 39 (2): 159–169.

Lehsten, V., M. T. Sykes, A. V. Scott, J. Tzanopoulos, A. Kallimanis, A. Mazaris, P. H. Verburg, et al. 2015. “Disentangling the Effects of Land-Use Change, Climate and CO_2 on Projected Future European Habitat Types.” *Global Ecology and Biogeography* 24: 653–663.

Lid, J., and D. T. Lid. 2005. *Norsk Flora*. Oslo: Det norske samlaget.

Lindborg, R., and J. Ehrlen. 2002. “Evaluating the Extinction Risk of a Perennial Herb: Demographic Data versus Historical Records.” *Conservation Biology* 16: 683–690.

Lundberg, A. 2011. “Climate and Land-Use Change as Driving Forces in Lowland Semi-Natural Vegetation Dynamics.” *Erdkunde* 335–353.

Moen, A. 1999. *National Atlas of Norway: Vegetation*. Hønefoss, Norway: Norwegian Mapping Authority.

Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Boerger, et al. 2015. “Global Effects of Land Use on Local Terrestrial Biodiversity.” *Nature* 520: 45–50.

Oke, O. A., and K. A. Thompson. 2015. “Distribution Models for Mountain Plant Species: The Value of Elevation.” *Ecological Modelling* 301: 72–77.

Olsson, E. G. A. 2004. “Summer Farming in Jotunheimen, mid-Norway.” In *Transhumance and Biodiversity in European Mountains*, edited by R. G. H. Bunce, M. Pérez Soba, R. H. G. Jongman, A. Gómez Sal, F. Herzog, and I. Austad, 25–30. Wageningen, the Netherlands: IALE Publication series nr 1.

Olsson, E. G. A., and K, Rønningen, S. K. Hanssen, and S. Wehn. 2011. “The Interrelationship of Biodiversity and Rural Viability: Sustainability Assessment, Land Use Scenarios and Norwegian Mountains In a European Context.” *Journal of Environmental Assessment Policy and Management* 13: 251–284.

Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, et al. 2012. “Recent Plant Diversity Changes on Europe’s Mountain Summits.” *Science* 336: 353–355.

Pereira, H. M., P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarres, M. B. Araujo, et al. 2010. “Scenarios for Global Biodiversity in the 21st Century.” *Science* 330: 1496–1501.

Phillips, S. J., and M. Dudík. 2008. “Modeling of Species Distributions with Maxent: New Extensions and a Comprehensive Evaluation.” *Ecography* 31 (2): 161–175.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. “Maximum Entropy Modeling of Species Geographic Distributions.” *Ecological Modelling* 190 (3–4): 231–259.

Randin, C. F., R. Engler, S. Normand, M. Zappa, N. E. Zimmermann, P. B. Pearman, P. Vittoz, W. Thuiller, and A. Guisan. 2009. “Climate Change and Plant Distribution: Local Models Predict High-Elevation Persistence.” *Global Change Biology* 15: 1557–1569.

Razgour, O., J. Hanmer, and G. Jones. 2011. “Using Multi-Scale Modelling to Predict Habitat Suitability for Species of Conservation Concern: The Grey Long-Eared Bat as a Case Study.” *Biological Conservation* 144: 2922–2930.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. “Global Biodiversity Scenarios for the Year 2100.” *Science* 287 (5459): 1770–1774.

Species Map Service 1.6. “Norwegian Biodiverstiy Information Centre and GBIF-Norway© 2007-2012.” Accessed October 2012. www.artsdatabanken.no

Tasser, E., J. Walde, U. Tappeiner, A. Teutsch, and W. Noggler. 2007. “Land-Use Changes and Natural Reforestation in the Eastern Central Alps.” *Agriculture, Ecosystems & Environment* 118 (1): 115–129.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. “Climate Change Threats to Plant Diversity in Europe.” *Proceedings of the National Academy of Sciences of the United States of America* 102 (23): 8245–8250.

Vandvik, V., and H. J. B. Birks. 2004. “Mountain Summer Farms in Røldal, Western Norway – Vegetation Classification and Patterns in Species Turnover and Richness.” *Plant Ecology* 170 (2): 203–222.

Wehn, S. 2009. “A Map-Based Method for Exploring Responses to Different Levels of Grazing Pressure at the Landscape Scale.” *Agriculture Ecosystems & Environment* 129 (1–3): 177–181.

Wehn, S., and G. Olsson. 2015. “Performance of the Endemic Alpine Herb Primula Scandinavica in a Changing European Mountain Landscape.” *Annales Botanici Fennici* 52: 171–180.

Wehn, S., B. Pedersen, and S. K. Hanssen. 2011. “A Comparison of Influences of Cattle, Goat, Sheep and Reindeer on Vegetation Changes in Mountain Cultural Landscapes in Norway.” *Landscape and Urban Planning* 102 (3): 177–187.

Wehn, S., G. Olsson, and S. Hanssen. 2012. “Forest Line Changes after 1960 in a Norwegian Mountain Region – Implications for the Future.” *Norwegian Journal of Geography* 66 (1): 2–10.

Wehn, S., S. Lundemo, and J. I. Holten. 2014. “Alpine Vegetation along Multiple Environmental Gradients and Possible Consequences of Climate Change.” *Alpine Botany* 124 (2): 155–164.