The importance of herbivore density and management as determinants of the distribution of rare plant species

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Abstract

Herbivores are often drivers of ecosystem states and dynamics and in many situations are managed either as livestock or through controlled or exploitative hunting of wild populations. Changes in herbivore density can affect the composition of plant communities. Management of herbivore densities could therefore be regulated to benefit plant species of conservation concern. In this study we use a unique spatial dataset of large herbivores in Norway to test whether herbivore density affects the distribution of rare red-listed plant species in tundra ecosystems, and to identify regions where herbivore density is the most important factor in determining the habitat suitability for the plant species. For all selected species a climatic variable was the most important determinant of the distribution, but herbivore density was an important determinant of some species notably *Primula scandinavica.* Herbivore density was the most important factor determining habitat suitability for this species in 13% of mainland Norway. Regions of Norway where the management of herbivore densities is most strongly linked to the habitat suitability of red-listed plant species are mapped. However, there was very low concordance in the localities of these areas; at any individual locality, habitat suitability was limited by herbivore density for only a small subset of the species. This suggests that management of herbivores for the benefit of rare plant species needs to be tailored for individual locations or species.

Keywords: Alpine; Biotic interactions; Conservation; Grazing; Red list; Species distribution modelling

1. Introduction

In many parts of the world, large herbivores are important drivers of ecosystem states and ecological processes. In the palaeo-historic context diverse assemblages of large herbivores, including many mega-herbivores occurred in many regions, but today, such communities exist only in African savannahs (Owen-Smith 1987). The herbivore assemblages in many other regions are now dominated by livestock and as such lack taxonomic and size diversity (Svenning et al. 2015). Current management of both wild herbivores and livestock does not closely mimic the expectations from natural herbivore assemblages (Bakker et al. 2015) nor necessarily replicate natural population dynamics (Gordon et al. 2004) as livestock and wild herbivores do not tend to be functionally equivalent (Knapp et al. 1999). Hence, ecosystems are unlikely to be in equilibrium with current dynamics in herbivore populations. Understanding the interactions between current herbivore assemblages and ecological processes and ecosystems is thus imperative.

Herbivores are not randomly distributed in landscapes, and factors that affect their distribution vary across spatial scales. Densities of large herbivores are managed directly in the case of livestock and through controlled or exploitative hunting of wild ungulates. Livestock distribution is controlled by livestock managers, and their decisions are guided by applicable policies, economics, past experience and recommendations (Mysterud 2006). Wild herbivore distribution is influenced by both regional management (Gordon et al. 2004) and anthropogenic disturbance. Herbivores themselves are selective, both at large spatial scales (across ranges) and small spatial scales (at the bite level) (Senft et al. 1987). This cross-scale selectivity of large herbivores influences their impact on ecosystems; shifts in plant communities can result from herbivory. For example, herbivory can lead to an increase in relative abundance of plant species that express tolerance traits (for example, certain grasses), while less tolerant species may be lost from a community (Augustine and McNaughton 1998; Hester et al. 2006). At larger scales, herbivores can cause, or prevent, shifts in ecosystem state (Estes et al. 2011; Van der Wal 2006). This can cause loss of habitat for some (non-generalist) plant species. Therefore, herbivores are likely to affect plant species distributions at large spatial scales. The implications of this increase in importance when considering climatic change (Van der Putten et al. 2010): plant species' responses to climatic change involve either adaptation to new climates *in situ*, or migration to new climates elsewhere. Habitat availability and herbivore density will constrain the options available for species that are directly or indirectly affected by herbivory. This is particularly important in the case of species of conservation concern that are also repressed by limited population size (Miller et al. 1999).

Species distribution models (SDM) have proven to be both popular and valuable tools in ecological research and management. SDM can provide insight into the ecology of species (Elith and Leathwick 2009) or predict how species distributions may shift under future conditions (Hijmans and Graham 2006). However, SDM usually utilise only climatic, land cover and/or edaphic variables. They have therefore been criticised for usually lacking biotic interactions (Araújo and Luoto 2007; Wisz et al. 2013) in their use of the niche concept (i.e. they use a Grinnellian rather than Eltonian niche concept (Trainor and Schmitz 2014). However, more recent work has started to incorporate biotic interactions into SDM (Kissling et al. 2012) including trophic dynamics (Trainor and Schmitz 2014). However, a call by Wisz et al. (2013) for large-scale biotic data along environmental gradients is still unanswered.

Livestock grazing is ubiquitous across the unenclosed mountain landscapes of Norway, with semi-domestic reindeer dominating in the far north, and sheep in the rest of the country. During the second half of the 20th century there has been relatively little temporal fluctuation in herbivore densities in mountain regions across Norway, but high spatial variation in this pattern (Austrheim et al. 2011). Changes in grazing pressure are regarded as the most important threat for red-listed species in Norwegian mountains today (Austrheim et al. 2010). In this study we use a unique national-level large herbivore density data set from Norway (Austrheim et al. 2011), to investigate whether large herbivore densities are key factors determining the distribution of plant species. We focus on rare vascular plant species (those on the Norwegian Red List) found in alpine habitats, where decreases in herbivore density have been linked to treeline advance and loss of alpine areas (Bryn et al. 2013; Speed et al. 2010). In this study we aim to (1) test whether herbivore biomass is an important predictor of rare vascular plant species in the Norwegian alpine zone and (2) identify regions where herbivore management could increase the habitat suitability for rare plant species.

2. Methods:

2.1. Species selection and data

We selected rare alpine vascular plants as our study species, taken from the vascular plants that are on the Norwegian Red List in 2010 (Kålås et al. 2010) or 2015 (Henriksen and Hilmo 2015). Species were selected from these lists that (1) were categorised as critically endangered, endangered, vulnerable or near threatened (CR, EN, VU or NT), (2) 'impact upon habitat' was cited as impact upon the species in Norway, and (3) the alpine zone was one of the main habitat types for the species. This gave a list of 20 species (Table 1).

Species occurrence data for these 20 species was downloaded from the Global Biodiversity Information Facility (GBIF) in February 2016 (GBIF.org 2016a). Synonyms used are shown in Table 1. Only georeferenced occurrence records from within Norway were used. Species occurrence points were projected onto a UTM grid (zone 32). Data were quality checked: points located in the sea or outside mainland Norway (i.e. occurrences in Svalbard and Jan Mayan) were removed. Duplicated records (same species and coordinates) were removed, as were data where the localities were given as "locality data withheld" or "locality data withheld. County and municipality estimated". Only species occurrence data from 1990 and onwards were included to reflect recent distribution. Following these quality control steps the number of occurrences per species ranged from 0 to 3662 (Table 1). Although some approaches exist to model species distributions with very small sample sizes (see below), we selected only species with over 150 occurrences in the recent quality controlled data set for modelling. This gave a list of seven species: *Botrychium lanceolatum* (Gmel.) Angstr., *Comastoma tenellum* (Rottb.) Toyok., *Gentianella campestris* (L.) Börner, *Kobresia simpliciuscula* (Wahlenb.) Mack., *Primula scandinavica* Brunn, *Pseudorchis albida* (L.) Á.Löve & D.Löve and *Pulsatilla vernalis* Mill. Basic ecological information on these species is given in Table 1 and the distribution of occurrence records shown in Figure 1.

2.2. Environmental data

2.2.1. Climate

Climatic data was downloaded for Norway from WorldClim at 30 arc sec resolution (Hijmans et al. 2005, http://www.worldclim.org/). All 19 bioclimatic variables were selected (O'Donnell and Ignizio 2012, http://www.worldclim.org/bioclim). WorldClim data were downloaded for the relevant tiles to give full coverage of mainland Norway, merged and masked to the Norwegian mainland to provide data across the study region.

We used principle coordinate analyses (PCA) to reduce the dimensionality of this data set (See Supplementary Figure A1). PCA identified two major axes in the bioclimatic variables across Norway: The first axis (61.7% of total variance) was correlated with precipitation and seasonality of temperature variables (i.e. an oceanic-continental axis). The second axis (19.9%) correlated with mean temperature variables (i.e. a latitudinal and elevational axis). A third axis (7.4%) showed a weaker correlation with precipitation seasonality. These three bioclimatic variables together explain 89% of the bioclimatic variation across Norway (Supplementary Figure A1). To facilitate interpretation of environmental variables in this study we selected one bioclimatic variable that was strongly correlated with each principle component (rather than the principle coordinate axes themselves) to use in the model. These were annual precipitation, mean temperature of the warmest quarter (referred to as mean summer temperature henceforth) and precipitation seasonality (coefficient of variation of monthly precipitation – higher values indicate a climate where a high proportion of annual precipitation occurs in few months) for principle components one to three respectively.

2.2.2. Herbivores and Land Cover

To quantify spatial variation in herbivore density we used a unique data set of the metabolic biomass of large herbivores across Norway (Austrheim et al. 2011). This dataset estimates the metabolic biomass (kg km^{-2}) of all large herbivore species (both livestock and wild herbivores) at the municipality scale across Norway from 1949 to 1999 (using the 435 municipalities that were in existence at that time, median area = 459 km^2). We used data from 1999 since this was the closest year available to the median year of record of the selected plant species occurrences (2003).

The herbivore assemblage dataset could not be reduced in dimensionality in the same way that the climatic data was (Supplementary Figure A1). The first three principle components explained only 62% of the variation in herbivore assemblage. Therefore, we summed herbivore metabolic biomass of the herbivore species that predominantly graze in tundra ecosystems (wild reindeer, semi-domestic reindeer and domestic sheep). We did not include moose, red deer or roe deer as these are predominantly forest herbivores, nor cattle, horses or goats since these mostly graze in pastures.

To quantify land-cover we used the AR50 land resources map of Norway (Norwegian Forest and Landscape Institute 2007). This classifies mainland Norway as built-up, agricultural, forest, other natural (non-forest) vegetation, mires, glaciers, ice and year round snow, freshwaters and sea at a scale of 1:50 000. Bedrock and soil pH are important determinants of plant species distributions. Soil pH at 5 cm depth was selected to represent these edaphic determinants and downloaded from SoilGrids1km (Hengl et al. 2014).

All environmental variables were projected on to the same UTM grid (zone 32) as the species occurrence data. These were then resampled to a 1 km x 1 km resolution using the nearest neighbour method for both continuous and categorical variables. The environmental data is shown in Figure A2. We investigated correlation between all pairs of selected continuous variables: the maximum absolute correlation coefficients was 0.43, between soil pH and mean summer temperature (Supplementary Figure A3).

2.3. Modelling

Species distribution models were built using MaxEnt version 3.3.3k (Phillips et al. 2006, https://www.cs.princeton.edu/~schapire/maxent/; Phillips et al. 2004) through the R Statistical Environment (R Core Team 2015) running the packages dismo (Hijmans et al. 2016) and raster (Hijmans 2015). The package rasterVis was used for visualisation (Perpiñán and Hijmans 2014). MaxEnt is a machine-learning based modelling approach that seeks to maximise the entropy between species presence points and environmental background data (Elith et al. 2011). It is increasingly widely used since it tends to perform well at small sample sizes and with presence-only data, and fits a range of complex response functions (Fourcade et al. 2014).

The use of MaxEnt has also been criticised due to (1) the common acceptance of default model parameters (Halvorsen 2013) and (2) widespread failures to recognise the approaches susceptibility to sampling bias (Fourcade et al. 2014; Yackulic et al. 2013). To ensure objective tuning of MaxEnt, we selected the combination of feature class and regularization multiplier that gave the most parsimonious model (minimum Akaike's information criterium corrected for small sample size AICc) for each species based upon a five k-fold cross-validation using the package ENMeval (Muscarella et al. 2014). Feature classes were chosen from the set (L, Q, H, LQ, LQH, LQHT, LQHTP where L = linear, Q = quadratic, H = hinge, T = Threshold and P = Product features) and regularization parameters were selected from the sequence from 0.5 increasing by intervals of 0.5 to 4.0. The selection of parameters for each study species is shown in Figure A4. To correct for potential sampling bias, we created a kernel point density surface across the study area of the total observations of vascular plants (Pteriodophyta, Pinophyta and Magnoliophyta) recorded in Norway (filtered from a GBIF download of all Plantae georeferenced within Norway; GBIF.org 2016b). This was used as a weighting for random selection of absence points (equivalent to using a biasfile; Fourcade et al. 2014). A weighted random sample of 10 000 background points was taken across the study region and used as background data for all species. This data is included as Supplementary Material (Supplementary Table A5). A systematic sampling approach often performs better in correcting for bias, however, we used the bias file approach since this does not affect the occurrence point distribution as may be the case for the systematic sampling approach (Fourcade et al. 2014).

After selecting the tuning parameters for MaxEnt, models were run for each species using a 5-fold cross-validation. The logistic output option was selected which quantifies the suitability relative to that at a typical presence site which was here set at 0.5 (Elith et al. 2011). The relative importance of the different predictor variables was quantified using the permutation importance of each variable to the replicated models (± standard deviations quantified through cross-validation). This approach uses the final model (and is independent of the path used to obtain it) randomly permuting the value across the presence and background points and measuring the difference in AUC value obtained, standardised to a percentage value. Response curves were constructed for each species and environmental variable. Finally, we created a limiting factors map (following Elith et al. 2010) to identify which environmental variable most affected the estimated relative occurrence rate for each species at a given location. This was used to quantify the parts of the study area where changed herbivore management practice could most influence the occurrence of the selected rare plant species, although it does not identify whether increasing or decreasing herbivore densities will increase suitability for the species.

3. Results

The number of occurrences used to model the distribution of the seven species varied from 187 to 2686 (Table 1). Model predictions from the selected Maxent model for each species are shown in Figure A5, along with the distribution of occurrence records. For all species, high suitability was found in the mountainous region of Southern Norway. For *Pulsatillia vernalis* this was the only part of Norway with high habitat suitability. For the others, regions of high suitability were also identified in Northern Norway. *Pseudorchis albida* and *Gentianella campestris* were the most widespread species in the selected, and a larger area of high suitability was identified for these (Figure A5).

The variable ranked top in terms of contribution to the final model for all species was a climatic variable (Figure 1). For most species this was mean summer temperature, but for *Pulsatillia vernalis* annual precipitation was ranked top. Tundra herbivore density was the second ranked variable in terms of contribution to the final model for *Primula scandinavica,* and the third ranked variable for *Kobresia simpliciuscula, Pseudorchic albida* and *Pulsatilla vernalis* (Figure 1). The contribution of herbivore density to the final model (permutation importance standardised as a percentage) ranged from 3% for *Comostoma tenellum* to 26% for *Primula scandinavica* (Figure 1).

Response curves for all species and variables are shown in Figure 2. For the climatic variables a general humped-backed is apparent in most cases, with peak suitability at intermediate precipitation, summer temperature, or precipitation seasonality. Higher suitability was found for *Comostoma tenellum* and *Pulsatilla vernalis* at low mean summer temperatures, whilst *Kobresia simpliciuscula* and *Pulsatilla vernalis* had higher suitability were precipitation was more seasonal. For most species, suitability was greatest at high herbivore densities, but for *Pseudorchis albida* and *Pulsatilla vernalis* suitability was greater at low herbivore densities. For all species, habitat suitability was greater in less acidic soils. Habitat suitability did not greatly vary between the land cover classes.

Herbivore density was the limiting factor (i.e. the factor that most affected the model predictions) (Elith et al. 2010) over 13% of mainland Norway for *Primula scandinavica* and 12% and 11% for and *Pseudorchis albida* and *Pulsatilla vernalis* (Table 2, Figure 3). The spatial overlap in where herbivore density limited the distribution of these species was not high (Figure 3). In around 69% of the study region herbivore density did not limit the suitability for any of the seven species. In 2% of the study region (Figure 4) herbivore density was the limiting factor for three or more species, and in 0.01% of Norway herbivore density was the limiting factor of all 7 species. The regions were herbivore density limited many species included parts of Nordland, the southern mountain region and the eastern part of central Norway and Trøndelag (Figure 4).

4. Discussion

Land-use change is an understudied and neglected aspect of global environmental change; far more research effort has been put into understanding the impacts of climate change on ecological systems and biodiversity (Titeux et al. 2016; Vitousek 1994). An important component of land-use change in many parts of the world involves changes in densities of managed herbivore species (Asner et al. 2004) and since ecosystems are not currently in equilibrium with herbivore communities understanding the role of herbivores in shaping ecological communities is highly important (Bakker et al. 2015). Species distribution modelling, as one approach for predicting responses of species to environmental change, exemplifies the lack of focus placed upon land-use variables: relatively little effort has been applied to understanding the role of land-use change and biotic interactions on species distributions relative to climatic factors (Wisz et al. 2013). In this study we demonstrate that managed herbivore densities are key determinants of the distribution of selected red-listed vascular plant species. Ungulate herbivore densities are currently in a state of flux within the study region (Austrheim et al. 2011) and further afield (Apollonio et al. 2010; Ripple et al. 2015); our results show that management of these species can have an important influence on conservation efforts for rare vascular plant species.

The regulation of plant diversity by herbivory has been acknowledged for a while and is well studied particularly at smaller spatial scales (Bakker et al. 2006; Olff and Ritchie 1998). However, ungulate herbivory may affect plant community structures at larger spatial scales (Austrheim and Eriksson 2001). In this study we operated at a very large spatial scale and identified that tundra herbivore density was an important factor in determining the habitat suitability for some of the selected red listed vascular plant species, notably for *Primula scandinavica*. While in the case of other species tundra herbivore density was not an important factor in determining habitat suitability. One or more climatic variables were the most important factors in the selected species distribution models across the selected species, with herbivore density being ranked at highest the second most important variable again for *Primula scandinavica*. This indicates that the influence of tundra ungulate herbivore densities is likely to be most pronounced on this species. *Primula scandinavica* has been classified as least-concern in the most recent version of the Norwegian Red List (Henriksen and Hilmo 2015), although it remains on the IUCN red list (Ericsson and Bilz 2013). This may suggest that recent temporal stability in the abundance of wild reindeer, semi-domestic reindeer and domestic sheep in mountain regions of Norway (Austrheim et al. 2011) has had a beneficial effect on the conservation status of these species.

A previous study did not find a strong impact of reindeer herbivory on the diversity or species richness of vascular plants (Olofsson and Oksanen 2005). However, both the richness of red-listed species (excluding near-threatened species), and the abundance of some red-listed plant species did increase with reindeer grazing (Olofsson and Oksanen 2005). The list of Finnish red listed species in Olofsson & Oksanen’s (2005) study had almost no overlap with the seven species investigated here. Only *Botrychium* spp. was common to both, and Olofsson & Oksanen found that to be unrelated to reindeer herbivory. Also note that *Antennaria* spp. were suggested to be weakly favoured by reindeer herbivory: however, our species selection criteria did not lead to inclusion of these species in our analyses (Table 1). Our study thus supports the role of ungulate herbivory in tundra environments in determining the distribution of red listed species in Fennoscandia; thus the management of ungulate herbivores can influence the conservation of these species.

Herbivory may have different effects on diversity with environmental conditions: Speed et al. (2013b) found that decreasing herbivory lead to an increase in species richness at high elevations and an decrease at low elevations. The dependence of the effect of grazing upon elevation for alpine plant species richness has also been observed in the Italian Alps (Dainese et al. 2015) while Sacconne et al. (2014) highlighted how grazing in tundra environments may shift the system's trajectory following environmental perturbation. The mechanisms through which herbivory may affect plant diversity in such systems include colonisation and extinction effects (Speed et al. 2012). We observed a hump-backed relationship between herbivore density and habitat suitability for several plant species. Many herb species (the majority of the species in the current study are herbs) are highly selected by grazing herbivores in mountain ecosystems (Evju et al. 2006). The abundance of these species is therefore often negatively impacted by high densities of grazing herbivores (Bråthen and Oksanen 2001). At low herbivore densities the response of plant communities to herbivory may be mediated through the impact of herbivores on woody plant species (Olofsson 2006). Herbivory in the tundra can reduce or prevent the establishment of shrubs (Olofsson et al. 2009; Ravolainen et al. 2014; Speed et al. 2013a) and plant species richness has been observed to show a humped-backed relationship with shrub height (Bråthen and Lortie 2016). Alternatively, herbivory may affect species richness through differential effects of herbivory on plant functional types (Dainese et al. 2015), particularly those that relate to ecosystem productivity (i.e. species with facilitative versus retarding effects on ecosystem productivity, Bråthen et al. 2007). Thus the humped-back relationship between herbivore density and habitat suitability is likely shaped by the negative effect of high levels of grazing on selected herb species, and the loss of suitable open habitat caused by woody plant expansion at low levels of grazing.

In this study we investigated the role of herbivore density in determining habitat suitability for red-listed vascular plant species at a large spatial scale: mainland Norway. We used open-sourced species occurrence data to do this. The quality of individual records when using such data is unknown, even given the quality control steps applied here (see Section 2.1). However, none of the occurrence records used here are outliers in geographic space (Figure A5). Nevertheless, results should still be interpreted with some caution. Species distribution modelling only quantifies habitat suitability as a function of the input environmental variables. Habitat suitability can also be influenced by factors not included in the model development, for example land-use history.

We corrected for spatial bias in this study by using a weighted background approach (Fourcade et al. 2014) and objectively parameterized the models ENMeval (Muscarella et al. 2014). Despite the objective paramaterization, the response curves (Figure 2) suggest some degree of overfitting. This may be related to the different scales of the environmental variables used. The climatic variables were rasterized from 30 arc-seconds resolution (ca. 1 km^2). This is obviously of a different magnitude to the herbivore densities that were estimated at a municipality scale (median area = 459 km^2, Austrheim et al. 2011). However, due to the hierarchical selectivity of herbivores (Senft et al. 1987), and the temporal variation in herbivore densities at smaller spatial scales (Blix et al. 2014), the scale of herbivore density that we used here is most relevant to the process studied. Similarly, climate variables are often used at coarse scales in species distribution analyses (Franklin et al. 2013), even though plants respond to small-scale climatic variation (Lenoir et al. 2013). Thus, while our study does not completely fulfil the call of Wisz et al. (2013) for fine grained biotic interaction data, it does suggest that regional-level ungulate densities provide good estimations of the influence of herbivory as a biotic interaction on plant species distributions.

4.1. Conclusions and Management Implications

Grazing of domestic sheep and reindeer (wild and semi-domestic) is widespread in boreal tundra ecosystems (Bernes et al. 2015; Ross et al. 2016). Therefore, the results we present here have relevance for management of rare plant species across a large area. Intermediate levels of herbivore density were found to be associated with higher habitat suitability for several of the rare plant species selected in this study. Previous work has recognised the importance of management of herbivores for the conservation of plant species (Pykälä 2003; WallisDeVries et al. 1998). However, in our study we found relatively little spatial concordance between regions where herbivory most influenced the suitability for the selected species. This implies that management of herbivore densities to benefit the conservation of these red-listed species requires a high context dependency, to either focus on individual species (i.e. Figure 3), or on the limited areas where herbivore density strongly affects suitability for multiple species (i.e. Figure 4).

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Tables

Table 1. Summary information of the selected study species, including growth form, red list categorisation and number of observations in the data set and recent records (records in or after 1990) that passed data quality control. SDM were built for the species with names shown in bold text.

Species	Growth form	Status (2010/2015)[a]	Recent quality controlled records[b]	Total records[c]	Notes[d]
Alchemilla oleosa	Herb	VU/NT	0	0	
Antennaria nordhageniana	Herb	VU/EN	3	14	
Antennaria porsildii	Herb	LC/VU	1	12	*Antennaria alpina*
Antennaria villifera	Herb	NT/VU	69	213	*Antennaria lanata*
Arenaria pseudofrigida	Herb	NT/NT	19	108	
Botrychium lanceolatum	Pteridophyte	NT/VU	187	253	
Braya glabella	Herb	VU/EN	0	129	
Carex bicolor	Sedge	NT/EN	81	200	
Comastoma tenellum	Herb	NT/NT	324	610	
Gentianella campestris	Herb	LC/NT	2686	3718	
Nigritella nigra	Orchid	EN/EN	114	114	*Gymnadenia nigra*
Kobresia simpliciuscula	Sedge	NT/LC	353	712	
Lysiella oligantha	Orchid	EN/EN	3	4	*Platanthera obtusata*
Primula scandinavica	Herb	NT/LC	930	1554	NT on IUCN global red list. Endemic to Norway and Sweden
Pseudorchis albida	Orchid	NT/NT	1175	2125	
Pulsatilla vernalis	Herb	NT/LC	703	891	
Stellaria hebecalyx	Herb	CR/VU	21	28	
Taraxacum aleurodes	Herb	LC/VU	1	4	
Tephroseris integrifolia	Herb	CR/CR	13	18	
Trichophorum pumilum	Sedge	VU/EN	85	144	

[a] The species status on the Norwegian Red List in 2010 and 2015 (Henriksen and Hilmo 2015; Kålås et al. 2010).

[b] The number of records after quality controlling the data (removing duplicates, data with withheld localities, records prior to 1990, removing points in the sea)

[c] The total number of records downloaded from GBIF on (GBIF.org 2016a). Only georefererenced records located within Norway and with no known coordinate issues were downloaded.

[d] Notes including species synonyms.

Table 2 Proportion of study area (total area 317 578 km^2) where the occurrence of each species is limited by each environmental variable (see Figure 4). Note that the study area differs from the total area of mainland Norway (i.e. excluding Svalbard and Jan Mayan, 323 772km^2) due to use of 1 km raster grid. Proportions are rounded to two decimal places.

	Land Cover	MAP	MST	Precipitation seasonality	Tundra herbivores	Soil pH
Botrychium lanceolatum	0.17	0.47	0.24	0.05	0.04	0.04
Comastoma tenellum	0.00	0.44	0.33	0.06	0.03	0.14
Gentianella campestris	0.05	0.38	0.26	0.10	0.01	0.19
Kobresia simpliciuscula	0.04	0.39	0.40	0.09	0.06	0.02
Primula scandinavica	0.03	0.19	0.21	0.24	0.13	0.20
Pseudorchis albida	0.00	0.04	0.56	0.08	0.12	0.20
Pulsatilla vernalis	0.00	0.66	0.10	0.04	0.11	0.08

Figures

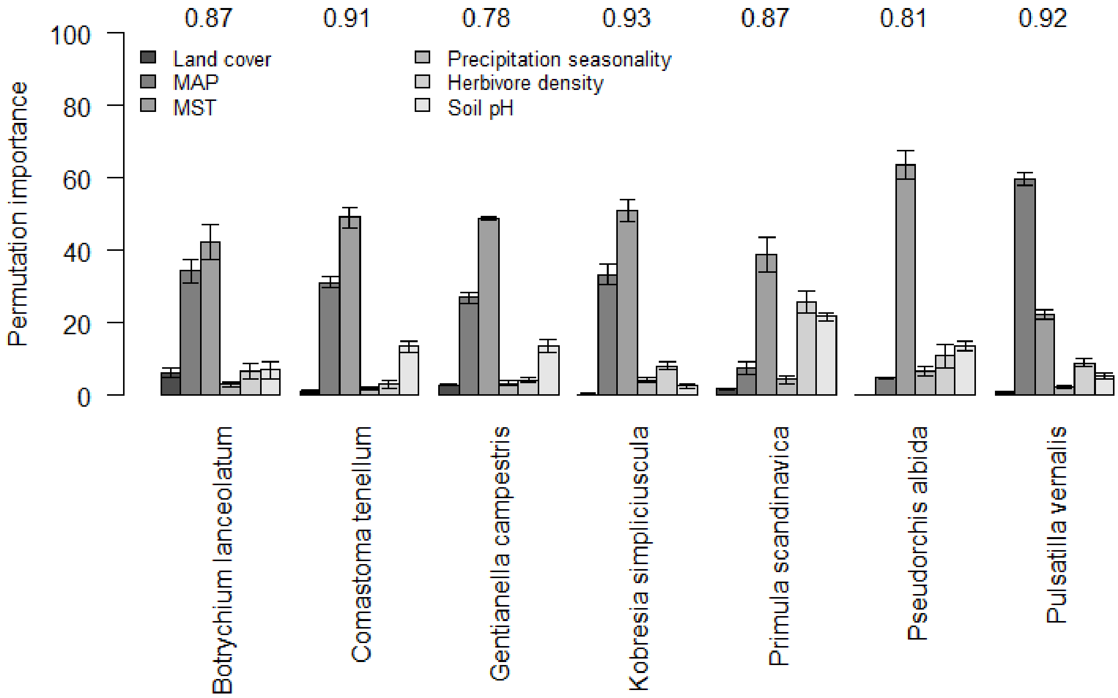

Figure 1 The permutational importance of each of the environmental variables to the final Maxent model for each species. Mean permutation importance values (expressed as a percentage) and standard deviations are shown from five cross-validated model runs. Values along the top axis show the mean AUC value for each of the species models. MAP refers to mean annual precipitation and MST to mean summer temperature.

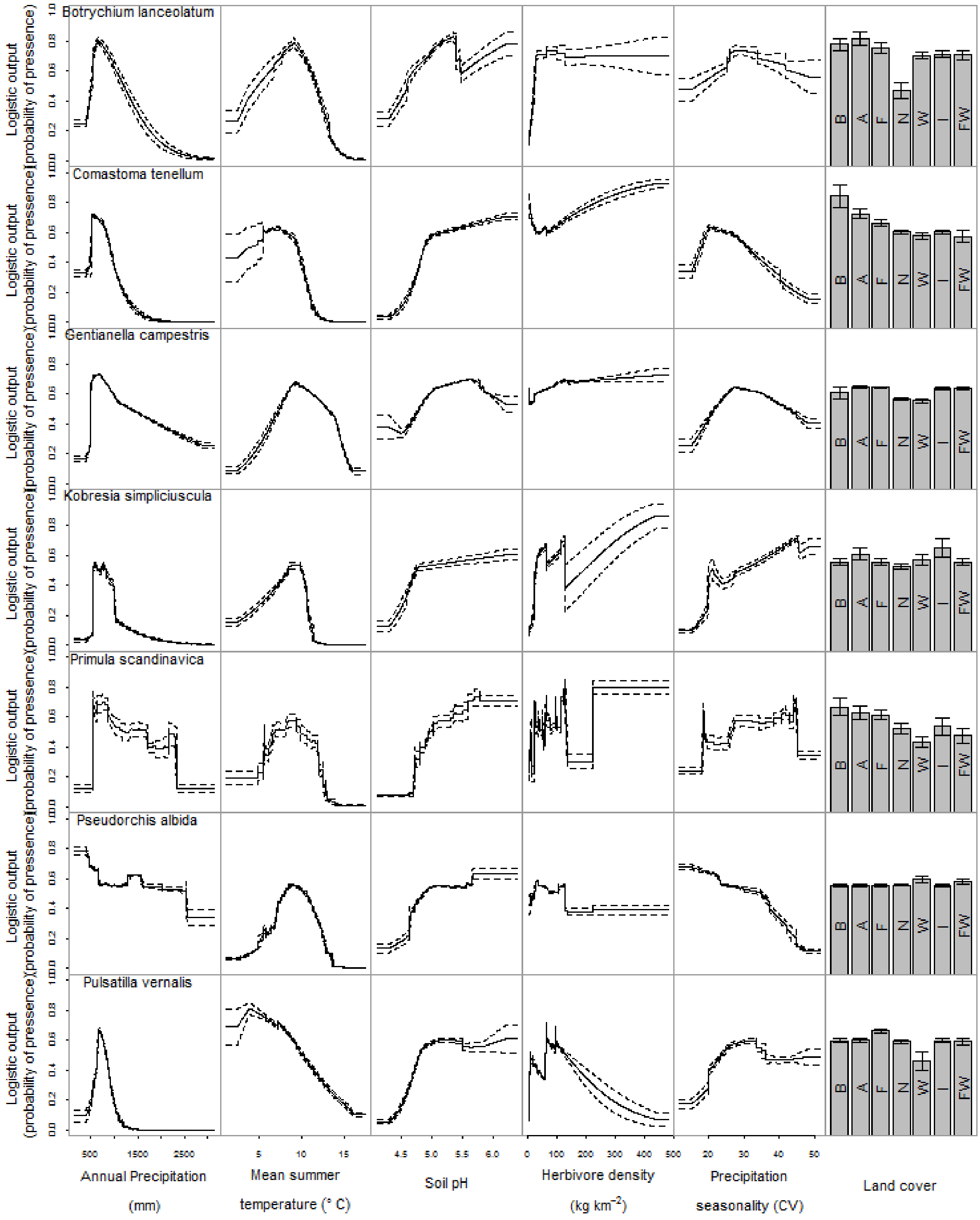

Figure 2 Response curves for all species and all variables. Means and standard deviations are shown. Species are ordered alphabetically, and variables by the contribution to the model predictions averaged across species (Figure 2). In the land-cover panels, B refers to build up, A to agricultural, F to forest, N to natural vegetation other than forest, I to ice and snow and FW to freshwater.

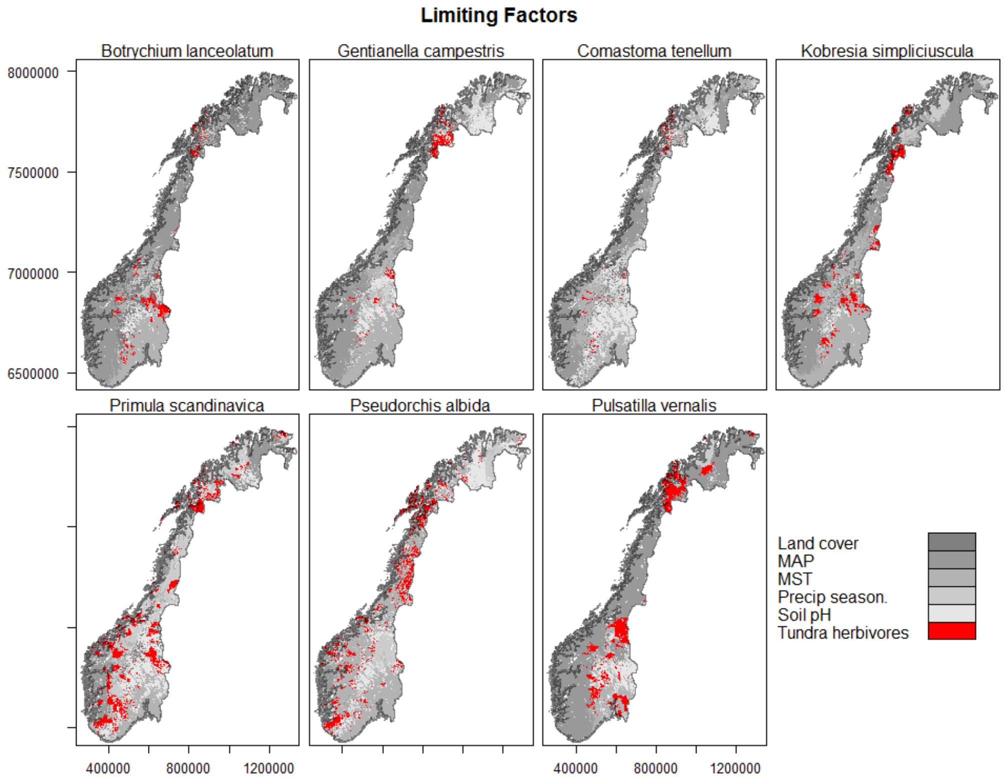

Figure 3 Limiting factors map for each of the species. The different colours represent the environmental variable that most limits the likelihood of occurrence of each species. The areas are presented in Table 2. UTM grid (zone 32). This figure is also provided as a KMZ file as supplementary material. MAP refers to mean annual precipitation and MST to mean summer temperature.

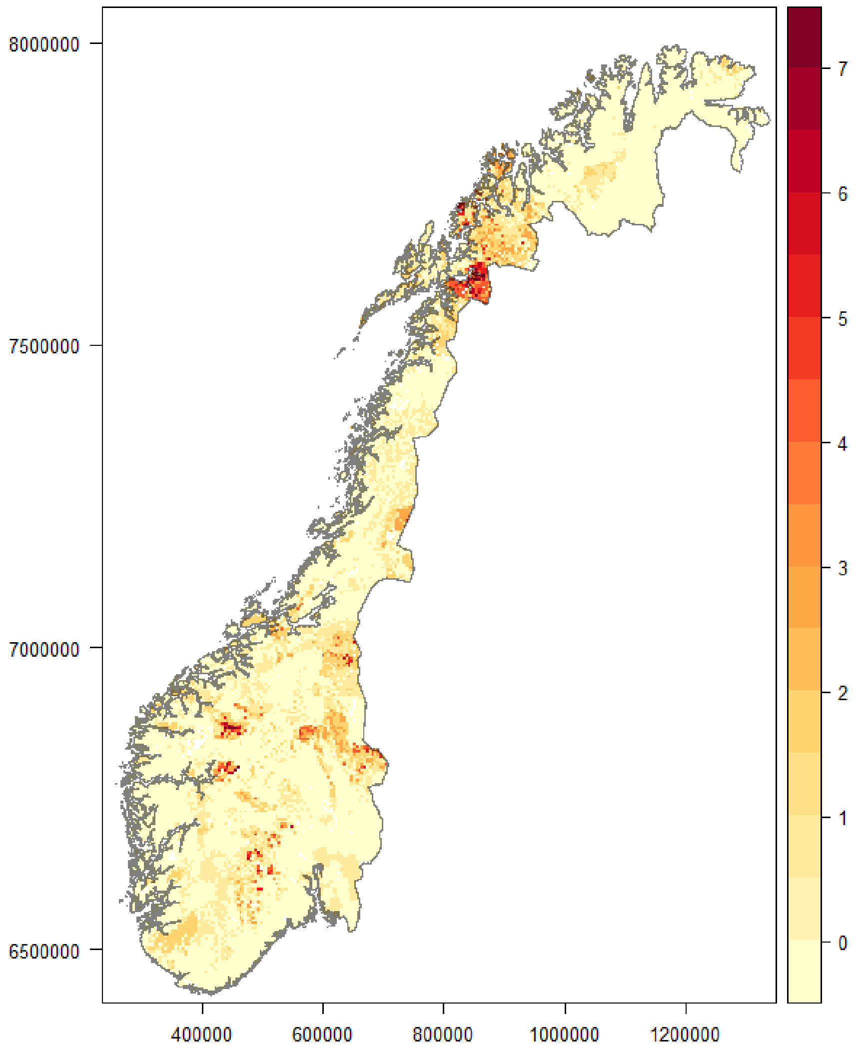

Figure 4 Map showing the number of species for which herbivore density is the factor most influencing the predicted suitability across Norway. Darker shades show where herbivore density limits a higher number of species. UTM grid (zone 32). This figure is also provided as a KMZ file as supplementary material.