

GIS-MODELLING OF POTENTIAL NATURAL VEGETATION (PNV): A METHODOLOGICAL CASE STUDY FROM SOUTH-CENTRAL NORWAY

GIS-MODELLERING AV POTENSIELL NATURLEG VEGETASJON (PNV): EIT METODE STUDIE FRÅ SENTRALE SØR-NOREG

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MASTER THESIS 30 CREDITS 2010



Preface

This study completes my work for a master's degree in Natural Resource Management at the Norwegian University of Life Sciences. It is part of the research programme 'Cultour' (KMB-project: 189977), initiated by The Norwegian Forest and Landscape Institute (TNFLI) and the Norwegian Hospitality Association and with financial support from The Research Council of Norway, as well as other partners. TNFLI provided me with financial support and has been a collaborating partner during the course of my work on this project.

I would like to thank my supervisor Terje Gobakken for helpful and constructive comments. Special thanks are also due to my secondary supervisor Dr Anders Bryn, who has provided support and good advice throughout the whole writing process. He deserves special thanks for assisting me with the vegetation mapping during the summer of 2009.

In addition, I would also thank the 'GIS-modelling group' at the Natural History Museum in Oslo for allowing me to participate in their internal Maxent seminar. Finn-Arne Haugen also deserves thanks for reviewing the manuscript and for valuable discussion on the mapping of PNVE prior to the mapping of my study area. I would also like to thank Catriona Turner for helping me with correcting the language.

I am especially grateful to my girlfriend, Elisabeth, for being patient and supporting me throughout the time spent in connection with this study.

Norwegian University of Life Sciences

Ås, 15. May 2010

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Summary

Potential natural vegetation (PNV) is a hypothetical natural state of vegetation that shows nature's biotic potential in the absence of human influence and disturbance. By comparing PNV with actual vegetation, anthropogenic influences can be assessed and quantified. Actual vegetation in a mid-south Norwegian mountain region, located around the village of Beitostølen in Valdres, was mapped during fieldwork in summer 2009. This vegetation map formed the basis for the development of PNV using three different modelling methods. The purpose was to explore the different methods and attempt to locate anthropogenic disturbances. The first method was based on an expert-validated manual mapped PNV map (PNVE) created simultaneously while mapping actual vegetation. The second model was created as a rule-based envelope GIS model (RBM), while the third model was created with a statistical predictive GIS modelling method, Maxent. RBM and Maxent were created with a basis in actual vegetation in addition to environmental predictor variables.

All models predicted the same vegetation types for 61% of total area, while different vegetation types were only predicted for 2% of total area. PNVE and Maxent were the two methods with highest accordance (87% of total area). Differences among modelling outputs were related to determine the upper potential forest limit for dominating tree species (birch and spruce), to model PNV for areas which are moderately to heavily disturbed by humans (e.g. farmland, housing estates, drained forests/swamps), and to model vegetation types that occur in their ecological extremities (e.g. humid types, rich types, successional state). The general tendencies for all three PNV models show a considerable increase and elevation of spruce forest, with a stable amount of birch forest, and decreasing amounts of boreal heath and meadow communities. Areas with boreal heath and meadow communities are transformed into mountain birch forest, whereas birch forest at lower altitudes is transformed into spruce forest.

PNV maps and actual vegetation maps were compared to reveal traces of earlier human disturbance; areas where vegetation types differed were considered as anthropogenically disturbed. All models predicted that more than 50% of vegetation from the actual vegetation map would be prevented from reaching its biotic potential. PNVE was the only model which captured human disturbance above the upper potential forest limit in the PNV maps. Shifts in forest distribution are known to be one of the major consequences of land-use changes in mountain areas.

Samandrag

Potensiell naturleg vegetasjon (PNV) er ein hypotetisk naturleg tilstand som vegetasjon syner naturens biotiske potensiale, forutsett at menneskeleg påverknad og forstyrring aldri har funne stad. Ved å samanlikne PNV og aktuell vegetasjon kan menneskeleg påverknad verta kartfesta og kvantifisert. Aktuell vegetasjonen vart kartlagt gjennom feltarbeid sommaren 2009. Dette vegetasjonskartet danna grunnlaget for seinare utvikling av PNV kart ved hjelp av tre ulike tilnærmingar for ein sentral Sør-Norsk fjellregion, lokalisert rundt Beitostølen i Valdres. Hensikta var å undersøkje ulike tilnærmingar, og forsøkje å kartfesta menneskeskapte forstyrringar av naturen. Første tilnærming er basert på eit ekspert evaluert, manuell kartlagt PNV kart (PNVE) som vart danna fortløpande med kartlegging av aktuell vegetasjon. Den andre tilnærminga er danna som ein regelstyrt konvolutt-modell (RBM) i GIS, medan den tredje tilnærminga er oppretta med ein statistisk prediktiv GIS-modellerings metode, Maxent. Dei to GIS-modellane vart danna på grunnlag av aktuell vegetasjon og miljøvariablar.

Alle tilnærmingane predikerte same vegetasjonstypar for 61% av det totale areal, medan berre 2% av totalt areal vart predikert med ulike vegetasjonstypar. PNVE og Maxent var dei to tilnærmingane med høgast samsvar (total 87% av areal). Skilnadar mellom tilnærmingmåtene var knytta til fastsetjing av øvre potensielle skoggrense for dominerende treslag (bjørk og gran), til å lage PNV for område som er moderat til sterkt forstyrta av menneskeleg endringar (t.d. jordbruksområder, boligfelt, drenerte skogar/myrar) og til å predikera vegetasjonstypar som førekjem i deira økologiske ytterpunkt (t.d fuktige typar, rike typar, ulike suksesjonsstadium). Generelle trendar for alle PNV tilnærmingane syner ei tydeleg auke i mengd og auke av granskogen, med stabil arealmessig mengde bjørkeskog, og ein betydeleg reduksjon av boreale lyngheiar, og boreale engsamfunn. Område med boreale lyngheiar og engsamfunn blir omdanna til fjellbjørkeskog, medan bjørkeskogen ved lågare høgder vert omdanna til granskog.

PNV kart og aktuellt vegetasjonskart vart samanlikna for å avdekke tidligere menneskeleg forstyrring. Område som førekom med ulike vegetasjonstypar vart sett på som påverka av menneskelege forstyrringar. Alle tilnærmingar predikerte at meir enn 50% av vegetasjon frå gjeldande vegetasjonskart vart forhindra frå å nå sitt biotiske potensial. PNVE var den eineste modellen som fanga opp menneskelege forstyrringar ovanfor øvre potensial skoggrensen i PNV karta. Endringar i skogfordelinga er kjent som ein av dei største konsekvensane av arealbruksendringar i sørnorske fjellområde.

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1 Introduction

Human activities have either directly or indirectly influenced almost every part of our world (Liu 2001), and are increasingly affecting the vegetation dynamics (Pickett 2005). These activities affect the landscape in numerous ways, ranging from landscape without any significant human impact to urban landscapes (Forman & Godron 1986). Land-use changes are identified as the major result of human influence (Chapin & Körner 1995), and in the Nordic region they are mostly related to altered agricultural activities (Hallanaro & Pylvänäinen 2002). Agricultural change is an ongoing process throughout Europe, where general trends show intensification of fertile and accessible areas, while poor and inaccessible areas are abandoned (MacDonald et al. 2000). The effects of agricultural abandonment are particularly noticeable in mountain areas (MacDonald et al. 2000). The same trends are identified for Norway (Fjellstad & Dramstad 1999). Changes may affect current landscape biodiversity, aesthetics, recreation, tourism, and agricultural management (Bryn et al. In press; Fjellstad & Dramstad 1999). It is important to understand the underlying processes due to their varying environmental consequences (Gellrich et al. 2007).

Norwegian mountain regions have been used for summer dairy farming for centuries (Reinton 1955). The oldest traces of this seasonal activity date back to the Late Neolithic, 2600–2400 BC (Prescott 1999). Such extensive farming practices included the clearing of pastures, grazing by domestic animals, and the collection of firewood and winter fodder (Aas & Faarlund 1995; Prescott 1999). The use of summer dairy farms reached its peak around the mid-19th century, when there were *c.*90,000 farms (Aas & Faarlund 1996). However, in the last 100 years the practice has decreased considerably, especially after World War II (Daugstad 2000). Today, there are only *c.*1300 mountain farms remaining in the whole of Norway (TNFLI 2008).

The decline in summer dairy farming affects the majority of outfields, which are no longer being used in traditional ways. This has led to a woodland succession all over Norway, but particularly in the subalpine vegetation zone (Potthoff 2007), where open areas and fields are gradually covered by shrubs and small trees (Øyen & Gjølshø 2007). Large-scale encroachment by trees and shrubs has led to decreasing biodiversity and extensive landscape changes (Sickel et al. 2004). Forest distribution shifts have been observed as the major consequence of land-use changes in rural districts and mountain areas (Bryn 2008; Gehrig-Fasel et al. 2007; Gellrich et al. 2008; Vittoz et al. 2008). These areas are also subject to another type of land-use change which alters and changes the mountain ecosystem, namely

the conversion of former summer dairy farming areas to tourist destinations and cabin villages (Taugbøl et al. 2001). This results in a fragmented and altered landscape where anthropogenic influences can be readily detected (Mæland 2005). In contrast, traces of former land-use are not as easy to detect as modern landscape changes. With increasingly modified and altered landscape structures, becomes it more important to understand how human disturbance affects the ecosystem and successions (Pickett 2005). Following disturbance, the ecosystem transforms through succession towards a dynamic balance between disturbance and development, until the disturbing factor no longer is considered a threat (Forman & Godron 1986). Former disturbed areas exist today as secondary regrowth successions towards a state of dynamic equilibrium. Through the application of ecological knowledge, such traces can be investigated and quantified using a number of Geographic Information System (GIS) related techniques (O'Sullivan & Unwin 2003).

The increased use of GIS tools for analysis and also statistical techniques has led to considerable use of GIS-models in ecology (Guisan & Zimmermann 2000). Simultaneous with improvements in methods and techniques, also species occurrence data with good precision and environmental data with high spatial resolution are more common and accessible (Bakkestuen et al. 2008; Elith et al. 2006). The variety of modelling methods available can be used to the benefit of a range of management activities (Barry & Elith 2006), such as the creation of species distribution models (Wollan et al. 2008), modelling of threatened species (Gibson et al. 2007), the application of spatial models for management and monitoring (Bryn et al. In press; Koniak & Noy-Meir 2009), large-scale spatial landscape models (Scheller & Mladenoff 2007), and models of vegetation and disturbance dynamics (Bryn 2008; Carranza et al. 2003; Gehrig-Fasel et al. 2007; Wallentin et al. 2008). In the latter case, has vegetation mapping proved useful as a reference for evaluating vegetation disturbance (Carranza et al. 2003).

Human influence on landscapes can be assessed and quantified through the comparison of actual vegetation and potential natural vegetation (PNV) (Ricotta et al. 2000). The idea of the development and mapping of potential natural vegetation was introduced by Tüxen (1956) as a hypothetical natural state for vegetation in order to show the biotic potential in nature. A hypothetical vegetation map can be constructed based on actual vegetation, where the existing vegetation serves as a reference point for potential distribution to sites of similar habitats, but where such vegetation is absent (Moravec 1998). The construction and use of PNV maps is increasing and such maps are evidently useful for determining the effects of human impact on vegetation patterns (Capelo et al. 2007; Carranza et al. 2003; Gehrig-Fasel et al. 2007; Ricotta et al. 2002).

The main purpose of this study is to explore three different methods to model potential natural vegetation maps. The second aim is to try to locate anthropogenic disturbances around Beitostølen, a rural district in the southern part of central Norway using these three modelling methods.

2 Materials and method

2.1 Study area

The study area is located in connection to the vicinity of Beitostølen and the rural district of Beito, in the northern part of Øystre Slidre Municipality, in the valley of Valdres, Oppland County, in southern central Norway (Figure 1). The study area stretches from Mount Bitihorn in the north (61°17'N) to Lake Øyangen in the south (61°14'N). The total mapped area is 34.2 km², and ranges in altitude from c.680 m a.sl. to c.1600 m a.sl.

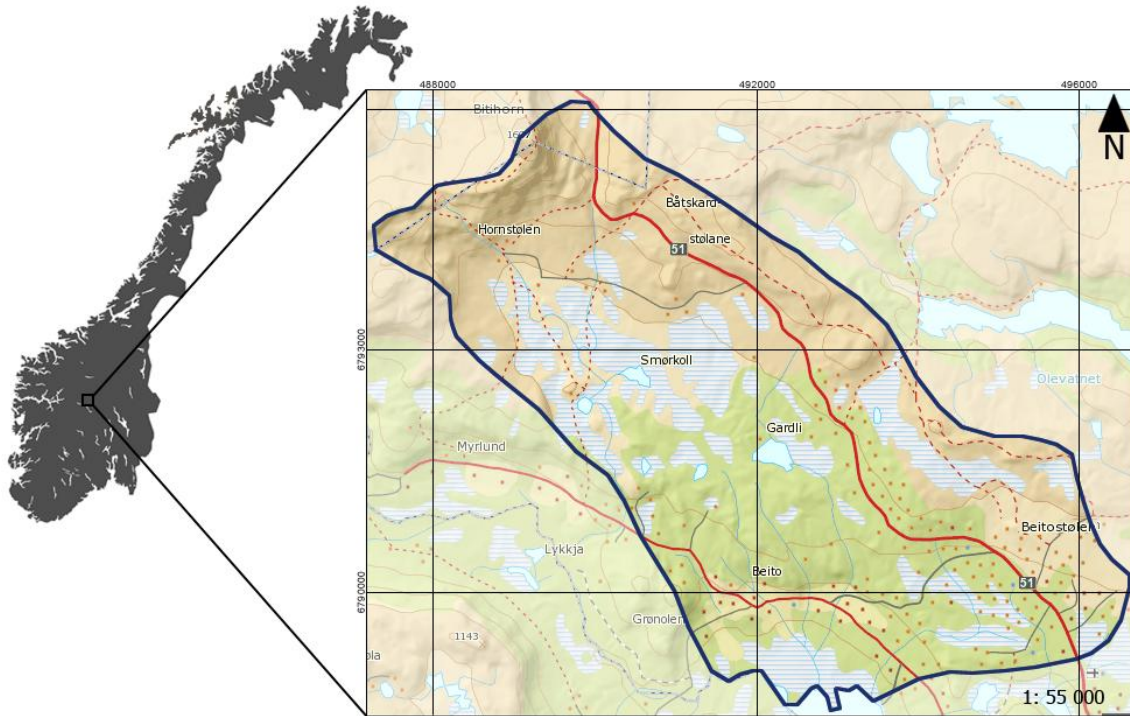


Figure 1: Location of study area, Map projection EUREF89/UTM zone 32N (source: www.gislink.no)

2.1.1 Geology

Most of the study area is situated on metamorphic sedimentary rock and volcanic rock consisting of primary quartzite/quartz schist and phyllite dating to the Cambro-Silurian era. The south-eastern part consists of metamorphic gneiss dating from the middle–late Proterozoic era. In the highest altitudes of the northern part of the area there is a small zone of Valdres-sparagmite. The bedrock is mainly covered by moraine from the last ice age, but large areas are also covered by peat and bogs (Lutro & Tveten 1996; Sollid & Trollvik 1991).

2.1.2 Climate

The precipitation for the area is registered at a weather station situated in Beito (754 m a.s.l.; WGS84/UTM33N, 6805398 N, 170565 E). The annual average precipitation recorded for the period 1895 to the present is 723 mm. This station does not record temperature data, so these are collected from the closest weather station (*c.* 17 km south-east), Løken weather station in Volbu (521 m a.s.l.; WGS84/UTM33N, 6790881N, 180348E). The annual mean temperature is 1.5°C; the coldest month is January, with an average of −9.9°C and July is the warmest, with 13.1°C. The average monthly normal temperature values for the growth season (June–August) was 12.4°C for the period 1962–2009 and has slightly increased over the years (Figure 2) (TNMI 2010).

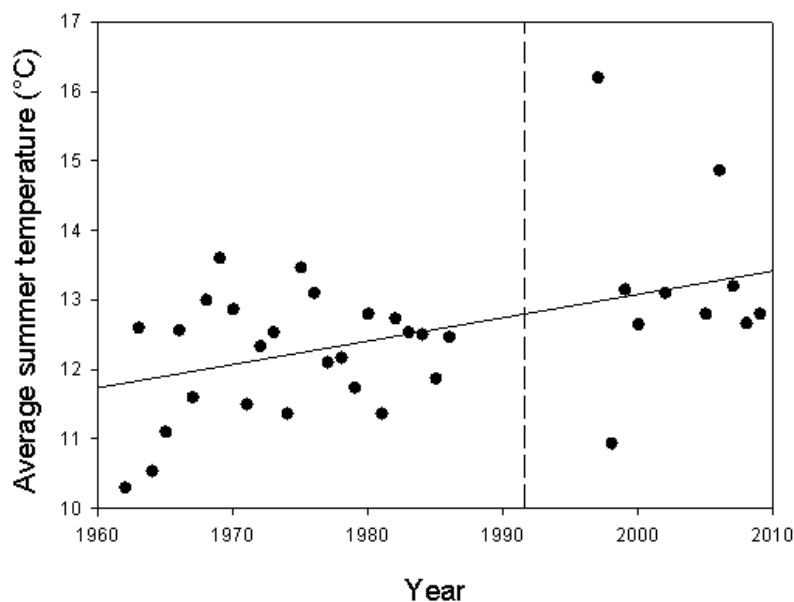


Figure 2: Yearly average summer temperature (June, July and August) from Løken weather station 1962 – 2009. Registrations from 1987 – 1996, 2001, 2003 and 2004 were not recorded. The registrations were divided into two groups (dashed line), older temperatures (1962–1986) and recent temperatures (1997–2009). Average temperature from each group were compared and tested statistically for differences.

2.1.3 Nature

The vegetation stretches from the middle boreal zone to the mid-alpine zone, where the border is situated at *c.* 850 m a.s.l. Beitostølen is located in a transitional climatic zone, an intermediate stage between a continental climate and an oceanic climate (Bakkestuen et al. 2008; Moen 1999). The lower part of the valley side up from Lake Øyangen towards Beitostølen is dominated by Norway spruce forest (*Picea abies*). Moderate to richer deciduous forest with birch (*Betula pubescens* ssp. *pubescens*) and aspen (*Populus tremula*) dominates the eastern part of the study area, around the agricultural landscape in Beito

(c.700–850 m a.s.l.). The area between Beito and Beitostølen has especially high productivity (Axelsen 1975). Fens and bogs are mainly located on the flattest areas within the study area, especially above present upper potential forest limit for birch, where there is a mosaic of mires and dwarf shrub heaths. Fens and bogs dominate also the lower lying plain to the north of Lake Øyangen and the area below Beitostølen. Forest stands of mountain birch (*Betula pubescens* ssp. *tortuosa*) were registered up to approximately 1090 m a.s.l. during the fieldwork. Forest stands of spruce were registered up to 920 m a.s.l., but smaller stands were observed up to 1020 m a.s.l. Podzol soil dominates the majority of the area in the municipality, but grey-brown podzols occur in places and improve the forest productivity, especially in sloping terrain (Axelsen 1975). Low-alpine vegetation types were observed down to 820 m a.s.l. The low-alpine zone is dominated by fens and dwarf shrub heath with small proportions of tall forb meadows and lichen heaths. Higher up, there is a mid-alpine zone dominated by dry grass heath, boulder fields, and exposed bedrock with small patches of snow-bed vegetation.

2.1.4 Historical land-use

There has been extensive human agricultural activity in the area around Beitostølen for centuries. Cultural remains indicate the earliest human settlement occurred in the Younger Stone Age (Møller 2003). Originally, Beitostølen comprised a summer dairy farm village, and summer dairy farming has been traditionally practised for more than 200 years. Around the year 1920 there were 16 summer dairy farms in Beitostølen, and the area was used for summer dairy farming until the last farm was abandoned there around 1970 (Møller 2003).

The traditional summer dairy farms in the area produced dairy products for their own households and for sale, and this required considerable amounts of firewood. In addition, all of the fields in the proximity of the summer dairy farms were managed, and when birch forest seedlings sprouted they were prevented from growing by immediate removal, grazing and manual clearing. The majority of the bogs contain large amounts of iron ore, and hence are a useful source of raw materials for iron production. The discovery of several early coal pits indicate that the production of iron was practised around Beitostølen for centuries, and this tradition continued until the beginning of the 19th century. This may indicate that large trees once grew in the area (Møller 2003). Matgrass (*Nardus stricta*) was harvested in the outlying fields, and sedges (*Carex* spp.) were cut from bogs for use as livestock fodder during the winter months. Foliage from birch, aspen and alder (*Alnus incana*) was collected and used in large quantities, both as new-grown leaves in spring and after defoliation in autumn. Different types of cup lichen (*Cladonia* spp.) were collected during summer and transported down to

the main farm during the winter (Gjesdahl 1965). Moss and peat for fuel were also collected on the summer farms (Møller 2003). According to Axelsen (1975), 20–25% of the area below the potential forest limit in Øystre Slidre Municipality has been deforested as a result of mountain farming activities.

Many domestic animals graze today in the outlying fields in Øystre Slidre Municipality. As the general trend in Norway, the total numbers have decreased the last decades (Bye et al. 2005). The total number of goats in Øystre Slidre Municipality started to decrease around 1950, when 2132 goats were recorded (Gjesdahl 1965), and by 2008 the number had fallen to 734 (SSB 2008). The numbers of sheep also decreased, from 4946 in 1989 to 2745 in 2008. Cattle, on the other hand, showed a small increase in the same period, from 2388 to 2594.

Valdres is among the areas in Norway where summer dairy farming was most widespread in the past (Reinton 1955) and the tradition still has solid roots there (TNFLI 2008). On a national scale this tradition is decreasing (Bryn & Daugstad 2001). This is also the case in Øystre Slidre Municipality, which had 502 summer dairy farms in 1939 (Gjesdahl 1965) but only 73 in 2008. Despite this fall in numbers, the municipality has the most summer dairy farms still in use in Norway. Out of the total in the municipality, six are located within the study area: three with goats, two with cattle, and one with both cattle and goats (TNFLI 2008). With the exception of one farm, all are located in the dairy farm cluster of Hornstølen, at a lower altitude south of Bitihorn (Figure 1).

Beitostølen has undergone enormous expansion as a tourist destination in the past century; the first 200 tourists came around the year 1900, and in 2004 more than 200,000 guest days were recorded (Alpinanleggenes Landsforening 2005). Especially during the last 50 years, Beitostølen has changed from a summer dairy farm cluster to a tourist destination and cabin village (Møller 2003). Today, cabins, hotels and ski lifts dominate the centre of Beitostølen.

2.2 Data material

2.2.1 Mapping actual vegetation

Actual vegetation was mapped using the Norwegian Forest and Landscape Institute's mapping system for vegetation at scales 1:20,000 to 1:50,000 in the period late July – early August 2009. The system has 45 vegetation types and 12 other land cover types (explained in Bryn 2006). Unique vegetation types are separated based on homogenous species composition, indicator species and vegetation physiognomy. Symbols were used to add additional information to vegetation types, such as ditched areas, sparse forest, and soil

characteristics (Appendix 3). Using portable lens stereoscopes in the field, vegetation types were drawn onto colour aerial photos at a scale of 1:35,000 (Appendix 1)(Rekdal & Larsson 2005). Almost all drawn polygons were visited during the course of the fieldwork and the minimum figure size was *c.* 0.2 hectares. Originally includes the system use of mosaic figures in combination of two vegetation types, this practice were excluded to simplify the later modelling of potential natural vegetation maps in GIS.

2.2.2 Environmental variables

Environmental predictor variables for the modelling were selected with results from the built-in jackknife test of variable importance in Maxent (Phillips & Dudik 2008). Environmental variables that showed low contribution to the development of the model were not used. The following available variables were tested: DEM (Digital Elevation Model), aspect, slope, soil nutrient, soil humidity, soil characteristics, bedrock, and sediments. The variables selected for the study, DEM and soil characteristics, were those which stood out from the others variables in the jackknife test.

A DEM with 2 m resolution was obtained from The Norwegian Forest and Landscape Institute. This DEM is based on LiDAR scanning performed by Blom Geomatics in 2007. The DEM formed the basis when designing both the rule-based model and the Maxent model. Due to the lack of environmental variables with proper resolution, the altitude (taken from the DEM) was used as a proxy factor for summer temperature (Austin 2002). Most researchers, however, agree that the uppermost potential climatic forest limit is mainly regulated by summer temperatures (Brockmann-Jerosch 1919; Bryn 2008; Bryn 2009; Danby & Hik 2007; Daubenmire 1954; Fang & Li 2002; Holtmeier 2003; Körner & Paulsen 2004; Mork 1968; Walter 1968; Wielgolaski 2005). Information about soil properties was derived from the actual vegetation map (AVM) grouped, prepared, and used in the statistical modelling to rule out inappropriate soil characteristics relating to the establishment of tree stands.

2.3 Modelling of potential natural vegetation

First, a manual PNV map based on expert knowledge (PNVE) was produced simultaneously with mapped actual vegetation in the study area. The construction of potential natural vegetation extrapolates present vegetation types to similar habitats, but where these classes do not presently exist (Moravec 1998). This expert-evaluated method relies on the fieldworker's judgment and understanding of ecology and natural succession. This type of subjective expert knowledge is crucial for defining potential natural vegetation based on the relationship between actual vegetation, vegetation dynamics, and environmental factors (Ricotta et al.

2000). Second, a rule-based exploratory envelop model (RBM) was produced in a GIS using the actual vegetation map as a basis. General rules of change were dedicated to each vegetation polygon at all altitudinal levels. This model captures key changes, and for the purpose of reducing uncertainty a qualitative outcome is more important than a quantitative outcome (Perry & Millington 2008). Third, a statistical modelling approach, Maxent (maximum entropy), was used for two of the dominating tree species in the most common forested vegetation types, in order to create a statistical PNV map. This is a machine learning method that uses environmental variables and evaluates the combinations and interactions among the variables to predict the distribution of suitable habitats for particular species (Newbold et al. 2009; Phillips et al. 2006; Wollan et al. 2008).

2.3.1 Mapping of expert-evaluated potential natural vegetation

The expert-evaluated potential natural vegetation and actual vegetation were mapped simultaneously. During the fieldwork, I (assisted by Dr. Anders Bryn), registered which type the actual vegetation type should have been originally, unless the vegetation already had reached the potential dynamic equilibrium state. Prior to the fieldwork, collective inspection of the area was performed to highlight any cases of doubt and to coordinate subjective judgments. This use of the expert-evaluated method to model PNV had been tried out earlier for two territories in western and northern Norway. The manually mapped PNV map was compared to the GIS-models, and was intended to serve as a control for the GIS-models' reliability. The accuracy of the modelled PNV maps was tested against actual vegetation maps (Chahouki et al. 2010).

2.3.2 Rule-based modelling of potential natural vegetation

A rule-based envelope model was developed with the intention of making rules for polygons, at all altitudinal levels. The rules for modelling were grounded on specific findings in nature from within the study area. Vegetation types from the actual vegetation map and the DEM was implemented together through a standard overlay procedure in ESRI's ArcMap 9.3 (Ormsby et al. 2001). Actual vegetation types were divided into elevation levels every 20th altitudinal metre. An attribute table connected to the actual vegetation map, with classes divided into altitudinal zones, was exported and reorganized for the implementation of modelling rules (Table 1) in Microsoft Excel 2010, and joined back using standard join procedure in ArcMap 9.3 to the actual vegetation map (Bryn 2006). Among other purposes, the model was designed to change a polygon with alpine vegetation, if it occurred lower than the identified upper forest limit, to the most reasonable forest type at that location. This is

dependent on the properties stored on the actual vegetation map, such as soil properties (moisture, nutrients and substrate), human influence, and altitude (Bryn 2008). Aspect was ruled out, since most of the study area is in a southern position.

Table 1: Altitudinal vegetation type transition rules for the rule-based envelope modelling. See Appendix 2 for vegetation type description and Appendix 3 for additional information relating to the vegetation types.

Vegetation group	Actual vegetation type	Altitude (m a.s.l.)	Potential vegetation type
Poor and dry vegetation types	2c%, 2e%	< 1100	4a]%
	2c%B	< 1100	4a]B
	2c>	< 1100	4a]B
	4a, 4a%]	< 1000	7a, 7a%]
	7a&	< 1000	7a
Intermediate vegetation types	2e, 2e!, 2e& 2eg, 2eF, 2ej	< 1120	4b
	2e!F	< 1100	8c&
	2e&<	< 1120	4b<
	2ev%	< 1120	4b]%
	1b, 1bB, 4b, 7b&	< 1020	7b
	4b]	< 1020	7b]
Rich vegetation types	3bs, 3b&s, 3bsg	< 1140	4c!
	3b, 4c	< 1140 – 1040	4c
	4c, 4c]	< 1040	7c, 7c]
	7c&	< 1040	7c
Wetlands and peatland forest	8c&, 8d&	< 1000	8c*&, 8d*&
	9cs, 9c!	< 1050 – 950	8c&!
	9cs, 9c!, 9c&!	< 950	8c*!
	9c&	< 1050 – 950	8d&
	9c&	< 950	8d*&
	9c&!k	< 1050 – 950	8d&!
Anthropogenic types	11a	< 1140	4c
	4g, 11b, 12d, 12e, 12f	< 1120 – 1020	4b
	4g, 11b, 12d, 12e, 12f	< 1020	7b
	12f	> 1120	2e
Ditched types	3bgT	< 1100	8d&
	4cT	< 1000	8d*
	9aT, 9cT	–	9a, 9c
	11aT, 8d&T	< 1000	8d*&
	11bT, 12dT, 12eT, 12fT	< 1100 – 1000	8c&
	11bT, 12dT, 12eT, 12fT	< 1000	8c*
Unchanged types	1a	–	1a
	1b	> 1120	1b
	2a, 2b	–	2a, 2b
	2c, 2e%, 2e., 2e:, 2eÅ	> 1100	2c, 2e%, 2e., 2e:, 2eÅ
	3a, 3b, 3b{	> 1140	3a, 3b{
	7a, 7b, 7c	–	7a, 7b, 7c
	8c&	> 1100	8c&
	9a, 9b, 9c, 9e	–	9a, 9b, 9c, 9e
	12b, 12c	–	12b, 12c

2.3.2.1 Defining upper potential forest limit

Since modelling rules had to be manually set for the rule-based model, the upper potential forest limit for birch and spruce needed to be manually identified. A forest is defined as an area consisting of trees > 2.5 m high with a crown cover of at least 25% (Rekdal & Larsson 2005). The upper potential forest limits were identified in five ways (Table 2). First, the upper potential forest limit was derived from the actual vegetation map and observations made during the fieldwork. Second, the upper potential forest limit was identified from the PNVE

model. Third, the upper potential forest limit for birch was identified on a regional scale by following the upper forest limit on eight surrounding topographic maps at a scale 1:50,000 (Norwegian Mapping Authorities N50 series, map number: 1616 I, 1616 IV, 1617 I, 1617 III, 1617 IV, 1716 IV, 1717 III, 1717 IV). The same method was also used for spruce, but was done by following the upper forest limit on The Norwegian Forest and Landscape Institute's area resource map (theme: type of wood) (TNFLI 2010) within the same area as for the topographic maps (where the theme cover corresponded). Fourth, the upper potential forest limit was found in registrations from a major subject survey carried out in the mid-1970s in Øystre Slidre Municipality (Axelsen 1975). Fifth, and finally, the upper potential forest limit was identified from Aas & Faarlund's (2000) registrations around Beitostølen from the early 1960s.

Table 2: Registration of upper forest limit and upper potential forest limit within and around the study area; p = poor forest, i = intermediate forest, r = rich forest.

Source	<i>Betula pubescens</i> (m a.s.l.)	<i>Picea abies</i> (m a.s.l.)
Vegetation map	990p/1100i/1070r	930p/850i/830r
Topographic map	1180	1080
Axelsen 1975	1130	1040*
Aas & Faarlund 2000	1100	975
Chosen upper potential forest limit	1140r/1120i/1100p	1040r/1020i/1000p

*Registration from Mellsenstølane dairy farm cluster located c. 26 km south-east of Beitostølen.

2.3.3 Statistical predictive modelling

Maxent version 3.3.1, based on a maximum entropy algorithm (Phillips et al. 2006; Phillips & Dudik 2008), was used to prepare a statistical predictive model for the potential distribution of birch and spruce. Since Maxent uses occurrence data to develop the model, random plots were assigned to vegetation types where birch and spruce occurred, either as primary or secondary type of wood, using the Hawth's analysis tools v.3.27 extension in ArcMap 9.3: 105 plots for birch and 75 plots for spruce. A few plots (< 10) were added for both species to ensure good spatial representation of both populations (Hengl et al. 2009). Since the vegetation figures with spruce were distributed to a lower part of the study area, 27 additional plots were assigned from single spruce stands identified from aerial photos to prevent bias in the sampling and to provide a better basis for the later statistical modelling (Figure 2). High resolution aerial photographs made it easy to identify separate spruce stands in the mountain birch forest (Figure 3). Random spruce plots tended to serve as supplementary species-presence data. Default values for all parameters (features, auto; regularization value, 1; convergence threshold, 10^{-5} ; maximum iterations, 500; and background points, 10,000) were

accepted when running the model (Gibson et al. 2007; Riordan & Rundel 2009), except for random test percentages, which were set at 25% for spruce and 30% for birch.



Figure 3: Aerial photo of spruce stands (a) and single spruces (b) in the mountain birch forest. (Scale 1:1500. (Source: www.norgebilder.no, photographed June 2008)

The predictions results from Maxent are evaluated by a threshold-independent receiver operating characteristic (ROC) analysis, known as AUC values, calculated within the program. The ROC curve evaluates a model's usefulness to predict the relative distribution probability of species (Elith et al. 2006). The closer to 1 these AUC values are, the greater the model's predictive ability is: AUC values < 0.5 are equal to those in a random prediction model (i.e. no different from random models); values < 0.7 indicate poor prediction ability, values 0.7–0.9 indicate moderate prediction ability; and values > 0.9 indicate significant prediction performance (Pearce & Ferrier 2000).

The prediction values are cumulative. A grid cell's value is the sum of probabilities of all grid cells with equal or lower value (Deblauwe et al. 2008; Phillips et al. 2006). The probability scales are all relative occurrence probabilities, and therefore a given value is not directly comparable to a value that is twice as high (Jimenez-Valverde & Lobo 2007). Sensible threshold probability needs to be set when converting a continuous relative model to a categorical map (Fielding & Bell 1997). Maximum sum threshold (MST) were used to set the thresholds for upper potential forest limit in the Maxent predictions of spruce and birch (Jimenez-Valverde & Lobo 2007). This is the value along the ROC curve which occurs at greatest distance from the $y = x$ line:

$$\text{MST} = \text{Sensitivity} (1 - \text{Training omission}) + (1 - \text{Specificity}(\text{Fractional area}))$$

Soil properties from the actual vegetation map were combined with Maxent distribution predictions for birch and spruce in ArcMap to divide the predicted forest distribution into poor, intermediate, rich, and peatland forest. For types 12d, 12e and 12f on actual vegetation map, soil properties were derived and implemented from PNVE.

2.4 Uncertainty relating to the models

Making prediction models is difficult and there are many uncertainties (Barry & Elith 2006). Two different uncertainty maps were designed to assess uncertainties between the different models and in the modelling of various vegetation types. An overlay procedure was run between the three prediction models to assess the differences among the prediction models. The predictions were compared on vegetation type level (without additional information). The uncertainty map for modelling vegetation types was based on expert knowledge of how different ecological characteristics can affect the development towards a natural dynamic equilibrium state.

2.5 Anthropogenic influence

The actual vegetation map was compared through a standard overlay procedure in ESRI's ArcMap 9.3 (Ormsby et al. 2001) with PNV maps, to identify anthropogenic influences on the nature and vegetation structure in the study area. The differences between the vegetation types on the actual vegetation map and the PNV maps were considered to be due to anthropogenic influences (Bryn 2009; Gehrig-Fasel et al. 2007), since these types have not yet reached their natural state of dynamic equilibrium (Bryn 2009).

2.5.1 Vegetation transitions

The vegetation group changes were derived from the area information relating to each PNV-map and exported for calculation and comparison in Microsoft Excel 2007. The comparisons of the upper potential forest limits were performed using a grid resolution of 100 m. The upper forest limit for each vegetation map was derived in the crossover to the grid. To assess the quantity of each vegetation type that was transformed to other vegetation type(s), a point grid with 50 m spacing was used, resulting in 13,695 representative points (Nakagoshi et al. 1998). Information about actual vegetation and PNVE vegetation was assigned to the points. Points with vegetation information were used to calculate the vegetation transitions among models.

2.6 Statistics

Statistical tests were performed using SPSS (Statistical Package for Social Science) Version 17. Differences between the models in mean altitudinal changes of potential upper forest limit were tested with the Kruskal-Wallis one-way analysis of variance with subsequent Mann-Whitney U-tests. Divergence in the previous average summer temperature (1962-1986) from the recent average summer temperature (1997-2009) were tested with the Mann-Whitney U-test. Non-parametric tests were used in both cases. The cause for this was non-normal data distribution and different variability in the data-sets (Mackenzie 2005).

3 Results

3.1 Model accordance

The three PNV-models predicted the same vegetation types for 61% of the study area (Table 3; Figure 4). Only 2% of the area differed among all three PNV models. Common to the vegetation types within the 2% is that they are influenced by different soil moisture levels. They grow in bog, peatland forest, drained agricultural land, or ditched non-productive areas, or where alpine heath and/or meadow communities occurring between different modelled potential forest limits. Only PNVE and RBM models predict the same vegetation type for 10% of total area (71% in total), which is mainly where the Maxent model predicts lower upper potential forest limits for both birch and spruce. Only the Maxent model and PNVE predicted same vegetation types for 26% of total area (87% in total), which is mainly between the upper potential forest limit for spruce and birch.

Table 3: Area calculations of model accordance among the different models.

Accordance among:	Area (km²)	% of total area
All models	21	61%
No models	0,6	2%
RBM and Maxent	0,4	1%
PNVE and Maxent	8,8	26%
PNVE and RBM	3,3	10%
Total	34,2	100%

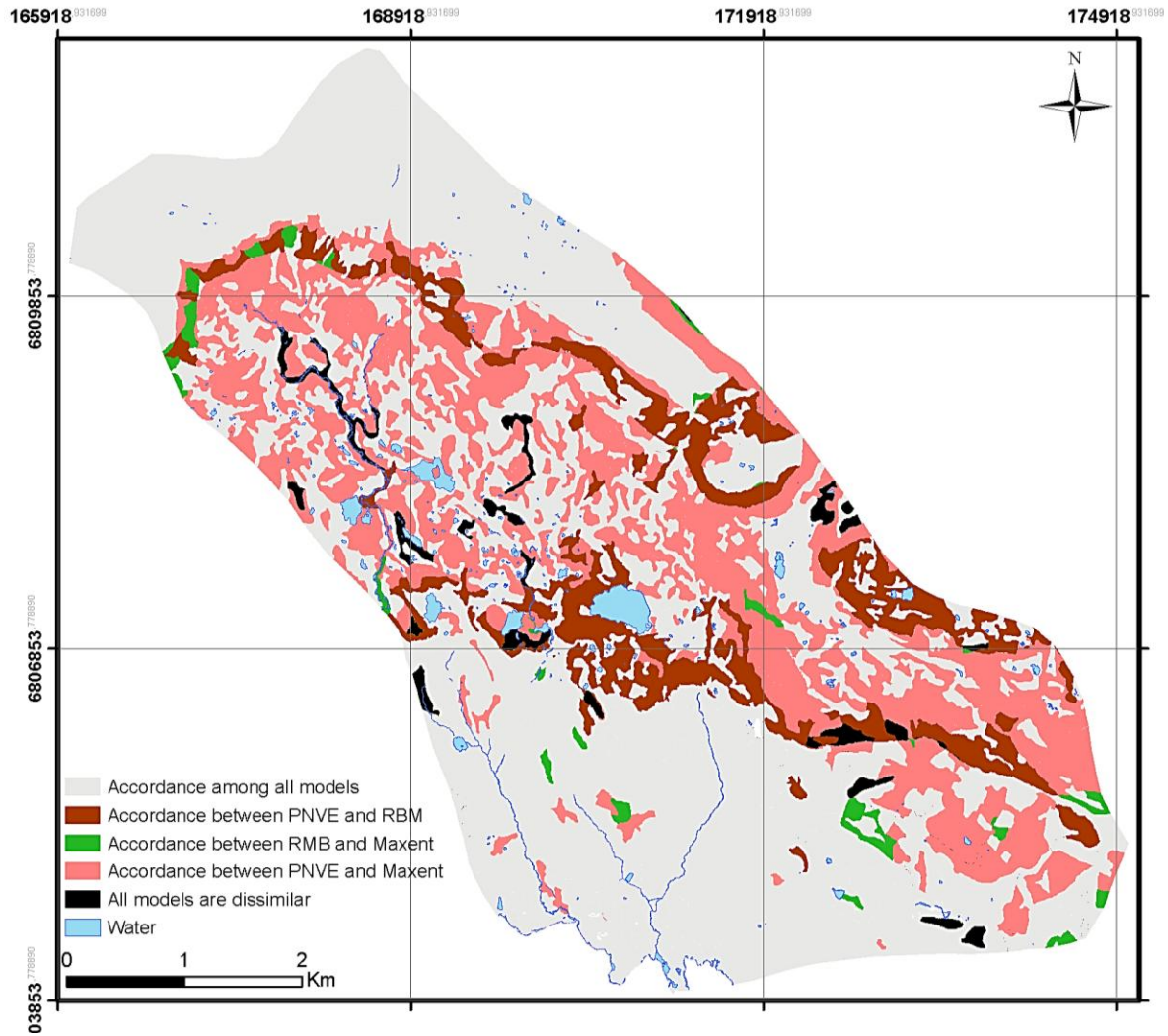


Figure 4: Accordance map of comparisons between the outputs of the different PNV models. Map projection WGS84/UTM zone 33N.

In general, there is greater uncertainty related to the modelling of PNV at higher altitudes in alpine heath or alpine meadow communities (Figure 5). Below the potential forest limit, the greatest modelling uncertainty relates to non-productive areas (12c, 12d, 12f), farmland (11a, 11b), and other areas which are largely under anthropogenic influences (e.g. drained forests). The greatest certainty for modelling at lower altitudes relates to wetlands and spruce forests. The large share of birch forest in the study area is modelled with comparatively less uncertainty.

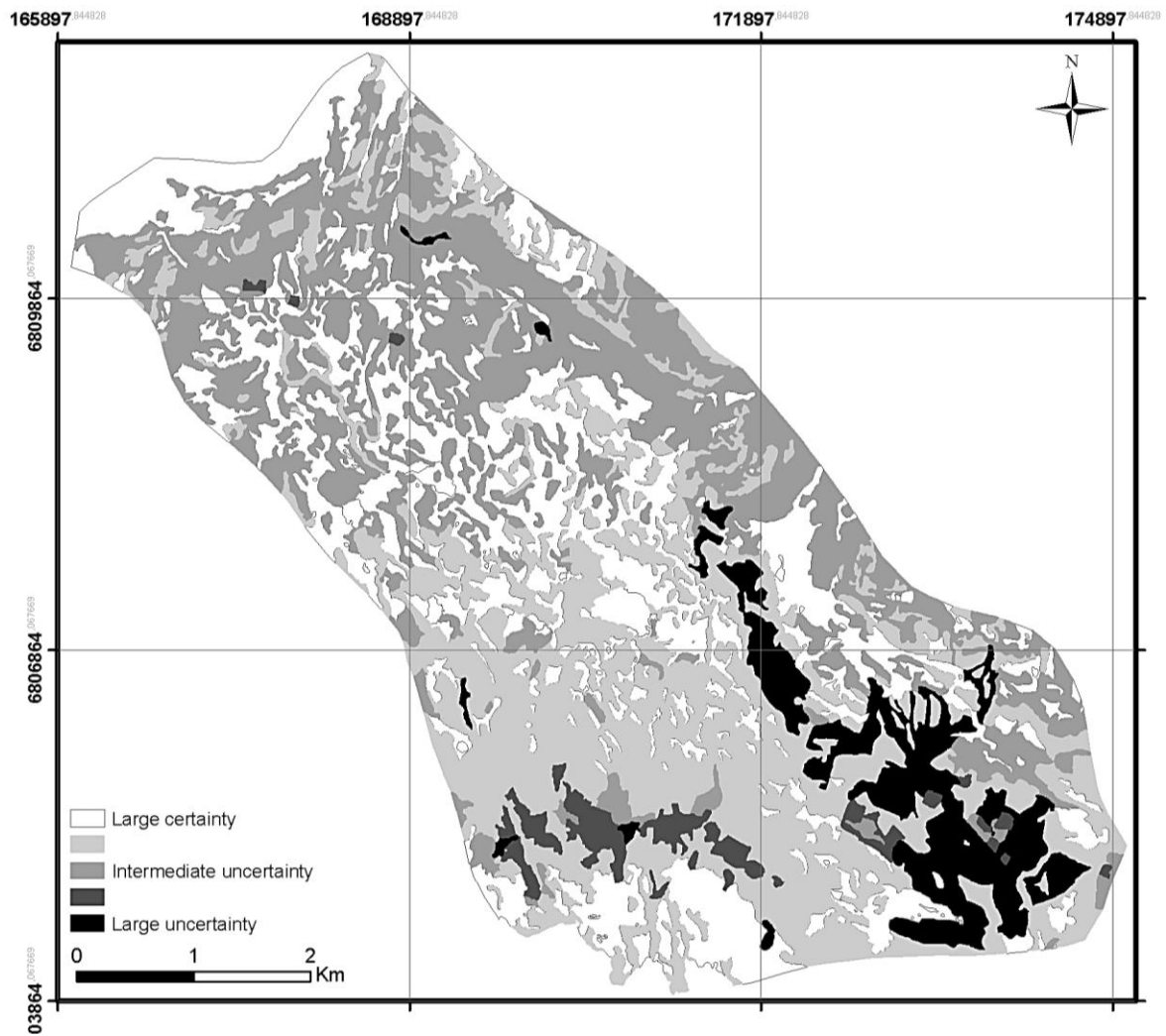


Figure 5: Map of uncertainty for modelling different vegetation types. Map projection WGS84/UTM zone 33N.

3.2 Anthropogenic influence

The divergence between the actual vegetation map of 2009 and the three PNV maps is probably a result of long and frequent human disturbances (see Discussion), and hereafter affected areas are referred to as anthropogenically influenced areas. All three PNV models estimated that more than 50% of vegetation recorded on the actual vegetation map still has not reached its expected natural dynamic equilibrium status (Figure 6; Table 4).

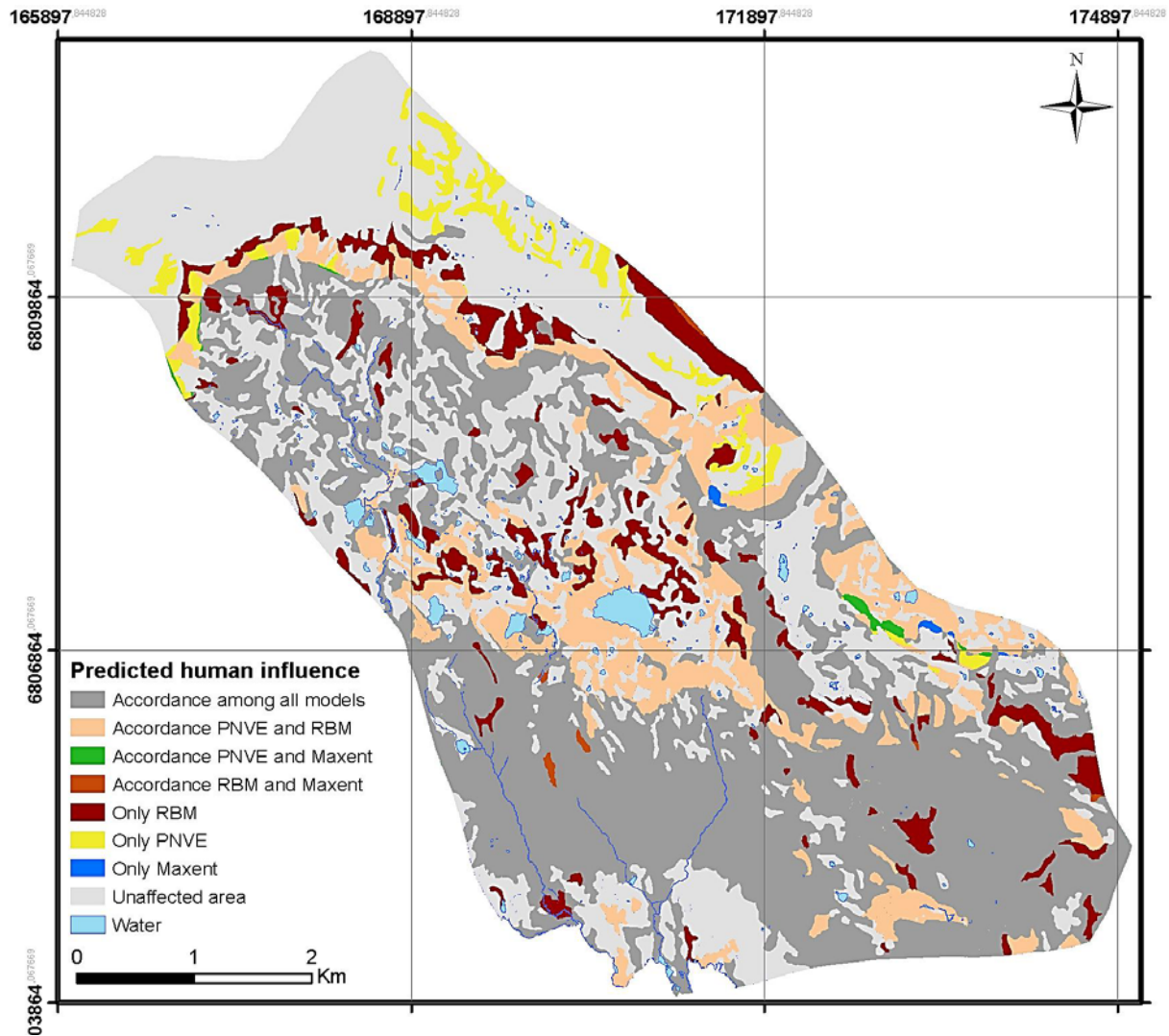


Figure 6: Variation between the models on predicted human influence within the study area. Map projection WGS84/UTM zone 33N.

The RBM predicted the highest difference from the actual vegetation map (60%) (Table 4), while the Maxent model predicted the lowest difference from the actual vegetation map (54%) (Table 4). The area with the greatest influenced is situated below the upper potential forest limit. The small shares of influenced areas situated above the potential forest limit are small units of pasture or non-productive areas on the actual vegetation map (Figure 7). The PNVE model is the only method which predicts human disturbance above the upper potential forest limit for vegetation types other than the 12 types. Further, it was found that anthropogenic influences had mainly disturbed the development of lichen heaths.

Table 4: Predicted anthropogenic influences among different PNV models.

Model	Anthropogenically influenced area (km²)	% of total area
PNVE	19.2	56%
RBM	20.6	60%
Maxent	18.5	54%

3.3 Vegetation type change

The actual vegetation situation (Figure 7) differs considerably from all three PNV maps (Figures 8–10). More than 50% of the area changes vegetation type on PNV maps. General tendencies for all of the PNV models show increasing amounts of spruce forest, with subsequent decreasing amounts of alpine heath and alpine meadow communities, and with a stable proportion of birch forest (Figures 8–10). Areas with alpine heath and alpine meadow communities are transformed into mountain birch forest, whereas birch forest at lower altitudes is transformed into spruce forest. In addition, all pastures, cultivated land, and human-made, non-productive areas were excluded from the PNV models.

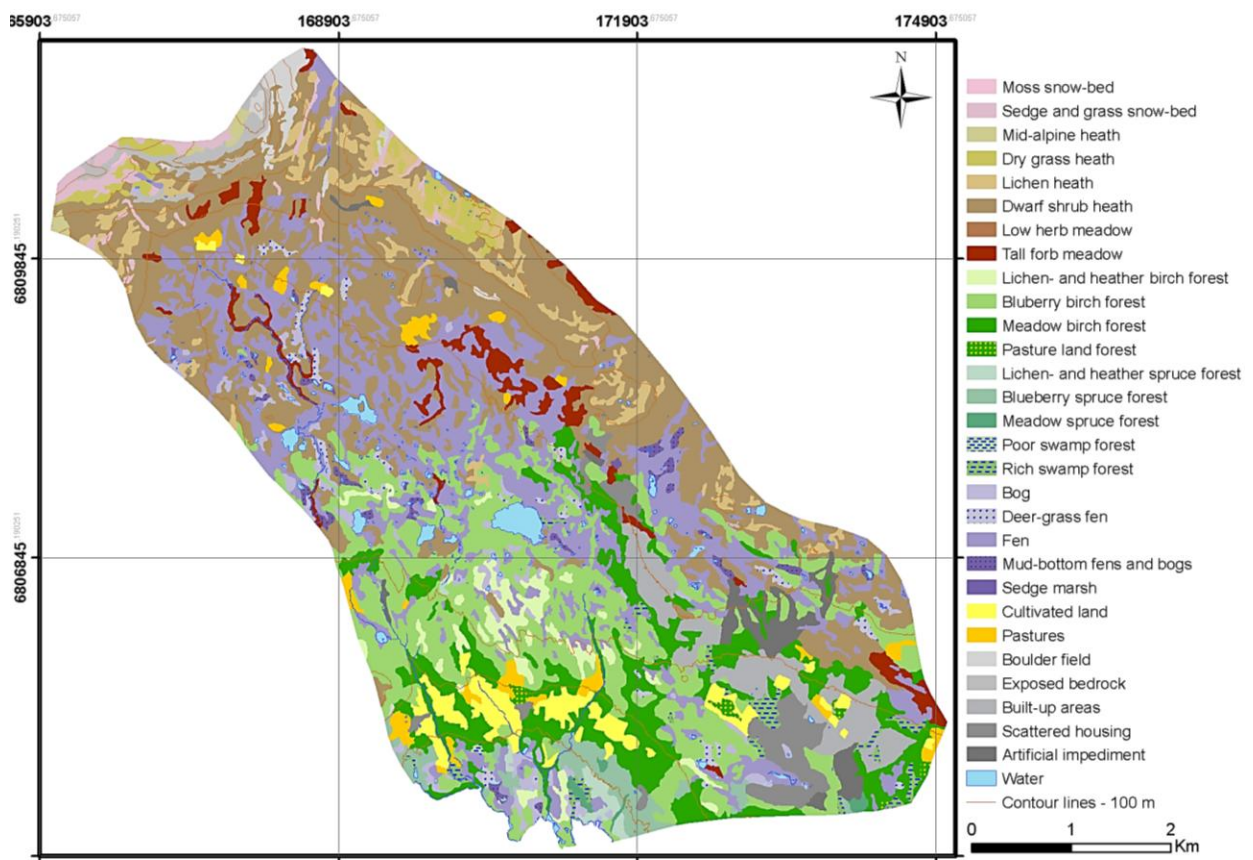


Figure 7: Vegetation map from the area around Beitostølen in 2009. Map projection WGS84/UTM zone 33N.

The landscape changes from the actual vegetation map to PNVE were dominated by the expansion of spruce forest and reduction in alpine vegetation types, particularly alpine heath communities (Figure 8). The expansion of spruce added 10.6km² to the total spruce forest in the area. Almost 80% of the actual birch forest has been transformed into spruce forest. Despite this, the amount of birch forest is roughly stable (aberration 0.1 km² compared to the actual vegetation map).

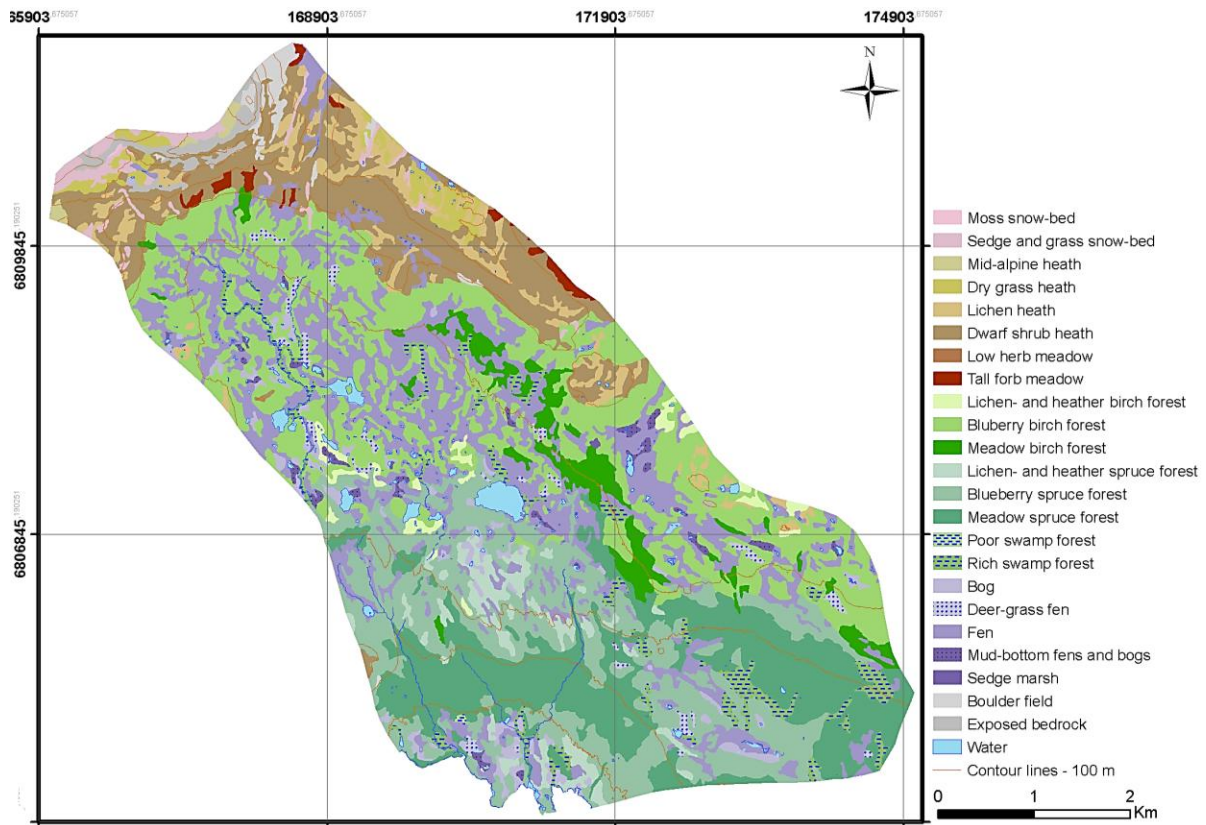


Figure 8: Vegetation map produced using the expert-evaluated PNV model (PNVE). Map projection WGS84/UTM zone 33N.

The landscapes changes from the actual vegetation map to the RBM were dominated by reductions in the alpine heath and meadow communities and birch forest, while the spruce forest advanced (Figure 9). Both spruce and birch forest advanced to higher altitudes, but there was a corresponding decrease in birch forest as spruce forest expanded. This PNV models predicts the highest amount of spruce forest (15.7 km²) and the largest advance for peatland forests (1.4 km²) at the expense of wetlands.

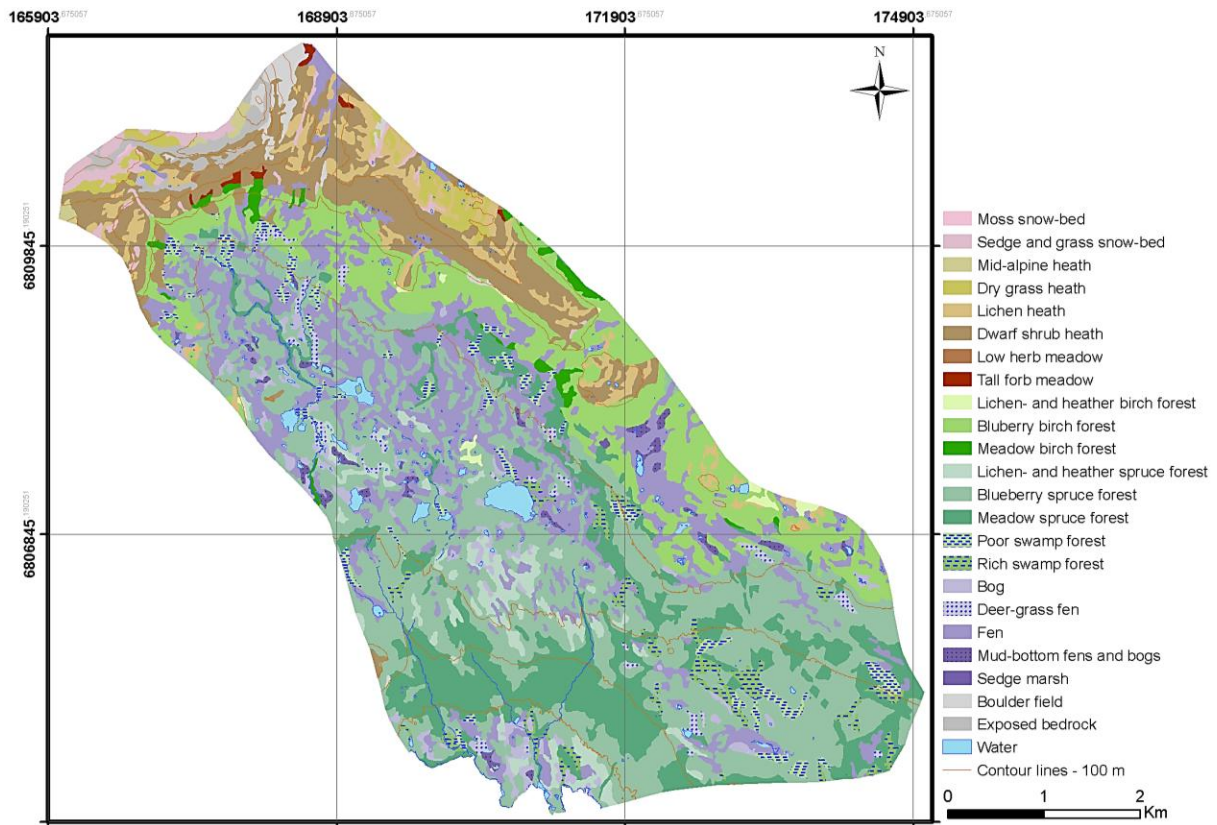


Figure 9: Vegetation map produced using the rule-based envelope PNV model (RBM). Map projection WGS84/UTM zone 33N.

The landscapes changes from the actual vegetation map to the Maxent model were dominated by a small reduction in alpine heath communities and the advance of spruce forest (Figure 10). This method models the lowest reduction in alpine vegetation types, and the smallest expansion of the spruce forest (9.1 km² in total). The total area with birch forest is almost equal to that on the actual vegetation map (8.3 km²), but is displaced to higher altitudes.

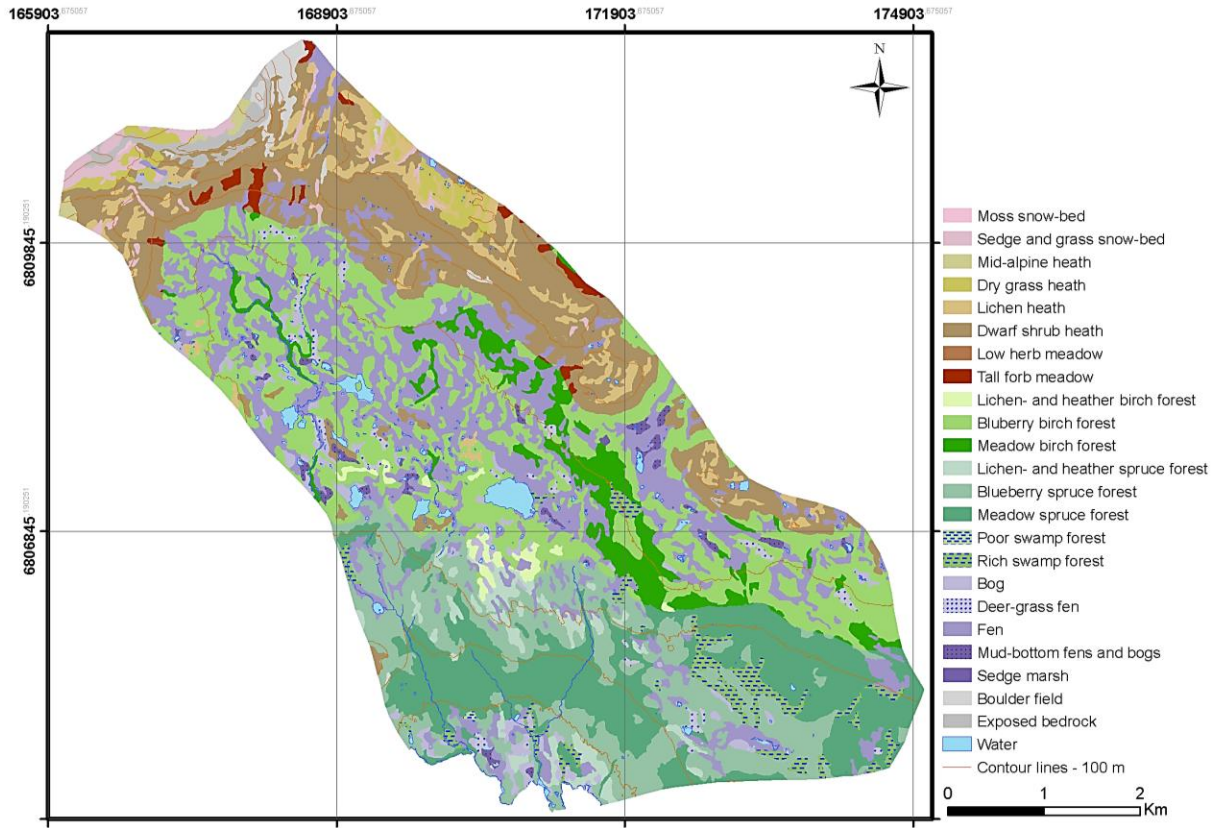


Figure 10: Vegetation map produced using the Maxent-predicted PNV model. Map projection WGS84/UTM zone 33N.

The elevation advance of birch and spruce forest to higher altitudes would reduce the alpine vegetation from 12.3 km² to 5.8 km² in the PNVE model, 5.1 km² in the RBM, and 7.8 km² in the Maxent model. Snow-bed vegetation would not be affected, but approximately half of the area of alpine heath communities and meadow communities would be replaced, and the majority of birch forest (Figure 12). In addition, a small share at lower altitudes would be replaced with spruce forest. All models predict that spruce will expand in terms of both altitude and land cover. On the actual vegetation map covers spruce forest only 2.4% of the total area. All models predict a considerable increase, to 30.9% in the PNVE, 46.2% in the RBM, and 26.7% in the Maxent model. The total area of birch forest is predicted to be stable according to the actual vegetation map in the PNVE model and the Maxent model, while in the RBM birch forest covers a considerably lower area (Figure 11).

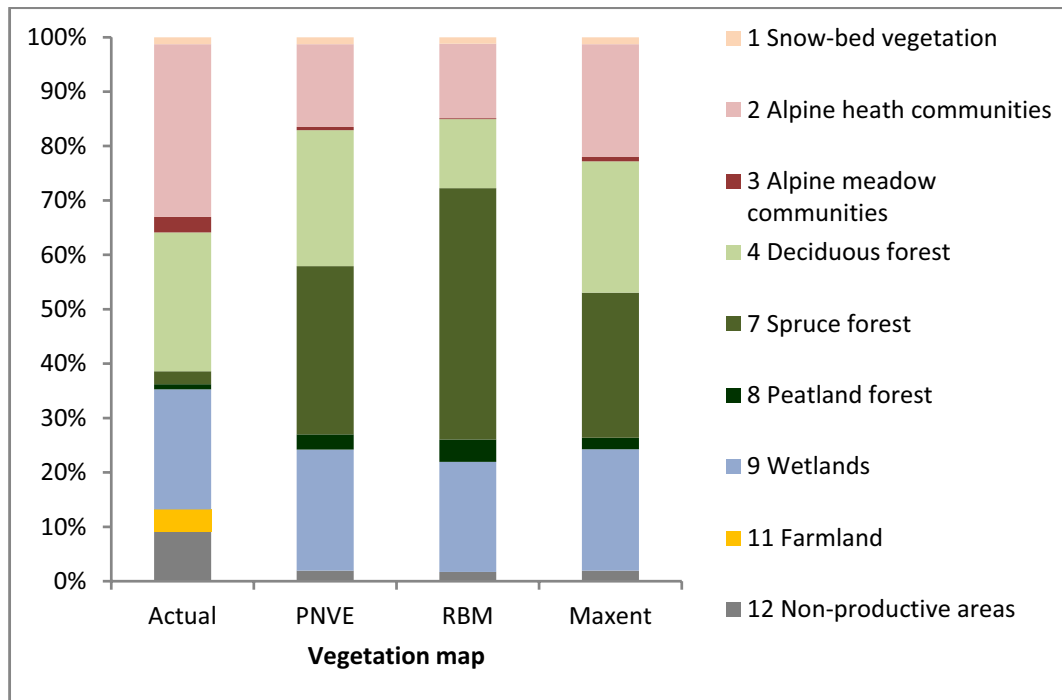


Figure 11: Vegetation groups as a percentage of total area (34.2 km²). Total area statistic for vegetation types in Appendix 2.

The vegetation group expected to show the largest advance is spruce forest. Almost every vegetation group has the potential for spruce forest, with the exception of snow-bed vegetation, peatland forest, wetlands, and natural non-productive areas. All models predict that peatland forest has a slightly larger potential than observed in the actual vegetation. The potential is located in the alpine meadow communities, non-productive areas, and wetlands. Despite this increased potential, a small share of the peatland forest has the potential for being wetlands (Figure 12). The proportion of wetland seems stable and undisturbed (Figure 11), but the low share (3.5%) that is transferred to peatland forest is replaced with very low proportions of non-productive areas, farmland, and alpine meadow communities. Among the alpine vegetation, alpine heath communities are expected to experience the largest reduction in total area. However, in the PNVE model, alpine meadow communities are predicted to experience the largest reduction in percentage (*c.*78%) of their original area. The majority of alpine meadow communities will be transferred to birch forest on firm ground. The small areas of humid types will be transferred to wetlands and peatland forest. The majority of the farmland on the actual vegetation map (73%) originally have the potential for being spruce forest, while smaller shares have the potential for birch forest (17.7%), wetlands (7.7%), and a negligible proportion of alpine meadow communities (Figure 12).

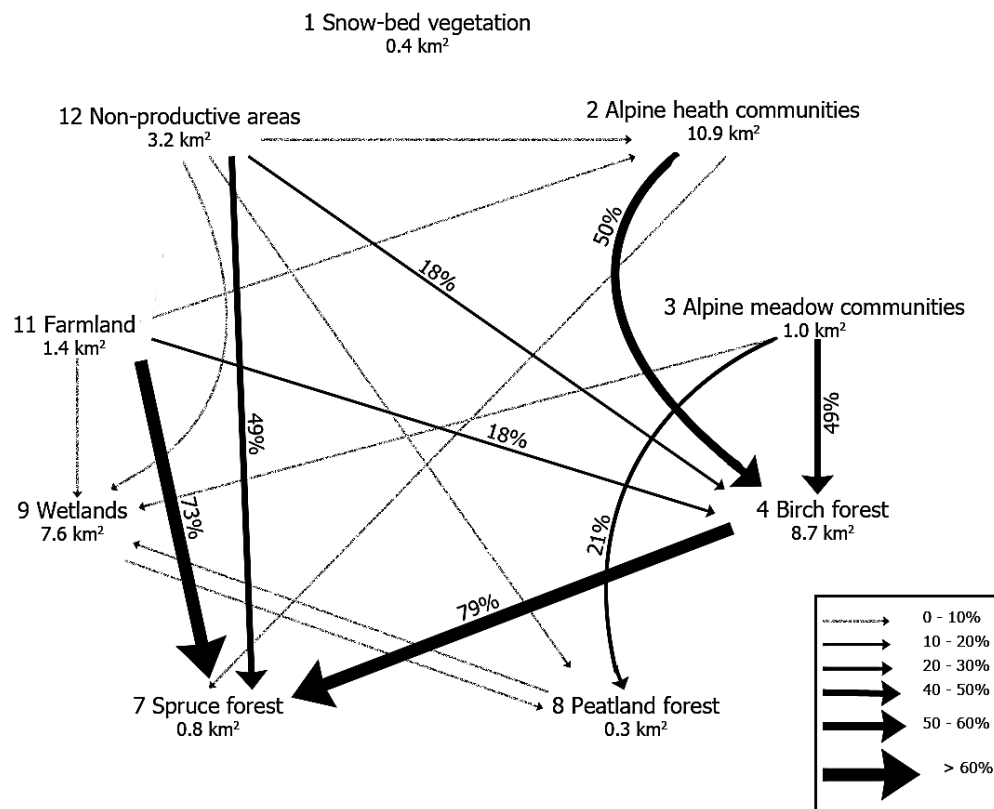


Figure 12: Main vegetation transition from present situation to expert-evaluated PNV model. The area given in square kilometres is the area in the present situation. The percentages refer to the proportion of the present vegetation group transferred to a given vegetation type.

3.3.1 Maxent prediction

The Maxent predictions for the distribution of spruce forest (AUC = 0.883)(Appendix 4) were better than predictions for birch forest (AUC = 0.769)(Appendix 5). According to the built-in jackknife procedure in Maxent, the proxy variable for temperature (DEM) contributed most to the potential spruce forest model (73%), while soil properties contributed considerably to the development of the potential birch forest model (56%). Calculation of MST resulted in choosing cumulative value 13 for spruce and 4 for birch when drawing maximum dispersal of the species.

3.4 Forest limit change

The RBM predicts the highest altitudinal average forest limit for both birch (1116 m a.s.l.) and spruce (1026 m a.s.l.), while the Maxent model predicts the lowest altitudinal average forest limit for both birch (1055 m a.s.l.) and spruce (950 m a.s.l.) (Figure 13).

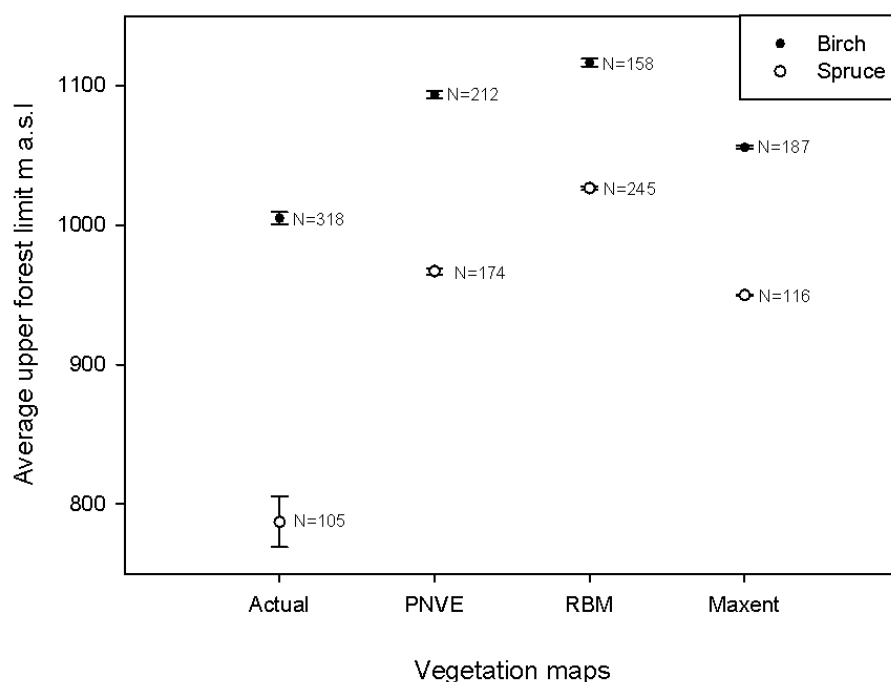


Figure 13: Average altitude for the present situation and the three vegetation models based on the grid dataset (Error bars: 95% CI).

The present mean continuous upper potential forest limit for birch and spruce is significantly reduced ($p < 0.001$) according to all three PNV models. The general situation shows that the quantity of birch forest recorded on the actual vegetation map will remain stable (Figure 11) on the PNV maps, but will become displaced to higher altitudes. The actual vegetation map shows that 25.5% of the area is covered with birch forest. This is almost equal to the PNVE and Maxent predictions, which respectively predict that 25.5% and 24.1% of the total area has the potential for birch forest at the theoretical dynamic equilibrium state (Figure 11). This is not the situation for the RBM, which predicted the elevation for spruce to be considerable higher and on this basis predicts the distribution of mountain birch to be less extensive, i.e. only 12.7% of total area.

The statistical test of difference in average summer temperature (June, July and August) showed a significant change ($p < 0.05$) on 1 °C from recent temperature registrations (1997-2009), 12.7 °C, compared to older temperature registrations (1962-1986), 11.7 °C.

4 Discussion

4.1 Modelling methods

Vegetation maps have proved to be useful in spatial GIS-modelling (Bryn 2008; Carranza et al. 2003; Chytrý 1998; Dirnbock et al. 2003; Moravec 1998; Tichý 1999). In the present study three different modelling methods were used, resulting in three different PNV maps. The three maps made predictions with a fault rate of $< 40\%$ according to corresponding vegetation types. In general, the different models result in similar trends on the PNV maps.

First, the three models predict different altitudinal levels for the upper potential forest limit. The RBM predicts the highest altitudinal forest limit with minimal vertical variation. This is not affected by ecological properties or altitudinal variations that may occur on a small spatial scale. Instead, is it related to the concepts of exploratory modelling, as well as envelope modelling. The goal of exploratory modelling is to capture key traits and general trends, and the details are less important (Perry & Millington 2008), whereas the methodology of envelope modelling restricts variations within the chosen envelope (Guisan & Zimmermann 2000). PNVE and Maxent are contrasting modelling methods to RBM, and make allowances for ecological differences and gradients to a larger degree than RBM.

Second, all modelling methods have problems with modelling PNV on types strongly influenced by human disturbance (i.e. types 11a, 11b, 12d, 12e, and 12f). Especially drained types from vegetation groups 11 and 12 are modelled differently among all models. Human-modified areas where the original vegetation has been completely removed and where restoration is impossible are hard to model. It was originally recommended that these types should be excluded from the modelling and left as open areas on the PNV map (Tüxen 1956). More recently, Moravec (1998) and Zerbe (1998) have recommended that these types should be manually interpreted on the PNV map to reduce uncertainty. This uncertainty is especially present in the RBM and Maxent models. Uncertainty in modelling these types is almost avoided on the PNVE map since this map is based on field observations and created by using the remaining fragments of intact vegetation as a reference point (Moravec 1998). The PNVE is the only model which gives good predictions for vegetation types 12c, 12d and 12e.

Third, modelling performs well on successional vegetation types, but is complicated where types occur in their ecological extremities. Especially factors such as humidity, nutrient richness, and successional state complicate the modelling. The fact that the PNVE model captures extremities for types is related to the PNVE model being compiled from actual vegetation in the field. Observations of species composition and physiognomy in field may

explain why some types are predicted to develop differently than when modelled with RBM and Maxent, and why variations in additional information that were meant to capture ecological extremities did not work as well in models as anticipated. For example, semi-humid types may appear in a state that is not humid enough to be identified using the additional sign of humidity. This may also be the case with the poorer types, e.g. poor types of dwarf shrub heath are modelled to lichen and heather birch forest in PNVE, while Maxent and RBM model the same polygons to blueberry birch forest. This may be due either to insufficient registration of additional information regarding poor/shallow soil, or insufficient implementation of rules in the RBM. The assumption during the vegetation mapping was that poor types were intercepted with additional information regarding bare ground, soil depth or lichen cover. Disturbance in lichen cover is an additional information sign that probably should be included in future surveys. PNVE was the only model that captured disturbance above the present forest limit in alpine heath communities. Disturbance was especially related to lichen cover in lichen heaths. Here, it is evident that additional information did not capture all essential information for later GIS-modelling of vegetation disturbance.

4.1.1 What is modelled?

From a literature search, the modelling from this study does not appear to fall into any specific classification, except for the general acknowledge that it models the potential distribution of species. Products from distribution models based on species data and environmental variables have been variously termed ‘habitat’ (Capelo et al. 2007), ‘fundamental/realized niche’ (Soberon & Peterson 2005) and ‘ecological niche’ (Li et al. 2009; Peterson et al. 2007), among other terms. Hence, it is the inconsistent use of terms and different understandings of the niche concept in species distribution modelling/models (SDM) which contributes to the uncertainty of what prediction outputs represents (Kearney 2006).

There are at least three main niche theories implemented in the various SDMs: i) Grinnellian niche, environmental characteristics needed by a species to survive in without immigration (Grinnell 1917); ii) Eltonian niche, species interactions with other species (Elton 1927); and iii) Hutchinson’s n-dimensional hypervolume, where species are not able to utilize their entire fundamental niche, but are limited to their realized niche due to biological interactions, mainly focused on competition (Hutchinson 1957). However, each of these concepts has been modified and criticized since they have been introduced (Hirzel & Le Lay 2008). Theories that have developed in recent decades, e.g. the metapopulation theory (see e.g. (Hanski 1999)) and the source-sink theory (see e.g. (Pulliam 1988)), have shown the limitations of these niche definitions.

The rule-based envelope model is considered an SDM (also named ‘habitat model’ or ‘ecological niche-based model’) (Guisan & Zimmermann 2000; Heikkinen et al. 2006). The statistical Maxent modelling technique used in this study is also an SDM (Phillips et al. 2006; Phillips & Dudik 2008). According to Phillips et al. (2006) is also Maxent a niche-based model where the output represents the modelled species niche in relation to the actual environment, due to Hutchinson’s niche terms. The purpose of SDMs is to spatially predict species distributions using the relationships between species occurrence data and environmental predictor variables as the basis (Raes & ter Steege 2007). According to Guisan & Thuiller (2005), the output of SDMs is a map of habitat suitability. Habitat suitability models (HSM) assume that a species-present geographical distribution reflects that species’ environmental habitat requirement (the species’ realized niche), while an ecological niche reflects the environmental variables that affects a species’ fitness.

However, HSMs make good contributions in revealing the niche characteristics of species (Hirzel & Le Lay 2008). Kearney (2006 p. 190) propose that the term ‘habitat’ can ‘describe the association between organisms and features of a landscape’. This term can be related to the vegetation classes used in this study. In other words, modelling of the vegetation maps might be considered a type of habitat modelling. However, it cannot be implemented in the HSM term since it models habitat distribution rather than possible habitats for species. The special advantage with the Maxent model in this study is that the predicted distribution for birch and spruce (species) forms the foundation for the potential spatial distribution of the vegetation types (habitats) associated with these species.

The modelling performed in this study did not include sufficiently complex environmental variables which may contribute to the modelling of species niches. However, the possible distribution of species is modelled on a spatial scale based on environmental variables. A better term for the Maxent modelling would therefore probably be spatial prediction modelling (SPM), a term coined by Rune Halvorsen (30. April 2010 at the University of Oslo).

4.1.2 Environmental variables

The GIS-based models are designed to be produced with minimal complexity with vegetation types where changes and succession patterns are known from an earlier study (Bryn 2008), where time series were used to identify a similar but more restricted modelling. In general, the selection of environmental variables is crucial and often relies on expert knowledge (Guisan & Zimmermann 2000; Manel et al. 2001). However, the purpose of modelling and scientific

experience was normative for the variables selected for the modelling (Metzger et al. 2005), together with the available variables (Bakkestuen et al. 2008). The DEM and the soil characteristics were the only two available predictors in proper resolution for our study area which contributed in the modelling of the PNV maps.

4.1.3 Time aspect

A high level of uncertainty is associated with determining the time aspect for the occurrence of the predicted changes to the PNV maps, or whether it will occur at all. A variety of biotic and abiotic factors may affect the successional regrowth rate and forest establishment, and hence the same vegetation type may transform at different rates at different locations due to different microclimatic conditions and historical use (Huntley 2005). This idiosyncratic regrowth pattern is also reflected in species' regrowth response, e.g. mountain birch establishes relatively fast, while spruce establishes more slowly. Hence, the history of anthropogenic disturbances and landscape properties affect the vegetation dynamics and regrowth patterns (Didier 2001). Regrowth does not react as a linear response to land abandonment (Bryn 2006). Therefore many areas that apparently seem to be in different successional stages have been abandoned at the same time. It is also difficult to assess when abandonment terminated, but increased time since abandonment favours succession and natural regrowth (Tasser et al. 2007). In addition to optimal climate conditions (Dalen & Hofgaard 2005), do successional regrowth speed depends on factors such as geology, elevation, exposure, and slope. After land abandonment do, especially elevation, soil moisture and nutrient status play an important role in successional regrowth speed (Bryn et al. In press; Tasser & Tappeiner 2002). Numerous factors might have influenced the vegetation disturbances around Beitostølen. Earlier, grazing, forage harvesting, logging, and other agricultural related activities dominated the use of outfields in the study area (Gjesdahl 1965). Decreased grazing in the outfields and the reduced need for firewood are the main controlling factors for forest regeneration after abandonment of summer dairy farms in the Swiss Alps (Gehrig-Fasel et al. 2007; Gellrich & Zimmermann 2007). Grazing by domestic animals especially affects birch forest where logging and mowing is also practised (Bryn & Daugstad 2001). Decline in these activities presumably can explain the established anthropogenic influence within the study area.

The recent increase in summer temperature within the study area (figure 2), have probably contributed to increased forest growth and elevated potential forest limits (Barnett et al. 2001; Bjune 2005). However, this would not have changed the PNV models of this study. Firstly, the recent climate improvement are not yet reflected in higher actual forest limits. Kullmann

(2001) proposed a time-lag of 30 years in Sweden for the forest limit to respond to changing climate. If the summer temperature continue to increase, the upper potential forest limit will be raised to higher elevations than expected in this study, because the upper potential forest limit is correlated with summer temperature (Bryn 2008; Mäkinen et al. 2002). If this is the case, the PNV models presented in this study will underestimate the potential forest regrowth, but at the same time you will be sure not to exaggerate the effect of human disturbance. Secondly, improved temperatures can increase the regrowth rate and subsequently speed up the succession towards the PNV condition (Rössler et al. 2008). Thirdly, increased summer temperature would drive the forest to higher elevations (Moen et al. 2004). However, this study models PNV related to the present environmental conditions. Raised summer temperatures would change the conditions and subsequently give other PNV models.

4.1.4 Reliability

The PNV maps are hypothetic models of a natural ecosystem, which probably will never be reached. The main purpose of preparing such maps is to gain an overview of which areas are influenced by humans and what these influenced areas will transform into when human use cease. These maps show the relationship between vegetation types and environmental variables, and will provide a good basis for decision making in management issues (Gallizia Vuerich et al. 2001). Besides being a good starting point in management issues, the PNV maps are a good null model for modelling climatic scenarios (Bryn 2009; Lapola et al. 2008; Rio & Penas 2006). Producing climatic scenarios without taking anthropogenic disturbances into consideration will give incorrect results and furthermore the estimates of vegetation response to climatic changes will be incorrect too. There is great difficulty in modelling climatic changes in relation to non-ecological factors (Rössler & Löffler 2007). This applies especially to the development of the forest limit (Hofgaard 1997; Holtmeier 2003). As a consequence, models which assume a direct relationship between the present forest limit and the climate will make incorrect predictions on a regional scale (Rössler & Löffler 2007).

4.1.5 Objectivity

It is difficult to model PNV without including a degree of subjective judgment (Capelo et al. 2007). PNVE is model with highest subjectivity since it is created with expert knowledge as the basis. The RBM is objective and based on ecological findings, but also has elements of subjectivity since some rules are implemented with a basis in knowledge and not based on findings from the study area. The Maxent model performs with the greatest objectivity since it is based on ecological findings which work as a foundation for statistical modelling. Even

though the RBM and Maxent are considered more objective methods for mapping compared to PNVE, they may also have been affected by subjectivity during the mapping of actual vegetation. The subjective decisions are related to the drawing of borders between different vegetation types during fieldwork (Tichy 1999). Also, Maxent will not perform very well in areas that have high levels of human disturbance. Maxent relies totally on the present distribution pattern of modelled species and might therefore underestimate the potential distribution of species that are highly influenced by the human disturbance. In contrast, RBM is more appropriate for modelling types or species which are suppressed by anthropogenic disturbance. Hence, objectivity is maintained by using findings from the study area which are adjusted based on ecological knowledge.

4.1.6 Scale

The PNV models discussed in this study present potential vegetation transitions on vegetation type level, representing the scale of the classification system used for field registrations. The use of another system, e.g. Naturtyper i Norge (Nature types in Norway) (NiN) (Halvorsen et al. 2008) or a more detailed vegetation mapping system, e.g. Fremstad (1997), would provide vegetation classification at a smaller scale. Identification of vegetation and vegetation transitions at smaller scale leads to more variation in the vegetation pattern, and hence predict greater amounts of human-influenced land. In contrast, vegetation classification on a larger scale would predict both less variation in vegetation and less anthropogenic influence.

4.1.7 Manual made expert-evaluated potential natural vegetation map

PNV map based on field registrations must be assumed to be the most precise and credible model, since they are based purely on field observations of remaining actual vegetation. According to Tüxens (1956) original proposal for creating PNV maps, this is one of the strengths with this method. The field-related method provides larger larger possibilities for capturing vegetation gradients, which occurs in ecological extremities, successions, or small-scale variation. This variations might be generalized and neglected in the actual vegetation maps, which are the basis for modelling PNV with RBM and Maxent. Thus, this method provides a better method in reconstructing areas exposed to heavily human alterations, since small patches of vegetation still may provide information of e.g. physiognomy, soil type and humidity, which contributes to reveal earlier vegetation types. However, heavily human disturbed areas are often proposed to be left outside in models of PNV (Moravec 1998).

4.1.8 Rule-based model

The RBM model is the most general model and captures the key traits rather than the small-scale changes (Perry & Millington 2008). The purpose of envelope modelling is described by Malczewski (2000 p. 21) who expressed that ‘one should emphasise that the purpose of any GIS-based decision analysis is to provide insights and understanding, rather than to prescribe a “correct” solution’. Even though this model captures the key traits, it was nevertheless developed to be as correct as possible (like PNVE). The greatest uncertainty related to this model, apart from modelling the heavily human-utilized areas, is probably connected with drawing the upper border of potential forest limit. However, PNV modelling at a larger scale than 1:25,000 reduces the problems connected with drawing exact borders (Bryn 2008; Chytrý 1998; Ricotta et al. 2002). Despite the model’s ‘simplicity’ it may still be used for detecting complex ecological systems (Perry & Millington 2008). Accordingly, are this strategy used for exploring human disturbance and testing the effects of different management strategies (Bryn 2006; Perry & Millington 2008).

4.1.9 Maxent

The use of presence-only data has proved useful for modelling species distribution (Elith et al. 2006; Riordan & Rundel 2009; Wollan et al. 2008). Maxent is among the GIS-modelling techniques that give the best predictions (Elith et al. 2006). In addition, it has the capability to make appropriate distribution predictions beyond the present *realized* distribution (Phillips et al. 2006). Even though models based on presence-only data are regarded as being less precise than presence/absence models, presence-only and presence/absence models are closely correlated (Hirzel et al. 2006).

Evaluation and defining threshold

Statistical Maxent models for birch and spruce performed better than moderately well ($AUC < 0.7$). This means that both predictions performed well, but not perfectly. However, AUC values tend to be higher for species with narrower ecological amplitude, without the model necessarily being better (Phillips & Dudík 2008). Since both birch and spruce are more generalists than specialists, both models can be more precise than evaluation through AUC values. This can indicate that the predicted distribution of both tree species is good overall.

The evaluation by predictive distribution models with a threshold-independent accuracy measure, such as ROC (AUC-values), is standard procedure for the evaluation of biological prediction models (Fielding & Bell 1997), but has received criticism in recent years (Austin

2007; Lobo et al. 2008). AUC is the only measure that can translate continuous prediction models as present/absence sites without threshold definition (Zucchetta et al. In press). Evaluation through AUC relates true positive predictions and false positive predictions to results in a continuous range of threshold levels (Cumming 2000; Erasmus et al. 2002). Identifying predictions' threshold level is the last step in a species distribution prediction procedure and is important for estimating a species' range (Liu et al. 2005). Continuous probabilities prediction from species distribution models needs to define a specific threshold for converting the predictions to presence/absence on a map. There are several ways of defining thresholds for conversion of continuous maps to categorical presence/absence maps (Jimenez-Valverde & Lobo 2007; Liu et al. 2005). In the present study threshold was derived from the values in a ROC plot, although ROC plots in themselves do not provide such classification rules (Fielding & Bell 1997). Jimenez-Valverde & Lobo (2007) found that defining thresholds based on the relationship between the ROC-plots sensitivity and specificity values (minimized different threshold (MDT) and MST) produced the most accurate predictions. Hence, these were most related to prevalence of the test species. MDT balances the relationship between sensitivity and specificity (Cantor et al. 1999), while MST favours the models 'sensitivity (Manel et al. 2001). MST was used in this study since it was more important for identifying the distribution of birch and spruce than identifying their absence.

Samples

There is no given rule on how many sample points are needed to form the basis for a satisfactory prediction. The number depends to a large extent on the properties of the study area and the selected species. In general, smaller sample sizes lead to lower levels of accuracy (Hernandez et al. 2006). However, accuracy is usually greater for species with more specialized niches (Chahouki et al. 2010; Hernandez et al. 2006; Phillips et al. 2006). Since birch and spruce can be classified as more general species (Lid et al. 2005), this may have affected the modelling performance by leading to lower AUC values (Phillips & Dudik 2008). However, Hengl et al. (2009) emphasize that the geographical representation of samples is much more important than the number of samples.

The statistical modelling of Maxent is one method for species distribution modelling (SDM). The purpose of SDM is to spatially predict species occurrence using the relationships between species occurrence data and environmental predictors as the basis (Raes & ter Steege 2007). The special advantage of this method is that the prediction models for birch and spruce form the foundation for the potential distribution of vegetation types (habitat).

Species distribution models (SDMs) attempt to predict the potential distribution of species by interpolating identified relationships between species presence/absence or presence-only data on the one hand, and environmental predictors on the other hand, to a geographical area of interest.

Maxent: Modelling of forest limit, treeline or species limit

Modelling based on species occurrence data, as mentioned above, results in a habitat suitability model (HSM) for actual species. When modelling the potential distribution of tree species, as was done in this study, the question arises as to whether the output map represents the upper potential forest limit of the trees, the treeline, or the upper potential presence for the actual species. For the present study, a tree is defined as a full-grown individual, standing 2.5 m tall in the case of birch and 5.0 m tall in the case of spruce. The treeline is the uppermost border for normally formed trees above the upper potential forest limit, while the species limit is the upper boundary at which the species occurs (Aas & Faarlund 2000).

The answer to the above question may be neither definite nor exact. The output from the models represents the input for the predictions. Thus, if the occurrence data represent the highest occurrences of trees within the area, the output will probably also represent the same. On the other hand, if the modelling is performed with upper findings from established forest of actual tree species, is it more likely that the prediction model will reflect the upper potential forest limit for that tree species within the actual area. Another aspect in this consideration is how the threshold for drawing the exact distribution border from the relative prediction scale is defined. Clearly, different threshold definitions result in a different predicted result (Jimenez-Valverde & Lobo 2007).

4. 2 Vegetation transitions and anthropogenic disturbance

The actual vegetation map (AVM) and PNV maps show differences for most of the investigated area. This indicates that a large share of the present vegetation still has not reached its natural state of dynamic equilibrium (Ricotta et al. 2000) and is prevented from reaching this state due to continued human disturbance and the time lag needed for forest establishment at these altitudes. Hence, the development of the disturbed areas is assumed to be prevented by anthropogenic influences (Ricotta et al. 2000), since the development of natural succession is known to be disturbed by such influences (Gellrich et al. 2007; MacDonald et al. 2000; Olsson et al. 2000).

Termination or strongly reduced management immediately initiates a state of natural succession (regrowth) (Fremstad & Moen 2001; Potthoff 2007; Tasser & Tappeiner 2002). Natural regrowth is an ongoing trend observed in all Norwegian mountain regions (Aas & Faarlund 1995; Bryn 2008; Bryn & Debell-Gilo 2010 In Press). The same trend is also observed in the Swiss Alps, where it has been observed as regrowth following agricultural abandonment (Gehrig-Fasel et al. 2007; Gellrich et al. 2008; Motta & Nola 2001). The influenced area around Beitostølen is primarily situated below the existing forest limit. This largely corresponds to most of the forested landscapes being influenced by humans (Bryn 2009; Garbarino et al. 2009). Large areas below the present upper potential forest limit are disturbed in the natural development towards the dynamic equilibrium state by human activities. Logging, grazing and mowing are among the historical activities with the greatest impact on this development. Hence, these activities decreased considerably in Norway after 1950s (Almås et al. 2004). Above the existing forest limit, alpine pastures, agricultural land, and land with grass and scrub vegetation are all primarily influenced by human activities (Gellrich et al. 2007). This trend has also been observed within the study area.

The identification of earlier anthropogenic disturbance and subsequent regrowth within the study area indicates a trend of decreased human nature utilization, where human actions are intensified and concentrated, with considerably greater ecological consequences. Modelling and mapping using PNV models substantiates this finding where the heavily disturbed classes (11a, 12c, 12d and 12e) were very difficult to model and map due to the fact that there were few traces of actual vegetation. Vegetation types exposed to medium disturbance (11b, drained forest, peatland forest and mires) were also mapped and modelled with high degrees of uncertainty, but more traces of actual vegetation, makes the construction of PNV for these types more reliable. This reflects the dominant trend for the development of the landscape in Norway. Where the introduction of machines and fertilizer has led to increasing demands for productivity and effectivity with subsequent intensification of the agricultural industry, the mosaic-dominated landscape has gradually disappeared (Dramstad & Puschmann 2008). Research from European mountain areas has revealed similar traces of reduced human utilization of outfields but decreased intensification of utilized areas (Gellrich et al. 2007; Gellrich & Zimmermann 2007; MacDonald et al. 2000). Gellrich & Zimmermann (2007) proved that abandonment of agricultural areas in Swiss mountains first occurred in areas with poor and shallow soil properties, where the slopes are steep or the road infrastructure is poor developed. Abandonment took place where most of the employees primarily worked in connection with the secondary and tertiary sectors. This corresponds well with the

employment situation in Øystre Slidre Municipality, where *c.*90% of workforce is related to these two sectors (SSB 2009).

Bryn (In press 2010) showed statistically that the intensity of human land-use within the outfields was higher closer to farms and summer dairy farms than further away. According to Bryn, the consequence of more intensive land-use was higher probability of deforested areas surrounding the farms and summer dairy farms. It is therefore likely that the findings reported here, also mainly relates to human disturbance. Alternative explanations, e.g. forest fires or caterpillar outbreaks, might have influenced the within vegetation type variation, but will most probably not have shifted the vegetation types *per se*. The vegetation type transitions modelled as the difference between PNV and AVM, is also spatially closely linked to the farms and summer dairy farms.

Forest regeneration will occur up to the upper potential forest limit if the abandonment of agricultural activities ceases, and natural succession will occur without interference (Gehrig-Fasel et al. 2007; Gellrich et al. 2007). This represents a natural succession to a dynamic equilibrium state dominated by coniferous forest. Clearings within coniferous forest initiate the first succession step back to coniferous forest with a colonization and regrowth session of birch (Aas & Faarlund 1996). Birch forest also constitutes a climax state between coniferous forest and alpine vegetation in Scandinavian mountains (Aas & Faarlund 1995).

4.2.1 Unchanged types

Several vegetation types have not been modified, particularly fens, peatland forest, and snow-bed vegetation. These types may either have been clear of former human land-use or the length of time since such disturbance has been sufficient that they are now in a late natural succession state (Bryn 2006). Formerly, scything and grazing on fens in Norway were commonly practised to accumulate stores of fodder, but mainly ceased after World War II (Almås et al. 2004). This was also a common practice on the fens in the study area (Gjesdahl 1965). Thus, it is probable that fen types in the area have been disturbed in the past and occur today in a later natural succession state.

4.3 Forest limit changes

The PNV maps indicate that there is great potential for forest distribution to increase in the investigated area, with elevated upper forest limits for birch and spruce. This reflects the potential for forest expansion into the mountain region of southern Norway (Aas & Faarlund 1995; Bryn 2008). The forest expansion is probably related to altered and decreasing

agricultural activities in the outfields. Earlier, logging cleared the forests and subsequent mowing and grazing in outfields prevented forests from establishing in mountain areas. Studies from Norway (Bryn 2008) and mountainous countries in Europe (Capelo et al. 2007; Carranza et al. 2003; Chahouki et al. 2010; Gehrig-Fasel et al. 2007; Wallentin et al. 2008) indicate that the observed expansion of forest limits is related to regrowth after earlier land-use and the abandonment of traditional agricultural management.

A northern and height-related expansion of the boreal forest has been observed since the beginning of the 20th century (Vittoz et al. 2008). This has been explained as due to the increasing temperatures after the Little Ice Age (Esper et al. 2002), since treeline vegetation in Fennoscandia is sensitive to climate-related environmental changes (Seppä et al. 2002). However, it is important to distinguish between the elevation of forest limits resulting from climatic changes and those influenced by land abandonment (Bryn 2009; Tinner & Theurillat 2003). Several authors agree that the observed forest limit expansion is a response to changing climate (Holtmeier & Broll 2005; Kullman 2001) since the upper potential forest line is constrained by air temperature (Körner 1998). This may be supported by the fact that the forest limit in Norway has fluctuated through time and forests have been established considerably higher than seen today. For instance, pollen analysis (Bjune 2005) and analysis of macrofossils (Aas & Faarlund 1988) have revealed that in the past birch forest has grown up to *c.*1300 m a.s.l. in Mid-Holocene in Jotunheimen. However, it has been documented by several researchers that most of the forest expansion that has appeared during the last 50 years in mountainous Norway has been primarily driven by the lack of human disturbance (Bryn 2008; Engum 2006; Rössler et al. 2008). These authors also point to climatically improved growth conditions in the last decade, and claim that this will probably speed up the future regrowth rate and further raise the upper potential climatic forest limit. In the last 50 years, however, the impact of climate changes on the regrowth rate and upper potential forest has been very low compared to the effect of reduced land-use (Bryn 2009). Monitoring treeline elevation is proposed as an ‘ideal and sensitive proxy indicator’ of climatic changes (Kullman 1998). This can lead to an overestimation of climatic consequences since the present treeline has been lowered as a result of human influence (Hofgaard 1997).

5 Conclusion

All three investigated models produce reasonable PNV maps, although the Maxent model is closest to the PNVE model with 87% accordance in matching vegetation types. The RBM and PNVE have weaker accordance, with 71%. In general, PNV models show the potential for spruce forest to increase in area, with stable proportions of birch forest and subsequent decreased amounts of boreal heath and meadow communities. Adjustment of additional signs used for supplementary information to vegetation mapping may contribute to better modelling of PNV in the RBM model. Uncertainty in making PNV maps relates to identifying the upper potential forest limit for dominating tree species, modelling areas that are exposed to moderate to high human disturbance, and modelling vegetation types that occur in ecological extremities. Modelling of PNV maps is easier on previously less disturbed areas than on areas exposed to more severe utilization today.

Comparison of the actual vegetation map with PNV maps showed that all models predicted that more than 50% of total area has been prevented from reaching its natural dynamic equilibrium state. These disturbances are assumed to be caused by anthropogenic influences and reveal that earlier human land-use was considerably more extensive than what is observed today. However, with decreased extent, the intensity and consequences of the human utilization have increased enormously.

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Appendices

Appendix 1: Information about colour aerial photos used for mapping actual vegetation

Company:	Blom Geomatic A.S
Date of photography	5. August 2006
Task number	06057
Picture:	Stripe 17-5, picture no. 24 Stripe 17-6, picture nos. 22 and 24

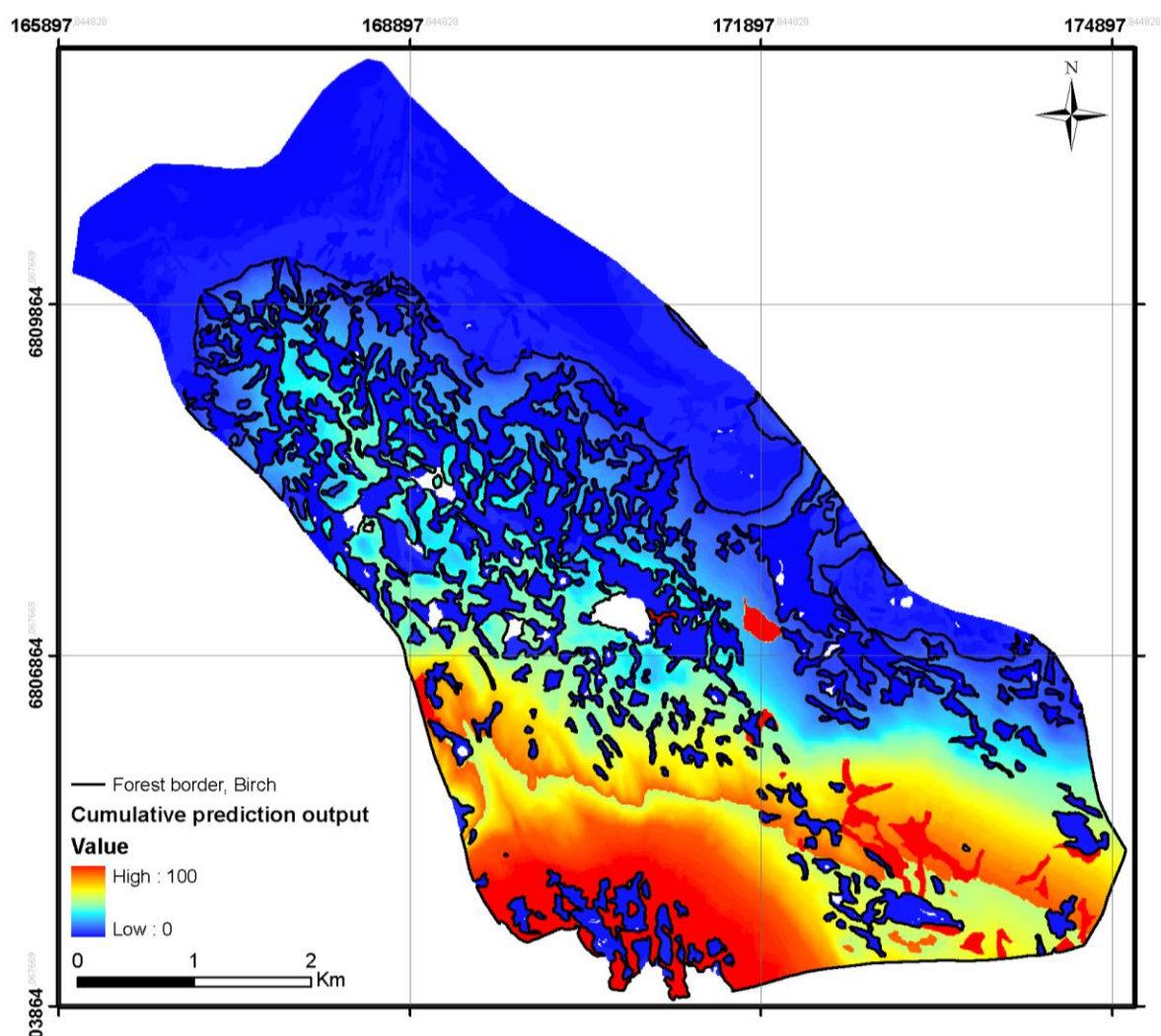
Appendix 2: Vegetation type description and area statistic for actual vegetation map and the different models.

Vegetation type	Actual situation (km ²)	PNVE (km ²)	RBM (km ²)	Maxent (km ²)
1a - Moss snow-bed	0.01	0.01	0.01	0.01
1b - Sedge and grass snow-bed	0.43	0.43	0.43	0.43
2a - Mid-alpine heath	0.08	0.08	0.08	0.08
2b - Dry grass heath	0.46	0.46	0.46	0.46
2c - Lichen heath	1.24	1.21	1.18	1.24
2e - Dwarf shrub heath	9.08	3.46	2.93	5.33
3a - Low herb meadow	0.004	0.004	0.004	0.004
3b - Tall forb meadow	0.97	0.20	0.10	0.27
4a - Lichen- and heather birch forest	0.66	0.35	0.12	0.22
4b - Blueberry birch forest	5.08	7.07	3.90	6.56
4c - Meadow birch forest	2.91	1.12	0.31	1.46
4g - Pastureland forest	0.09	-	-	-
7a - Lichen- and heather spruce forest	0.14	0.75	0.91	0.60
7b - Blueberry spruce forest	0.59	5.17	10.40	4.15
7c - Meadow spruce forest	0.08	4.67	4.43	4.35
8c - Poor swamp forest	0.01	0.01	0.80	0.01
8d - Rich swamp forest	0.32	0.94	0.59	0.70
9a - Bog	0.64	0.66	0.64	0.64
9b - Deer-grass fen	0.30	0.30	0.30	0.30
9c - Fen	6.30	6.34	5.63	6.40
9d - Mud-bottom fens and bogs	0.28	0.28	0.28	0.28
9e - Sedge marsh	0.02	0.02	0.02	0.02
11a - Cultivated land	0.87	-	-	-
11b - Pastures	0.55	-	-	-
12b - Boulder field	0.28	0.28	0.28	0.28
12c - Exposed bedrock	0.38	0.38	0.38	0.38
12d - Built-up areas	1.14	-	-	-
12e - Scattered housing	0.70	-	-	-
12f - Artificial impediment	0.59	-	-	-
Total	34.21	34.21	34.21	34.21

Appendix 3: Additional signs used for adding additional information to vegetation types.

o)	Deciduous trees, unspecified
+	Scots pine
*	Norway spruce
⊖	Aspen
j	More than 50% cover of <i>Juniperus communis</i>
♢	25-50% cover of <i>Salix</i> sp.
s	More than 50% cover of <i>Salix</i> sp.
o))	Unspecified deciduous shrub
g	More than 50% cover of grass
n	More than 50% cover of <i>Nardus stricta</i>
v	25 - 50% cover of lichens
x	More than 50% cover of lichens
^	25 – 50 % of area < 30 cm soil thickness
⌒	> 50 % of area < 30 soil thickness
Δ	25-50% cover of stone block
◊	50-75% cover of stone block
□	25-50% cover of bare ground
⌞	50-75% cover of bare ground
.	25-50% cover of earth, stone and gravel
:	50-75% cover of earth, stone and gravel
⊥G	Abandoned pastures and cultivated land, with more than 50% grass cover
⊥U	Abandoned pastures and cultivated land, with less than 50% grass cover
F	Moisture types of 2c, 2e, 3a, 10a, 10b
TE	Bare ground, no potential of forest because of peak power
~	Unproductive areas, with 10 - 25 % cover of vegetation
r	Rich fen (9c)
k	Lime-demanding subtypes
]	25-50% cover of trees
T	Drained areas

Appendix 4: Output map from Maxent with cumulative probability values for birch. Map projection WGS84/UTM zone 33N



Appendix 5: Output map from Maxent with cumulative probability values for spruce. Map projection WGS84/UTM zone 33N

