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The rare liverwort *Scapania nimbosa* – new knowledge about distribution and ecology in Norway

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The globally disjunct liverwort *Scapania nimbosa* is only known from eastern Himalaya and northwestern Europe. *Scapania nimbosa* has since 1907 only been known from one locality in Norway. After reinvestigation of the locality in 1998 it was suspected to be extinct due to mining activity in the area. However, new investigations in 2003 revealed a new locality and further investigations up to present have resulted in 26 populations including 144 patches being found. All known populations are lying within an area of about 12 × 20 km, 5–20 km from the outer coast line, 200–550 m a.s.l., in north facing mountains slopes in Fræna, Eide and Gjemnes municipalities, Møre and Romsdal county. The climate is euoceanic, with mild winters (January mean temperature near 0°C), heavy precipitation (yearly >2000 mm) and 220–250 days per year with >0.1 mm precipitation. Fog formation around the mountains is common and is believed to be important. *Scapania nimbosa* was found at less than 50% of the seemingly suitable localities, and we suggest that the extent of occurrence is restricted by dispersal. *Scapania nimbosa* is red-listed both in Norway and Europe, and possible threats are discussed.

Scapania nimbosa Taylor ex. Lehm has a clearly disjunct global distribution and is only known from the eastern parts of Himalaya (Nepal, Sikkim), western China (Yunnan) and northwestern Europe (Hill et al. 1991, Fig. 1A). This type of disjunction is shared with a small group of bryophytes belonging to the "Oceanic Boreal Montane element" (Hill and Preston 1998). With few exceptions none of the big liverworts in this element is known to have sexual reproduction or gemmae, making the disjunct distribution patterns even more puzzling.

This group of species grows in a boreal oceanic climate, characterised by high annual precipitation and air humidity, winters include at least periods with snow cover, especially at higher elevations above the forest limit (Ratcliffe 1968, Lye 1970). The species are typically found in northwest Europe, the west coast of North America, eastern Himalaya and coastal parts of East Asia (Schofield and Crum 1972). There are a few exceptions to this general pattern like *Scapania ornithopodioides* (Dicks.) Waddell occurring in Hawaii and *Anastrophyllum donnianum* (Hook.) Steph. in central European mountains. In Norway the liverwort species of the Oceanic Boreal Montane element all occur in the western, most rainy and humid parts of Norway, from Ryfylke in Rogaland in the south, to Nordmøre in Møre and Romsdal in the north.

In Europe *S. nimbosa* is found only in Scotland, Wales, Ireland and Norway. The occurrences in the British Isles constitute the main European population (Fig. 1B). Most localities occur in northwestern Scotland, while scattered localities are present in Wales and along the west coast of Ireland (National Biodiversity Network Gateway 2008). *Scapania nimbosa* is among the most narrowly distributed species in the Oceanic Boreal Montane element (Hill and Preston 1998).

In Norway *S. nimbosa* was first recorded by Albert LeRoy Andrews in 1907, in Sleppskardet, Fræna municipality, Møre andRomsdal county (Andrews 1919). Later, it was collected in the same area by E. Jørgensen in 1921 and 1931 (Jørgensen 1934, herb BG). Hassel et al. (2000) were not able to relocate it during an excursion to Sleppskardet in 1998, and proposed that it might be extinct due to dramatic changes in the landscape the last 60 years caused by limestone mine activities. However, in 2003 a very small population was detected about 6 km further east in the same mountain range, on a steep northeast facing slope in Eide municipality (Ramsgrøhammaren). In 2005

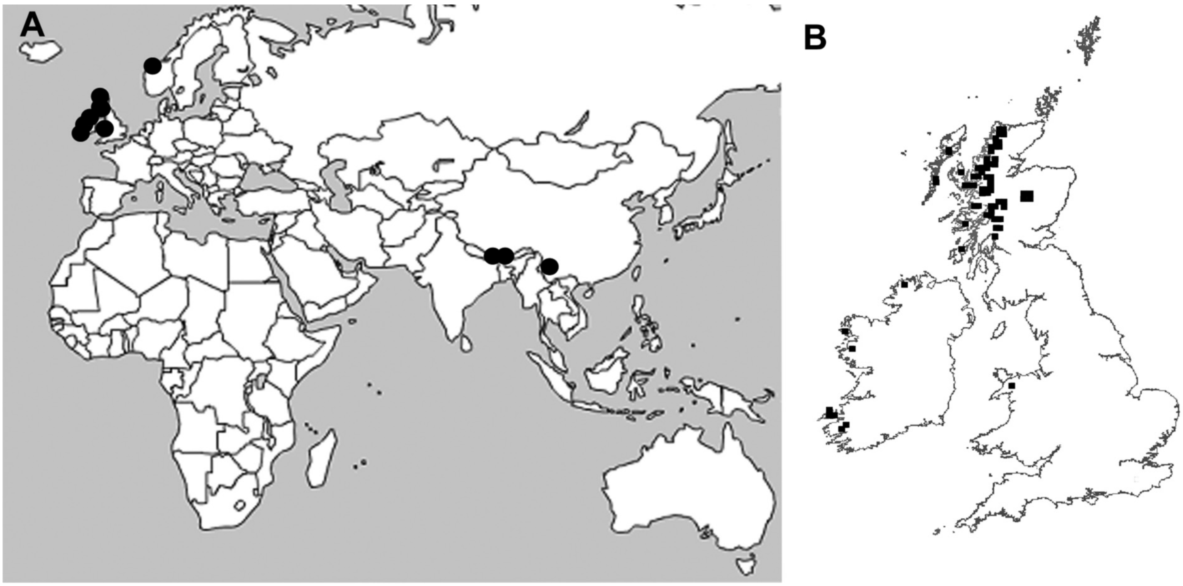

Figure 1. (A) Global distribution of *Scapania nimbosa* (based on data from Hill et al. 1991). (B) Distribution of *Scapania nimbosa* in the British Isles (National Biodiversity Network Gateway 2008).

an additional locality was discovered near Hældalsvatnet, also in Eide municipality (Gaarder and Hassel 2005).

The only mode of dispersal in these species today, seems to be by fragmentation. The disjunct distribution patterns could have resulted from a wide boreal distribution during the Tertiary period, with only the relicts left today (Schofield and Crum 1972, Damsholt 2002). However, phylogeographic studies usually support dispersal rather than ancient geographical vicariance as the preferred explanation of disjunct distribution in bryophytes (reviewed by Heinrichs et al. 2009).

The ecology and population biology is poorly known for this group of species in Norway. However, the genus *Herbertus* has been studied in detail by Løe (1999). In the British Isles there is quite good knowledge of the ecology of the species and their habitats are systematically monitored (Joint Nature Conservation Committee 2005). All the species in this Oceanic Boreal Montane element are highly dependent on high air humidity, and primarily grow in north facing rocks and heath lands, and along creeks and waterfalls so far not exploited by hydroelectric power projects. Fog or spray from waterfalls is an additional source of humidity and is important for some of these species (Damsholt 2002).

Scapania nimbosa was considered as critically endangered (CR) in the 2006 red list of Norway (Flatberg et al. 2006), and is also present on the European red list (as R – rare, European Committee for Conservation of Bryophytes 1995). In the UK it occurs in 19 vice counties and is considered as "nationally scarce" (Joint Nature Conservation Committee 2008).

Several of the other Norwegian species in this Oceanic Boreal Montane element are also considered threatened, such as *Anastrophyllum joergensenii* Schiffn., *Herbertus borealis* Crundw., *H. aduncus* (Dicks.) Gray*, H. stramineus* (Dumort.) Trevis. and *Anastrophyllum donnianum,* which are all present on the Norwegian red list (2006 red list: Flatberg et al. 2006). Others, like *Pleurozia purpurea* Lindb. and *Scapania ornithopodioides,* also belonging to this group are more widely distributed and not included in the Norwegian red list.

Aims

This study aims to improve knowledge about the local distribution of the threatened species *S. nimbosa* in Norway and also to increase knowledge about its population status and ecology. This is achieved through field inventories during 2007–2009, focusing on finding new populations of *S. nimbosa* at Romsdalshalvøya in Møre and Romsdal. In addition we want to discuss possible explanations of the current distribution of *S. nimbosa* in Norway.

Material and methods

Study species

Scapania nimbosa was originally described from Ireland in 1844, and belongs to the family Scapaniaceae. The genus

Scapania is the most species rich in the family and has its highest species diversity in boreal and arctic regions. The genus is in general characterized by having conduplicate leaves with a large dorsal lobe and a smaller ventral lobe. *Scapania nimbosa* and *S. ornithopodioides* are the only Nordic representatives of the subgenus *Protoscapania* (Damsholt 2002). This section is separated from the rest of the genus by their very short or lacking keel between the conduplicate lobes (Fig. 5A). The section includes among the largest species of the genus and shoots of *S. nimbosa* are often more than 5 cm long while *S. ornithopodioides* is even larger. The two species are easily separated in the field by *S. nimbosa* being small, bright red-brown and having few, long irregular spiny teeth along the leaf margin compared to the larger, dark red-brown shoots, with many regular and relatively smaller teeth along the leaf margin in *S. ornithopodioides* (Damsholt 2002). *Scapania nimbosa* has no smell while *S. ornithopodioides* is strongly aromatic (Paton 1999). The two species grow in mats either alone, together or intermixed with other bryophytes (Fig. 5B, Table 2).

Study area

The study area is lying in northwestern Norway (Fig. 2A), in central parts of Møre and Romsdal county, and covers the municipalities Eide, Fræna, Molde, Gjemnes and Averøy. It ranges from the coast line to about 20–25 km inland, i.e. including the coast and outer fjord district of this region (Fig. 2B).

The study area has a rough topography with many steep mountains up to 1000 m a.s.l., often with an alpine structure, but there are also lower, more rounded hills (Fig. 3). Fjords penetrate the landscape. The landscape along the outer coast is dominated by low, rocky heaths and rocky sea shore; there are also many small and larger islands. Parts of the lowland are cultivated for agriculture.

Geologically the area is dominated by gneiss, but amfibolite is also present. Smaller limestone areas are exploited by mining activities. The soils at higher altitudes are partly of glacial origin (moraine), partly scree material and partly organic material from forests, mires and heaths. During the Pleistocene the area was glaciated several times. During the last glacial maximum (the Weichsel period) about 22 000 years BP, the glacier extended into the sea some 100 km away from the present coast in this part of Norway (Andersen and Karlsen 1986).

The climate in this region is humid and oceanic. The mean temperature (1961–1990) of the coldest month (January) at local meteorological stations near sea level in Fræna and Eide is between –0.2 and +0.2°C; but colder at higher altitudes. The mean temperature of the year is between 5.9 and 6.2°C and of the warmest month (August) between 12.7 and 12.9°C. The local winds are predominately coming from west or north across the sea. When the air from the sea meets the mountain ranges it will be pressed up and cooled down, cause fog formation or loose its moisture as rain or snow. The mean yearly precipitation at the local meteorological stations lies in the interval 1400–2300 mm and shows a great variation due to influence by the mountain ranges. Areas close the

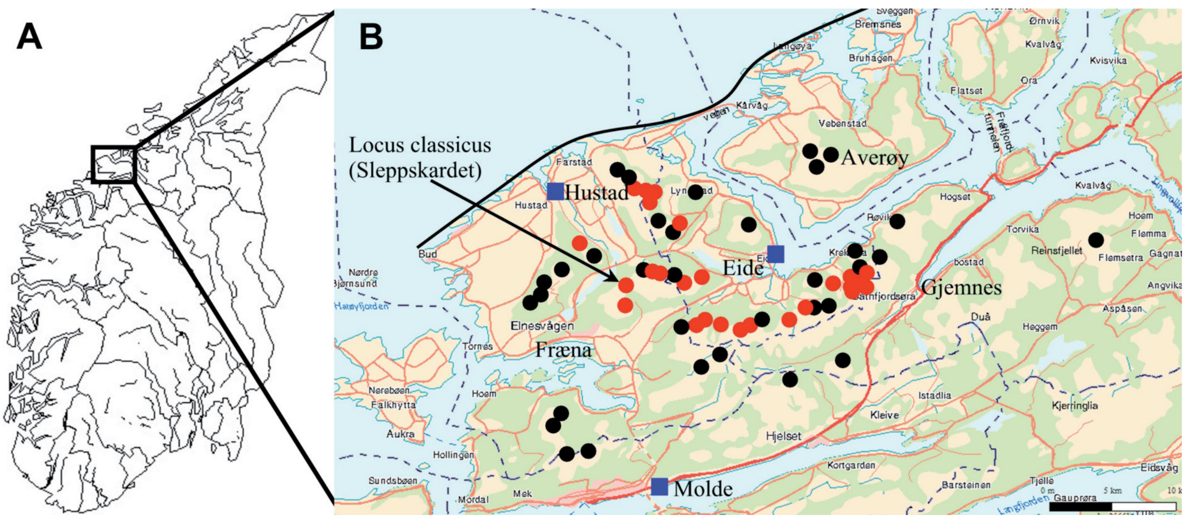

Figure 2. (A) Map of southern Norway with the study area enclosed by a square. (B) Distribution of *Scapania nimbosa* in Norway. Red dots: localities with *S. nimbosa*. Black dots: localities where *S. nimbosa* was searched for but not found. Names of municipalities are given, and borders between them are indicated by broken lines. The black line indicates the outer coast line used in Fig. 6. Blue squares indicate position of the weather stations used in Fig. 4. Norwegian collections of *S. nimbosa* are stored in the herbaria TRH (Trondheim), BG (Bergen) and O (Oslo).

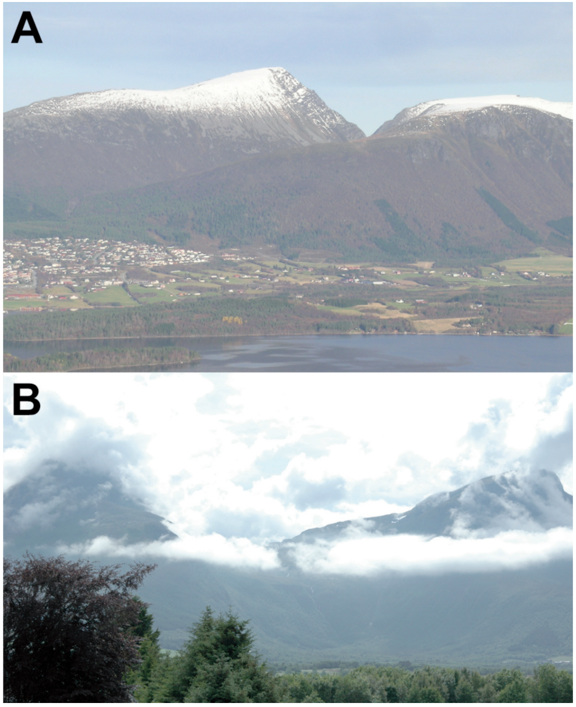

Figure 3. (A) Mountains between Elnesvågen and Eide (Talstadhesten, Allia and Sandnestindan) in October. Photo J. B. Jordal. (B) Fog formation in June at the Tussfossen locality in Eide municipality. Photo K. I. Flatberg.

mountains and 10–20 km from the coast (e.g. Eide) have considerably higher precipitation than areas at the outer coast (e.g. Hustad), and also higher than the fjord districts south or east of the mountains (e.g. Molde, Fig. 4). Mean monthly precipitation (1961–1990) lies above 100 mm for all months at Eide station except for 98 mm in May, and increases to nearly 300 mm monthly in September and October (Fig. 4). Eide is closest to most *S. nimbosa* localities and is thus the most relevant station. There are approximately 220–250 days with a precipitation >0.1 mm, i.e. 60–70% of all days (The Norwegian Meteorological Institute 2010).

Lower altitudes are covered by forests (pine or birch, but with some spruce plantations), mires and coastal *Calluna* heaths. At higher altitudes birch forest dominates and forms the forest limit. Above the forest there are moist heaths and mires, but also large scree areas with ferns, grasses or tall herb vegetation, and rock walls with more scattered vegetation.

Field investigation

In 2007 one of the hitherto largest known populations was detected, and this gave us new information on the ecology of the species in this area, and more systematic investigations have been conducted in the period 2007–2009.

North- and northeast-facing mountain slopes between 100 and 600 m a.s.l. have been systematically selected by map studies and field observations. We have looked for open areas, small rock walls or moist heaths near the forest limit. Based on experience from the first 4–5 localities it seemed to be possible to predict new localities with some success. In total we have selected about 80 potential localities. Until now, 60 of these have been investigated. At most localities of this species in 2007–2009 the following data were collected: 1) the altitude and the position of each patch of a population in the UTM grid system (EUREF89, 32V) were measured by a handhold GPS, with accuracy of ± 5–10 m. 2) Area covered by *S. nimbosa* was estimated in dm^2. 3) The most common accompanying species of vascular plants, mosses and liverworts were noted. In addition photos were taken at most localities. The distance to the coast line (Fig. 2B) was measured on the map. Collected material is deposited in herbarium TRH.

The term locality refers to geographic restricted area that in most cases hold one population, but some large localities can hold more populations. Each population consists of one or more patches. Each patch is separated from other patches by at least 10 m with vegetation without *S. nimbosa.*

Results

Distribution

The known Norwegian distribution of *Scapania nimbosa* now includes 26 localities restricted to the municipalities of Eide, Fræna and Gjemnes in Møre and Romsdal county. *Scapania nimbosa* were found at 40% of the investigated localities. It occurs 5–20 km away from the coast line, mainly in mountain ranges parallel to the coast (Fig. 2B). The species occurs in an area of about 12 × 20 km. In comparison, there are at minimum 100–120 localities of the close relative *S. ornithopodioides* all along the Norwegian west coast (Artsdatabanken and GBIF Norway 2010), representing a distribution area which is about 500 km long and 20–70 km broad.

In addition to the new populations found, 34 seemingly potential localities for *S. nimbosa* have been investigated with negative outcome (Fig. 2B, black dots).

The vertical distribution of *S. nimbosa* patches ranges from 200 to 550 m a.s.l. There are 34 patches between 200 and 300 m, 54 between 300 and 400 m, 43 between 400 and 500 m and 12 above 500 m. The average altitude of the *S. nimbosa* populations increases by approximately 140 m from the localities closest to the coast line towards the inland (Fig. 6).

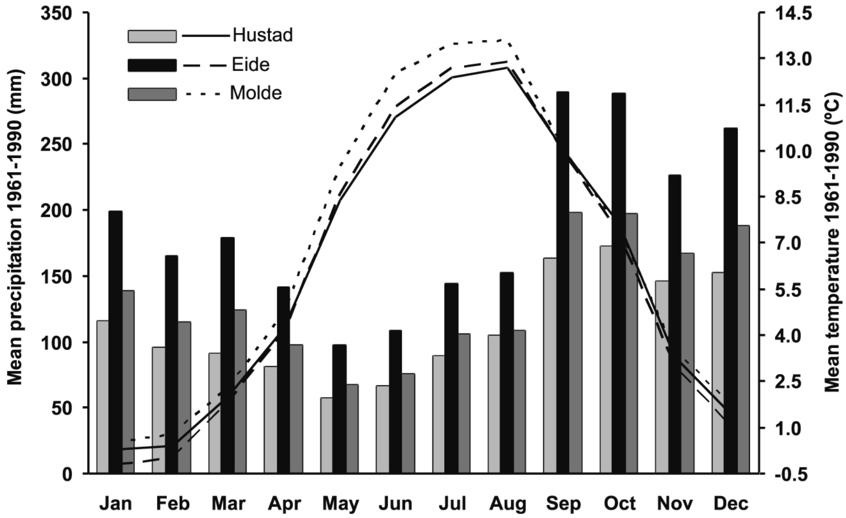

Figure 4. Mean annual precipitation and temperature by month at the three weather stations Hustad (1 km from the coast line), Eide (13 km from the coast line) and Molde (22 km from the coast line). The positions of the weather stations are also shown at Fig. 2B.

At most localities selected as potentially suitable for *S. nimbosa*, its close relative *S. ornithopodioides* was found. Comparing localities with *S. ornithopodioides* only with localities were both species were growing, with respect to spatial distribution (altitude and distance from coast line), no clear differences were found (Fig. 6). However, there seem to be more *S. ornithopodioides* localities close to the coast.

Population data

The survey made in 2007–2009 has revealed several populations of different size, but most consist of 1–3 patches (Table 1). *Scapania nimbosa* always has a more restricted occupancy at the localities than *S. ornithopodioides*. At localities with both species, *S. ornithopodioides* populations often are 2–10 times as large as those of *S. nimbosa*, and

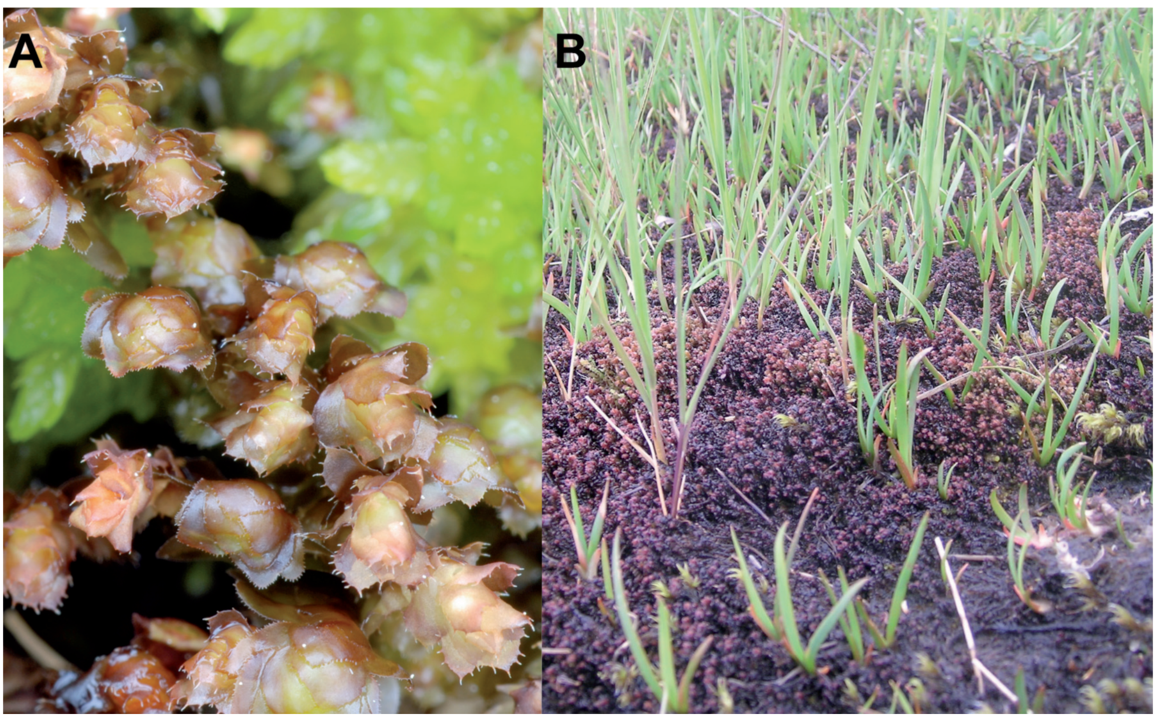

Figure 5. (A) *Scapania nimbosa* (long leaf teeth) growing intermixed with *S. ornithopodioides* short leaf teeth). (B) *Scapania nimbosa* growing with *Racomitrium lanuginosum* in a *Narthecium ossifragum* dominated community. Both photos J. B. Jordal

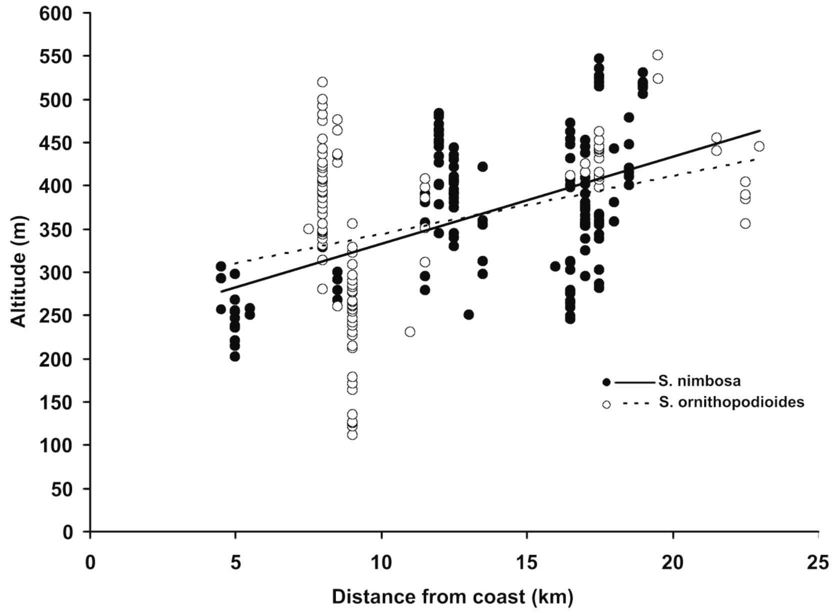

Figure 6. Altitude of *Scapania nimbosa* and *S. ornithopodioides* patches plotted against distance from the coast, with regression lines *S. nimbosa* $R^2 = 0.25$ and *S. ornithopodioides* $R^2 = 0.13$. The coast line is indicated in Fig. 2B. The *S. ornithopodioides* patches included are only from localities where *S. nimbosa* was not found. In addition *S. ornithopodioides* occurs at all localities and most patches with *S. nimbosa* (excluded in the figure).

also have a wider spatial distribution, i.e. growing at lower altitudes.

Scapania nimbosa has been collected at 144 different patches (positions >10 m apart) in 26 populations (>300 m apart). Table 1 show that the known population covers an area estimated to be at least 5.6 m^2, but including all populations brings the estimate up to 7 m^2. Five populations were >0.5 m^2. Eide municipality has 19 populations and 109 patches covering an area estimated to 6 m^2. Fræna municipality has 6 populations with 32 patches covering an area supposed to be 1 m^2. The only population in Gjemnes municipality is very small. Over all municipalities the largest population, 3.5–4 m^2, is found 15–20 km from the coast line. Only 1.2 m^2 is found 4.5–10 km from the coast, and 1.5–2 m^2 at 10–15 km distance from sea.

None of the populations were registered with sporophytes or male and female gametangia. Gemmae were neither observed.

Ecology in Norway

All localities with *S. nimbosa* are in open habitats facing towards the northwest, north or northeast. The typical habitat is a protected depression on a north facing slope, around the forest limit. The localities often have a rough topography, the landscape thus offering a great variety of different microhabitats.

Based on experience in 2007–2009, the species can grow in rather acid circumstances where no calciphytes are found. Most localities have either amphibolites or gneisses. No records of *S. nimbosa* have been made directly on limestone. The localities seem to have in common high soil moisture and a low probability of drying out. *Scapania nimbosa* never grows on flat places, but prefers slopes where trickling water keeps the soil saturated by moisture most of the time. The typical substrate of *S. nimbosa* in this area is moist, peaty soil, but some populations grow at small, constantly moist rock walls or rock slopes, in those cases mostly at the edges near close vegetation.

Most of the localities of *S. nimbosa* are located 12–17.5 km away from the coast line (Fig. 6), this coincides with mountain ranges up to 1000 m high, and in addition to frequent fog formation this area has much higher precipitation than areas closer to the coast and areas further inland (Fig. 4). Based on data from the Eide meteorological station and general knowledge on the impact of coastal mountains on the local climate, we suppose that most localities have a yearly precipitation of 2000–2500 mm. In winter the localities are normally covered by snow for 3–6 months. The liverworts will in this way be protected and avoid many of the dry frost periods during the winter. The patches are often situated in depressions acting like snow beds, places where the snow will accumulate and melt late in the spring.

The typical vegetation is moist heaths with transitions to sloping fens, in addition very often with scattered, small

Table 1. Population data of *Scapania nimbosa* in Norway. 'Area covered' is the estimated area (in dm^2) covered 100% by the species. NE = not estimated. Number of different patches per population is indicated. N = north, E = east, S = south, W = west. Persons: GG = Geir Gaarder, JBJ = John Bjarne Jordal, KH = Kristian Hassel, TP = Tommy Prestø.

A. Data on localities.

Date(s)	Munici-pality	Locality	Position (UTM grid system)	Altitude (m)	Found by	Area covered (dm^2)	No. of patches
27.11.2009	Eide	Bollihaugen	MQ 136-137, 796	268–300	JBJ	20	4
01.07.2008	Eide	Finnseterdalen	MQ 198, 714-715	343–357	JBJ	21	2
30.07.2005, 27.05.2007, 18.06.2007	Eide	Hældalsvatnet	MQ 139-143, 752-754	330–444	GG, JBJ, KH	>100	19
23.09.2008, 25.06.2009	Eide	Herskedalsfjellet N	MQ 272-274, 753-756	282–367	KH, JBJ	50	9
25.06.2009	Eide	Herskedalsfjellet S	MQ 275, 744	478	JBJ	8	1
25.06.2009	Eide	Herskedalsfjellet SE	MQ 282, 750	381	JBJ	7	1
25.06.2009	Eide	Herskedalsfjellet W	MQ 271, 748	358	JBJ	2	1
09.10.2007	Eide	Klokkhuset	MQ 240-241, 722-723	506–531	KH	NE	6
01.07.2008	Eide	Luten N	MQ 178, 722	306	JBJ	0.5	1
15.07.2008	Eide	Mælen N: V of Årøyan	MQ 118-125, 823-825	202–297	JBJ	90	10
11.07.2008	Eide	Mælen NE: Sandsbekken	MQ 121-122, 819	250–258	JBJ	2.5	2
09.11.2009	Eide	NW of Kjølasetra	MQ 251-252, 748-750	353–453	JBJ	77	9
27.02.2003	Eide	Ramsgrøhammaren	MQ 160, 755	250	GG	1	1
28.06.2008	Eide	Surndalsheia	MQ 188-192, 713-718	355–472	JBJ	77	13
12.11.2009	Eide	SW of Galtvatnet	MQ 283-284, 757	515–547	JBJ	9	6
24.06.2008	Eide	Trolldalsheia NE	MQ 170, 711-712	338–353	JBJ	22	3
24.06.2008, 22.09.2008	Eide	Trolldalsvatnet N	MQ 164-167, 714-715	245–312	JBJ, KH	34	12
20.06.2007, 16.10.2008	Eide	Tussfossen	MQ 223-224, 719-720	295–420	KH, TP, GG	NE	8
01.07.2008	Eide	Vassgårdheia N	MQ 205, 724	398	JBJ	0.5	1
10.11.2009	Fræna	Allia	MQ 093-095, 729-732	298–421	JBJ	25	7
15.07.2008	Fræna	Mælen N: Sluppen	MQ 111-113, 824-825	256–306	JBJ	7.5	5
16.10.2008	Fræna	Raudtuva E	MQ 068, 774	328	JBJ	0.5	1
28.10.2009	Fræna	Seterdalen	MQ 115, 755-756	357–391	JBJ	1	3
07.10.2007	Fræna	Sleppskardet	MQ 095-098, 748-750	378–484	KH	NE	14
30.10.2009	Fræna	Stordalen	MQ 126, 756-757	279–380	JBJ	1	3
25.06.2009	Gjemnes	Skredfjellet N	MQ 282-284, 747-750	442–447	JBJ	1	2
Total						560–700	144

Table 2. Some vascular plants and bryophytes frequently growing together with *Scapania nimbosa* in Norway.

Vascular plants	Bryophytes
Andromeda polifolia L.	*Anastrepta orcadensis* (Hook.) Schiffn.
Betula nana L.	*Bazzania tricrenata* (Wahlenb.) Lindb.
Calluna vulgaris (L.) Hull	*Bazzania trilobata* (L.) Gray
Carex panicea L.	*Campylopus atrovirens* De Not.
Empetrum nigrum L.	*Diplophyllum albicans* (L.) Dumort.
Erica tetralix L.	*Hypnum jutlandicum* Holmen & E.Warncke
Eriophorum angustifolium Honck.	*Lepidozia pearsonii* Spruce
Euphrasia wettsteinii var. palustris (Jørg.)	*Marsupella emarginata* (Ehrh.) Dumort.
Huperzia selago (L.) Bernh. ex Schrank & Mart.	*Mylia taylorii* (Hook.) Gray
Lycopodium annotinum L.	*Pleurozium schreberi* (Willd. ex Brid.) Mitt.
Molinia caerulea (L.) Moench	*Racomitrium lanuginosum* (Hedw.) Brid.
Nardus stricta L.	*Rhytidiadelphus loreus* (Hedw.) Warnst.
Narthecium ossifragum (L.) Huds.	*Sarmentypnum sarmentosum* (Wahlenb.) Tuom. & T.J. Kop.
Pedicularis sylvatica L.	*Scapania ornithopodioides* (Dicks.) Waddell
Pinguicula vulgaris L.	*Sphagnum compactum* DC. ex Lam. & DC.
Potentilla erecta (L.) Raeusch.	
Selaginella selaginoides (L.) P.Beauv.	
Succisa pratensis Moench	
Tofieldia pusilla (Michx.) Pers.	
Trichophorum cespitosum (L.) Hartm.	
Vaccinium uliginosum L.	

rock surfaces. The field layer has to be low and open to allow light to pass through to the liverworts, and this does not occur at low altitudes. *Scapania nimbosa* most often grows on peat with scattered heath vegetation . The most typical vascular plants accompanying *S. nimbosa* in the area are *Narthecium ossifragum* (Fig. 3B) and *Trichophorum cespitosum*, further species are mentioned in Table 2.

The bryophyte species most commonly growing together with *S. nimbosa*, is its close relative *S. ornithopodioides*. The latter has been found at all localities, the two are growing in mixed populations, or growing just a few meters apart. Other bryophytes frequently growing together with *S. nimbosa* are listed in Table 2.

Discussion

The many new localities discovered have allowed development of knowledge concerning the distribution and the ecology of *S. nimbosa*. The increase in known localities from three in 2006 to the present 26 will certainly have impact on the future management of the species.

Climate and distribution

The humid and oceanic climate in this region is probably an important factor explaining the current distribution of *S. nimbosa*. Climatic factors in combination with topography, exposure and soil moisture make the microhabitat humidity stable and high much of the growing season. The 'fog effect' may also be of importance, which is also indicated by its species epithet 'nimbosa' – 'growing in the clouds' (also underlined by Damsholt 2002 p. 11). The precipitation increases considerably from the coast line to the mountain ranges 10–20 km away from the coast before it decreases again further inland (Fig. 4), and this might explain the main distribution pattern of the species in the investigated area. Lye (1970) used the same pattern of precipitation to explain the main distribution of oceanic bryophytes rather far away from the coast in Rogaland, southwestern Norway. During the winter season there is often a quite stable and protecting snow cover at the altitudes where *S. nimbosa* grows. The resistance of *S. nimbosa* to freezing and desiccation is not known, but we assume that it can survive at least shorter periods of desiccation and freezing. Closer to the coast and at lower altitudes the snow cover is more variable with many freezing and thawing cycles and together with a drier and more windy climate this may explain the absence of *S. nimbosa* here. Further towards the inland (more than 20 km away from the coast) the snow cover is usually quite stable during winter, but summer precipitation and air humidity is lower, causing a higher probability of desiccation. Thus it seems like the combination of relatively stable snow cover during winter, high summer precipitation and high and stable air humidity is favourable for *S. nimbosa*.

The main factor explaining the distribution of *S. nimbosa* seems to be precipitation as most occurrences are found from 12 to 17.5 km away from the coast (Fig. 6), where the high mountain ranges are situated and the rain fall is high and fog formation is common. The increasing average altitude of *S. nimbosa* occurrences with distance from coast is not surprising as vegetation zones, including the climatic forest limit, are changing in nearly exactly the same way, rising approximately 150 m across the study area (Moen 1999). Suitable habitats will then be found at increasing altitudes towards the inland.

In the British Isles, *S. nimbosa* is found between 400 and 1070 m a.s.l. in subalpine and alpine habitats (Paton 1999). The difference compared to Norway can be explained by a generally warmer climate and thus higher altitudinal limits of similar vegetation zones. It is found in similar habitats, described as damp, generally well-drained acid or less often mildly base-rich soil or humus in constantly humid, shaded north to east-facing montane environments, like base of crags, steep grassy slopes, scree and among dwarf shrubs (Paton 1999). In Yunnan it is known from 3500–3800 m a.s.l., and this is also a fog area (Damsholt 2002, Hill et al. 1991).

Distribution in historical perspective

There should potentially be a large number of other suitable localities for *S. nimbosa* along the west coast of Norway. Størmer (1969), in his treatment of southern and western mosses in Norway, discusses the distribution of three of the mosses (*Andreaea alpina* Hedw., *Racomitrium ellipticum* (Turner) Bruch & Schimp. and *Oedipodium griffithianum* (Dicks.) Schwägr.) in the Oceanic Boreal Montane element according to Hill and Preston (1998). These three mosses have rather wide distribution ranges, from the southwest to the northern part of Norway (Nordland and Troms), while the liverworts confined to the same element show a much more restricted distribution and are mainly found from Rogaland to Sogn and Fjordane (Artsdatabanken and GBIF Norway 2010). There is one striking difference between the mosses and liverworts. The liverworts lack spore production, while this is rather common among the mosses. The restricted distribution of the liverworts seems to be linked to limited dispersal. *Scapania ornithopodioides* and *S. nimbosa* have almost the same distribution in the British Isles (National Biodiversity Network Gateway 2008). However, this is not the case in Norway, as *S. ornithopodioides* is one of the most widely distributed Oceanic Boreal Montane liverworts found along the whole west coast of Norway (Artsdatabanken and GBIF Norway 2010). Our results indicate that there are no obvious differences between localities were both *S. nimbosa* and *S. ornithopodioides* were found and localities with only *S. ornithopodioides* (Fig. 6). This indicates that *S. nimbosa* has not yet reached all available localities. A possible explanation for this is the restricted dispersal capacity combined with very special habitat demands and/or too short time available to fill all suitable localities.

Although nunataks are indicated in the study area during Pleistocene, organisms which today cannot live above 1000 m a.s.l. in Norway probably could not survive the Weichsel period here (Dahl 1998 p. 34). All lowland liverworts present today, including *S. nimbosa* and *S. ornithopodioides,* are therefore supposed to have spread from refugia south or west of the ice cap and established in the area during Holocene. Dispersal in *S. nimbosa* probably occurs by shoot fragments (or rarely gemmae) spread by the wind or by animals. It is hard to see any other possibility for colonisation during the Holocene than transport by wind from Atlantic areas like the British Isles. The chance for a successful establishment by wind over such a long distance (about 900–1000 km from Scotland, and even more from Ireland) must be very low and will happen very rarely. What we now see might be the result of just one successful dispersal event. Small samples have been collected at most of the localities and will be used to elucidate the inter population relationships by DNA-analyses. *Anastrophyllum joergensenii* is also present in only one small area in West Norway, and may represent a similar story. The dispersal ability of *S. nimbosa* seems to be lower than that of *S. ornithopodioides*, which has been rather successful in its dispersal in Norway during the Holocene period. *Scapania ornithopodioides* also seems to be a better competitor against shadow from herbs, ferns and grasses, and this may explain the occurrence of this species at low altitudes down to 100–200 m a.s.l., where the vegetation generally is taller.

Even if *S. nimbosa* has quite special habitat requirements we think it has a much wider potential distribution area in Western Norway. The smaller populations compared to *S. ornithopodioides,* the small and concentrated distribution area and absence at many potential localities in our study area, could be explained by lower dispersal ability. But it could also mean that *S. nimbosa* is less competitive than *S. ornithopodioides*. This could result from smaller size, lower establishment ability, slower growth or less shade tolerance. These are all factors that need to be explored to get better understanding of the distribution.

Threats, management and red list status

The locality in Sleppskardet has been strongly changed by mining activities during the last 60 years, and this could also be a future threat to other populations as these activities are still expanding at some places. As we have shown *S. nimbosa* has survived in an unexploited area by Sleppskardet (Table 1), but seems to be extinct at the low altitudes indicated by Andrews (1919) and Jørgensen (1934) and searched for by Hassel et al. (2000). The populations here must have declined considerably. The population by Trolldalsvatnet is close to a road leading to a drinking water reserve, and former populations may have been influenced by the construction of this road and the water pipe. New roads for different purposes and water pipes in connection with e.g. small hydroelectric power projects may become threats at some localities. The construction of power transmission lines and building of new huts are also possible threats. A power transmission line was planned through the locality west of Årøyan (to transport energy from a windmill project at sea) before *S. nimbosa* was discovered at this site, but this project was never realized. The use of motor vehicles outside roads is increasingly common and may be a future threat. The populations of red deer and roe deer in western Norway have been increasing for a long time (Austrheim et al. 2008), and erosion of liverwort mats by deer trampling has been observed several places. This is certainly harmful to *S. nimbosa* as establishment and regeneration seems to be slow, but on the other hand it may also increase the rate of dispersal to new localities. The species has relatively small populations and may also be subject to accidental events like screes and snow avalanches. The current populations seem to avoid localities with a regular scree frequency.

Climate change will possibly lead to more unstable winters and warmer summers (Hanssen-Bauer et al. 2003). Longer periods without an isolating snow cover in the winter may increase the chance of drying out. The same will be the case if the summers get warmer. Increased tree cover and rise of the tree line are possible threats for many of the localities as most of them are lying just above the current forest limit. The two main reasons for increased tree cover are warmer climate due to climate change, and less intense grazing pressure from sheep in this region. The latter may lead to increased tree seedling recruitment success (Speed et al. 2010), and especially birch *Betula pubescens* recruitment is an important factor as this species is dominating the forests of higher altitudes in the area. Ceased grazing may also result in increased shading and competition from grasses and herbs at the current localities.

Localities with *S. nimbosa* populations are now available to everyone on the Internet (The Directorate for Nature Management 2010, Artsdatabanken and GBIF Norway 2010). This knowledge is very important to avoid or stop projects which could be harmful to the populations. It is also necessary to look at the possibility of legal protection of the most important localities, e.g. as natural reserves or landscape protection areas.

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