Conservation genetics and ecology of four red listed vascular plant species in the high arctic archipelago of Svalbard

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Forord

Dette masterprosjektet har vært en del av et UNIS (universitetssenteret på Svalbard) prosjekt som ble startet opp av Inger Greve Alsos i 2009, med støtte fra Svalbards miljøvernfond. Veiledere har vært Inger G. Alsos og Anne Krag Brysting. I tillegg har Reidar Elven vært sterkt involvert i prosjektet og bidratt med veiledning.

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Idunn E. B. Skjetne

Abstract

Nearly one third of the vascular plant species of the remote high arctic archipelago of Svalbard are listed on the regional Red List for Svalbard, and there is a need for information to evaluate their conservation status, and improve conservation management. Here I study distribution, population sizes, ecology, and threats in *Carex capillaris*, *Comastoma tenellum*, *Puccinellia angustata* ssp. *palibinii*, and *Tofieldia pusilla* which are all restricted to some of the warmest local areas of Svalbard. Further, I use Amplified Fragment Length Polymorphism (AFLP) to evaluate whether the Svalbard populations are genetically depleted compared to other arctic-alpine populations of the species, investigate their phylogeographic history, and resolve taxonomic problems. All species have larger populations than previously assumed and new populations of *C. tenellum* and *T. pusilla* were discovered. *Carex capillaris* is thriving, and is associated with high substrate moisture and temperature at its only Svalbard locality. Local expansion potential was indicated. The population is genetically depleted, and forms a distinct genetic subgroup of ssp. *fuscidula*, with N Norway as the most likely source region. The results indicate that *C. capillaris* may have colonized Svalbard during the warmer early-middle Holocene, but a more recent introduction is also possible. Possible threats include reduced evolutionary potential, inbreeding depression, and stochastic events. *Comastoma tenellum* is growing in bird cliff vegetation at its three known localities. The populations are genetically depleted, and although clearly related to the most probable source region, NW Russia, they form a distinct genetic subgroup. This suggests an early-middle Holocene introduction of the species to Svalbard, associated with a strong founder effect. Possible threats include reduced evolutionary potential, inbreeding depression, and fluctuating population sizes. The population of *P. angustata* ssp. *palibinii* in Bockfjorden has been erroneously classified and belongs to the Svalbard endemic *P. svalbardensis*. This species exhibits a highly specialized ecology and is locally abundant in other parts of Svalbard. High levels of genetic diversity were detected, and no genetic threats are apparent. *Tofieldia pusilla* is found in different types of habitats, but temperature might restrict local expansion. The populations are not notably genetically depleted, which indicates that *T. pusilla* is doing comparatively better than many other thermophilous vascular plants in Svalbard. Based on the results, *C. capillaris* and *C. tenellum* were downgraded to less critical Red List categories, and *T. pusilla* was taken out of the Red List. As temperature probably is the limiting factor to *C. capillaris*, *C. tenellum* and *T. pusilla* in Svalbard, they are expected to benefit from a warmer climate.

Contents

Introduction

The flora of the remote high arctic archipelago of Svalbard includes around 165 native species of vascular plants (Elven and Elvebakk 1996), of which nearly one third (50 species) are listed on the regional Red List for Svalbard, which is part of the Norwegian Red List (hereafter referred to as the Norwegian Red List) (Solstad et al. 2010). Anchored in the Svalbard Treaty (1920), and further the Svalbard Environmental Protection Act (2001), the Norwegian authorities aim Svalbard to be among the best managed wilderness areas in the world (White Paper Report no. 22 2009). Still, key information to evaluate conservation status, including population numbers, sizes and threats, is insufficient for many species (Vistad et al. 2008, Lydersen et al. 2009). There is also a need to gather knowledge about the ecological requirements of the red listed vascular plants, as habitat preservation is crucial to save rare plants (Conservation of Arctic Flora and Fauna (CAFF) 2002). Furthermore, although the IUCN Red List criteria (World Conservation Union (IUCN) 2001), which are used in the Norwegian Red List (Kålås et al. 2010), do not take genetic diversity into consideration, endangered species often face genetic concerns (Frankham 1995, 2005). Information on levels and partitioning of genetic diversity can be a major contribution in prioritizing to which endangered populations and species conservation resources should be allocated (DeSalle and Amato 2004). At last, as climate change is emerging as the major stressor on Arctic biodiversity (Conservation of Arctic Flora and Fauna (CAFF) 2010), knowledge about species responses to past climatic changes might provide valuable insights into how they may respond in the future (Alsos et al. 2009, Cordellier and Pfenninger 2009). Here, I put focus on four vascular plant species, which were all listed on the Norwegian Red List when this study was initiated in 2009 (Elven et al. 2006): *Carex capillaris* L., *Comastoma tenellum* (Rottb.) Toyok., *Puccinellia angustata* ssp. *palibinii* (T.J. Sørensen) Tzvelev, and *Tofieldia pusilla* (Michx.) Pers.

Very few (perhaps three) vascular plant species are endemic to Svalbard, and many are, as arctic plants in general, widely distributed throughout the Arctic region (Elven et al. 2011). Since its origin, the Arctic flora has been subjected to repeated glacial cycles (the last from about 110,000 years before present). Evidence from fossil records and studies of the distribution of genetic diversity have revealed that species shifted their ranges in response to these glacial cycles (Comes and Kadereit 1998, Abbott and Brochmann 2003, Brochmann et al. 2003, Williams et al. 2004). During the maximum ice extent of the last glaciation (about

20,000 years before present), Svalbard was almost completely glaciated (Landvik et al. 1998, Landvik et al. 2003, Ottesen et al. 2007), and evidence suggesting *in situ* glacial survival is only found for one vascular plant species (*Arenaria humifusa* Wahlenb.) (Westergaard et al. 2011b). The retreat of the ice, about 10,000-11,000 years before present (Lehman and Forman 1992, Salvigsen and Hogvard 2005, Forwick and Vorren 2010), was followed by warmer climatic conditions, and evidence from e.g. thermophilous marine molluscs and plant macrofossils suggest that the summer temperatures in Svalbard were about 1-2 ºC higher than today during early and mid Holocene (about 9500-4000 years before present) (Birks 1991, Salvigsen et al. 1992, Salvigsen 2002). During this period, thermophilous species like *Salix herbacea* L. was found outside its current distribution in Svalbard (Birks 1991). Although it has been suggested that even the thermophilous plants in Svalbard are glacial survivors (Hadač 1963, Rønning 1963), this is highly unlikely (Brochmann et al. 2003), and most of them probably colonized Svalbard during the warmer Holocene periods and established a wider distribution than they have at present (Alsos et al. 2002, Engelskjøn et al. 2003, Alsos et al. 2007). However, some species may have more recently colonized Svalbard, with the most likely candidates found among those with only one present locality in Svalbard.

The majority of the most threatened species in Svalbard are a group of thermophilous species which have their present small and few populations restricted to small 'pockets' with favorable conditions (Engelskjøn et al. 2003, Alsos et al. 2004, Solstad et al. 2010). Such favorable 'pockets' may include thermal springs and south facing slopes (Walker 1995). Three of the four species studied here, *C. capillaris*, *C. tenellum*, and *T. pusilla* can be considered thermophilous (Elvebakk 1989), and all four are found disjunctly distributed in the warmer inner fjord areas of Spitsbergen. Temperature is a major determinant of the spatial distribution of plants in the Arctic, both at a local and regional scale (Walker 1995). In arctic plant communities, temperature may direct the number of species (Rannie 1986), and as plants differ in their temperature preference, it may also direct the species composition (Brooker and van der Wal 2003). In Svalbard, only the three coldest of the five bioclimatic zones of the Arctic are represented (Elvebakk 2005b, Walker et al. 2005). Consequently, under the present climatic conditions, most areas are too cold for the thermophilous species.

In the last 100 years, average temperatures in the Arctic have increased at almost twice the global average rate (Intergovernmental Panel on Climate Change (IPCC) 2007), and a continued warming is expected (Christensen et al. 2007). There is already evidence for species shifting their ranges towards higher latitudes due to the ongoing climatic changes

(Parmesan and Yohe 2003, Root et al. 2003, Chen et al. 2011), and shifts in vegetation types within the Arctic have also been observed (Sturm et al. 2001). Thus, climate change is emerging as a major impact factor on Arctic biodiversity (Conservation of Arctic Flora and Fauna (CAFF) 2010) and may affect it at all levels: genetic-, species-, and ecosystem diversity (Conservation of Arctic Flora and Fauna (CAFF) 2002). While climate warming may have a negative impact on many arctic species (Alsos et al. 2012b), we might expect that some species, like the red listed thermophilous plants in Svalbard, will take advantage of a warmer climate and expand their present distributions (Walker 1995, Crawford 2008).

However, their present small and isolated populations are expected to harbor less genetic diversity (Frankham 1996, Cole 2003), be more inbreed, and suffer greater inbreeding depression (Ellstrand and Elam 1993, Keller and Waller 2002, Frankham et al. 2010) than larger and less isolated populations, and consequently, they might be more prone to extinction (Frankham 2005). Nevertheless, as the current levels and distribution of genetic diversity are shaped by a wide range of factors, including history (e.g. population fragmentation, bottlenecks, refugia, and range shifts) (Young et al. 1996, Hewitt 2000, Petit et al. 2003, Meirmans et al. 2011), life history traits (e.g. life span, breeding system, and dispersal mode) (Hamrick and Godt 1996, Nybom and Bartish 2000, Nybom 2004, Thiel-Egenter et al. 2009), and geographic range (Loveless and Hamrick 1984, Hamrick and Godt 1989), the levels of genetic diversity and inbreeding depression, and the genetic distinctiveness of the populations of red listed vascular plants in Svalbard, may vary greatly among species. Consequently, the capability of individual species to respond to climate change will vary greatly.

Although we expect larger areas of Svalbard to become suitable for the red listed thermophilous species with a warmer climate, there may be other parts of their ecology which could restrict their expansion potential. Substrate chemistry is an important determinant of the distribution of plant communities and individual species (Elvebakk 1982, Elvebakk 1997). As the bedrock types covering most of Svalbard are weakly acidic (Elvebakk 1997), areas suitable for calciphilous species are smaller and disjunctly distributed. Moisture may also influence the distribution of species, and the moisture preference and tolerance of arctic vascular plants varies highly among species (Raup 1969), also within Svalbard (Kojima and Wada 1999). Further, as nutrient levels are generally low in arctic soils, some plants depend on the nutrient enrichment by sea birds, and can only be found in the distinct and species rich bird cliff vegetation (Eurola and Hakala 1977, Elvebakk 1994).

There are other aspects which also might influence the prospects of red listed plants in Svalbard. Competition is expected to increase in a warmer Arctic, and arctic species with conservative nutrient-use strategies, slow growth, and inflexible morphologies may become outcompeted by more responsive, faster growing, taller species immigrating from southern latitudes (Callaghan et al. 2005). Arctic ecosystems are also vulnerable to human impact (Jónsdóttir 2005), and red listed plants may face threats from an increasing human traffic. The number of cruise ship tourists visiting Svalbard has nearly doubled since 1998, and is currently about 30,000 per year (Governor of Svalbard 2010). And although 65 % of the land area of Svalbard is protected, including most localities of the focus species in this study, cruise ships often visit such vulnerable areas (Lydersen et al. 2009, White Paper Report no. 22 2009). Furthermore, there is considerable research activity taking place in the archipelago (White Paper Report no. 22 2009). Another potential threat for red listed plants is disturbance from geese and reindeer (*Rangifer tarandus platyrhynchus*). In particular, the populations of barnacle goose (*Branta leucopsis*) and pink-footed (*Anser brachyrhynchus*) geese in Svalbard have increased greatly during the last decades (Norwegian Polar Institute 2012), and in 2006-2007 their population sizes in Svalbard were estimated to be about 25,000 and 55,000 individuals, respectively (references in Tombre et al. 2008). Large-scale vegetation destruction due to geese grazing is known e.g. from Arctic Canada (Jefferies et al. 2006). However, species exhibit different competitive abilities and tolerances to disturbance (Raup 1969, Grime 1977), and are therefore expected to respond individualistically to these potential threats.

At last, although the vascular flora of Svalbard is reasonably well studied, and its taxa are mostly well known, taxonomic problems remain in several genera, including *Puccinellia* (Elven and Elvebakk 1996). Thus, for some taxa, the major problem for conservation management might in fact be taxonomic uncertainties (Frankham et al. 2010). This applies to one of the focus species in this study, *P. angustata* ssp. *palibinii*, as morphological re-investigations conclude that the Svalbard material, from a population in Bockfjorden, was erroneously classified (Elven et al. 2011). This population is therefore hereafter referred to as *Puccinellia* sp.

To gather information useful for conservation management of each of the four focus taxa (*C. capillaris*, *C. tenellum*, *Puccinellia* sp., and *T. pusilla*) in Svalbard, this study aims to:

1) Map as many as possible of their current population locations and population sizes in Svalbard, and evaluate the population status, including identification of possible environmental threats.
2) Study their ecological requirements at the visited localities, and evaluate whether the species have local expansion potential.
3) Use Amplified Fragment Length Polymorphism (AFLP) markers to determine whether the Svalbard populations are genetically depleted compared to populations from other parts of their distribution area, and investigate the phylogeographic history of the Svalbard populations. For *Puccinellia* sp. the relationship to two other *Puccinellia* taxa in Svalbard, *P*. a*ngustata* (R. Br.) Rand & Redf. ssp. *angustata* and *P*. *svalbardensis* Rønning, will be investigated based on morphology (i.e. inspection of herbarium vouchers) and AFLP markers, and levels of genetic diversity among populations of the taxa will be compared.
4) Discuss implications for conservation in Svalbard.

Materials and Methods

Focus species

Carex capillaris L. (Cyperaceae) (Figure 1) is a perennial caespitose sedge with an uncertain ploidal level due to difficulties in inferring basic chromosome numbers in the genus (Brochmann et al. 2004). It grows in wet habitats like stream banks and mires, or in mesic tundra, on calcareous substrates (Rønning 1996, Brochmann and Steen 1999, Aiken et al. 2003, Elven 2005, Elven et al. 2011). Information on the reproductive biology of *C. capillaris* is limited. Although its flowers appear wind pollinated, it has been suggested that caespitose *Carex* species are predominantly autogamous (Ford et al. 1991, Jonsson et al. 1996). However, this pattern is not consistent (Ford et al. 1998). Nevertheless, Brochmann and Steen (1999) suggested that *C. capillaris* may be mainly autogamous in Svalbard. The *C. capillaris* complex is associated with taxonomic controversy, and two species are currently recognized by the Panarctic Flora Project **(**PAF**)** (Elven et al. 2011): *C. capillaris* and *C. krausei* Boek.. Based on morphology, three subspecies/varieties of *C. capillaris* can be recognized: ssp. *capillaris* is mainly temperate-boreal with an amphi-Atlantic, European and Asian distribution; var. *elongata* Olney ex Fernald is mainly boreal and southern arctic with an amphi-Beringian, Asian, and North American distribution; and ssp. *fuscidula* (V.I.Krecz. ex T.V.Egorova) Á.Löve & D.Löve is mainly arctic with a circumpolar-alpine distribution (Elven et al. 2011). In 1960, *C. capillaris* was reported from Svalbard, growing in 'quite considerable quantities' close to the thermal springs, Trollkjeldene, in Bockfjorden (Haakon VII Land) (Rønning 1961a), which is still its only known locality in Svalbard (Figure 2). Elven et al. (2001) classified the population as ssp. *fuscidula*. *Carex capillaris* was listed as critically endangered on the 2006 Norwegian Red List (Elven et al. 2006).

Comastoma tenellum **(**Rottb.) Toyok. (Gentianaceae) (Figure 3) is (in Svalbard) an annual or biennial, diploid herb (Rønning 1996, Brochmann and Steen 1999, Elven 2005, Elven et al. 2011). It is often restricted to relatively disturbed sites, in Svalbard found in bird cliff vegetation, on calcareous substrates (Elven 2005, Solstad et al. 2010). *Comastoma tenellum* has insect-pollinated flowers, but is mainly autogamous (Brochmann and Steen 1999, Schönswetter et al. 2004). The species has a disjunct circumpolar-alpine distribution (Elven et al. 2011). The first report of *C. tenellum* in Svalbard was from Wijdefjorden in 1873 (Elvebakk and Nilsen 2002), and the species was, when this study was initialized, only known

from two Svalbard localities: Flatøyrdalen in Wijdefjorden (Ny-Friesland), and Ossian Sarsfjellet in Kongsfjorden (Haakon VII Land) (Figure 4, Table A1). *Comastoma tenellum* was listed as critically endangered on the 2006 Norwegian Red List (Elven et al. 2006).

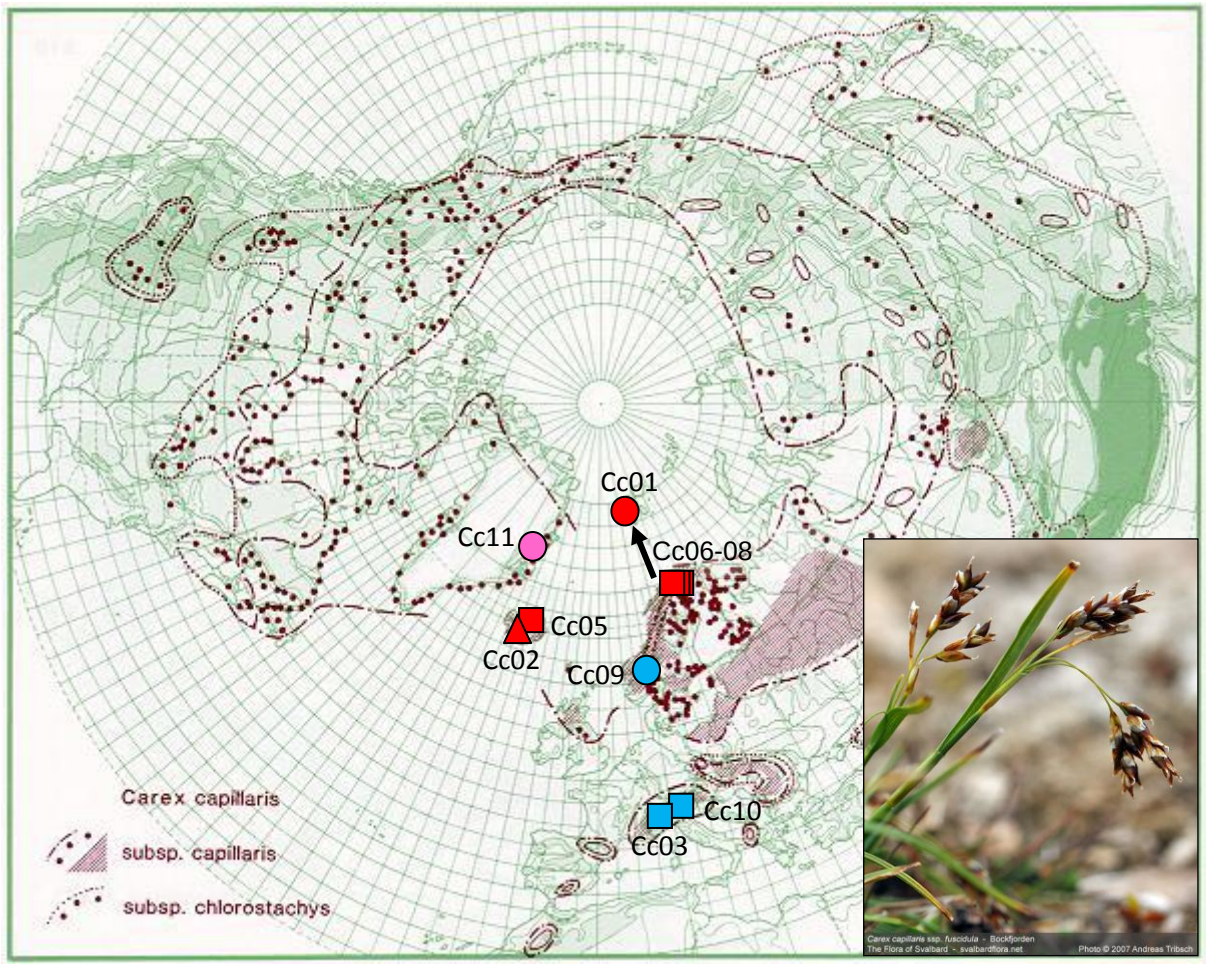

Figure 1 Geographical distribution (Hultén and Fries 1986), sampled populations, and genetic groups (inferred from AFLPs) of *Carex capillaris*. Colors represent main genetic groups, symbols represent subgroups within these. One individual from population Cc02 belongs to the subgroup otherwise consisting of population Cc05-08 (not shown). Arrow indicates the most likely source region of the Svalbard individuals (inferred from assignment tests with a minimal log-likelihood difference threshold of 0). Population ID follows Table 1. Photo of *C. capillaris* ssp. *fuscidula*: Andreas Tribsch (Alsos et al. 2012a).

Figure 2 Distribution and sampled population of *Carex capillaris* in Svalbard, modified after Alsos et al. (2012a).

***Puccinellia* sp.** A population of the taxonomic challenging (Elven and Elvebakk 1996, Elven et al. 2011) temperate to arctic grass genus *Puccinellia* was recognized from Bockfjorden (Haakon VII Land) in 1981 (Elvebakk and Spjelkavik 1981) (Figure 5). It was later classified as *P. angustata* ssp. *palibinii*, found nowhere else in Svalbard, and until then only reported from Novaya Zemlya and Franz Joseph Land (Elvebakk et al. 1994). However, morphological re-investigations conducted by the Russian *Puccinellia* expert, and *P. angustata* ssp. *palibinii* author, N. N. Tzvelev, conclude that the population in Bockfjorden does not belong to *P. angustata* ssp. *palibinii* (Elven et al. 2011). Therefore, this population was examined together with populations of the two morphologically most similar (and presumably closely related) *Puccinellia* taxa in Svalbard: *P. angustata* ssp. *angustata* (hereafter referred to as *P. angustata*) and *P. svalbardensis*. *Puccinellia angustata* has a circumpolar distribution (Elven et al. 2011), and is widespread in Svalbard (Alsos et al. 2012a), where it is known since 1868 (Svalbard Herbarium database 2006). *Puccinellia svalbardensis* was first described from Lovénøyene in Kongsfjorden (Rønning 1961b). During the last decade 15 large populations of this Svalbard endemic have been discovered in

Wijdefjorden (Elvebakk and Nilsen 2002, Elvebakk and Nilsen 2011) and a large population in Pyramiden (Dickson Land) was recently rediscovered (I. G. Alsos pers. com.). All three taxa are perennial and hexaploid, and caespitose (Elven 2005, Elven et al. 2011). They also have a similar ecology, but *Puccinellia* sp. and *P. svalbardensis* are restricted to the most dry, highly saline and calcareous substrates (Rønning 1961b, Elvebakk and Nilsen 2002, Solstad et al. 2010, Elvebakk and Nilsen 2011). They all have wind-pollinated flowers, but Brochmann and Steen (1999) suggest that *P. angustata* and *P. svalbardensis* are mainly autogamous in Svalbard. Since *P. angustata* is widespread (Alsos et al. 2012a), and *P. svalbardensis* relatively widespread (Figure 5), in Svalbard, they were not listed on the 2006 Norwegian Red List, while *P. angustata* ssp. *palibinii* (i.e. *Puccinellia* sp. from Bockfjorden) was listed as critically endangered (Elven et al. 2006).

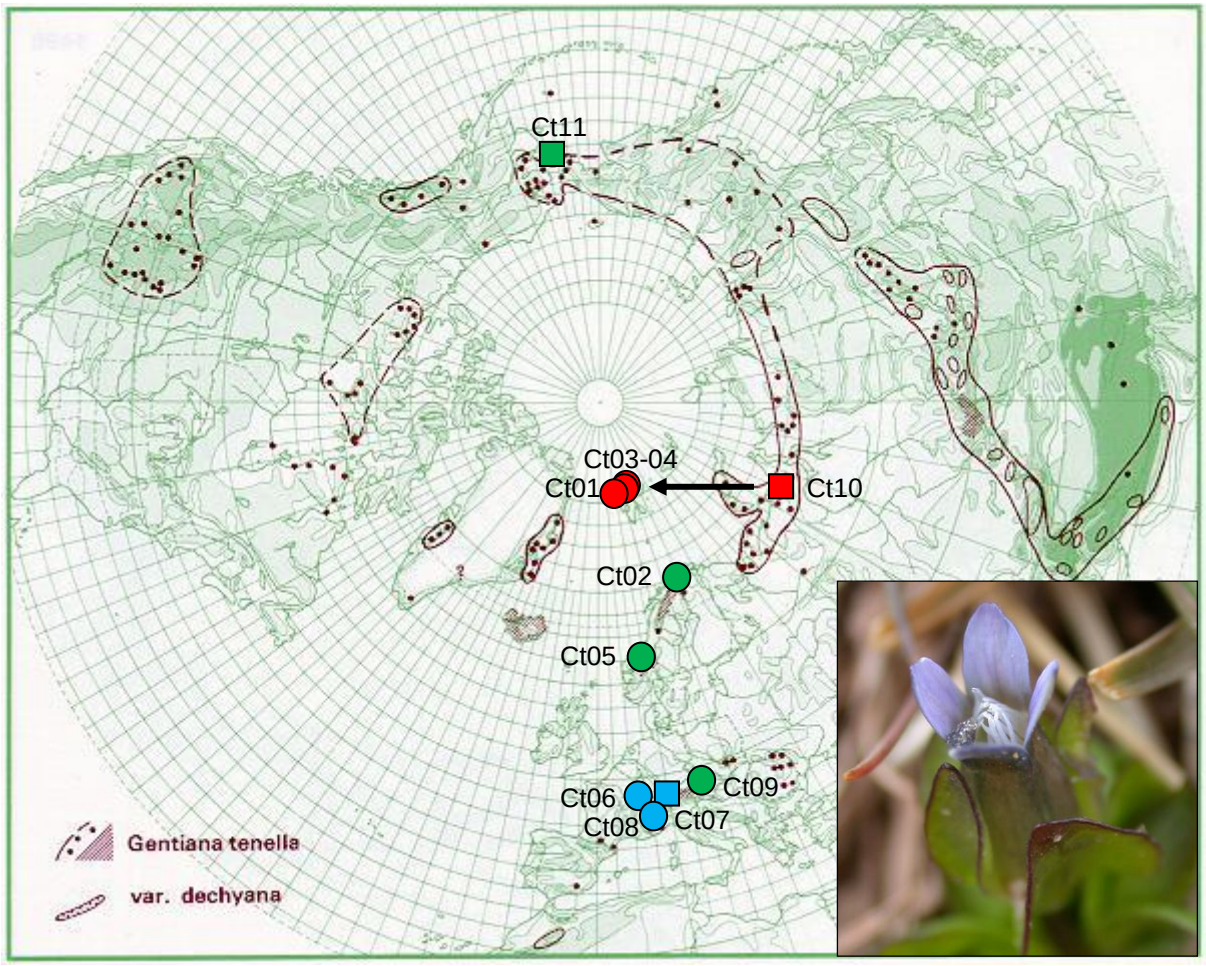

Figure 3 Geographical distribution (Hultén and Fries 1986), sampled populations, and genetic groups (inferred from AFLPs) of *Comastoma tenellum*. Colors represent main genetic groups, symbols represent subgroups within these. Arrow indicates source region of the Svalbard individuals (inferred from assignment tests with a minimal log-likelihood difference threshold of 2). Population ID follows Table 1. Photo of *C. tenellum*: Inger Greve Alsos (Alsos et al. 2012a).

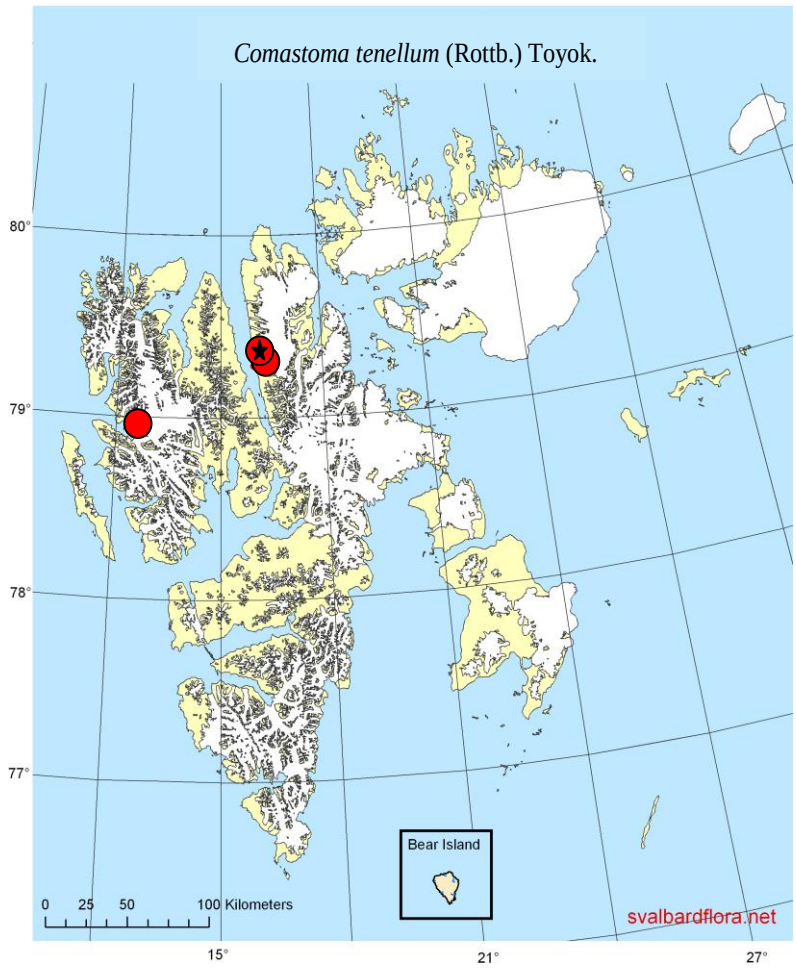

Figure 4 Distribution and sampled populations of *Comastoma tenellum* in Svalbard, modified after Alsos et al. (2012a). The population discovered for the first time by this study (Ringhorndalen) is indicated with a star.

Tofieldia pusilla (Michx.) Pers. (Melanthiaceae) (Figure 6) is a perennial and diploid, caespitose monocot (Rønning 1996, Brochmann and Steen 1999, Elven 2005, Elven et al. 2011). It is growing in mesic tundra or wetland areas, on calcareous substrates (Rønning 1996, Elven 2005, Elven et al. 2006). Although there is limited knowledge about *T. pusilla*'s reproduction, its flowers indicate that it is insect-pollinated, probably by small flies (A. Tribsch pers. comm., pers. obs.). In Svalbard, *T. pusilla* is reported to be autogamous (Brochmann and Steen 1999), but Line (2006) found that the species is mainly allogamous in northern Canada, and it also reproduces asexually via short rhizomes (Cranston and Valentine 1983). *Tofieldia pusilla* has a (sub-) circumpolar–alpine distribution (Elven et al. 2011). The first report of the species in Svalbard was from Dicksonfjorden (Dickson Land) in 1882 (Rønning 1972). During the last decades several new localities have been discovered, and there are at present 13 known (groups of) occurrences in Svalbard, in the districts Dickson Land, Haakon VII Land, James I Land, and Ny-Fries Land (Solstad et al. 2010) (Figure 7,

Table A1). *Tofieldia pusilla* was listed as near threatened on the 2006 Norwegian Red List (Elven et al. 2006).

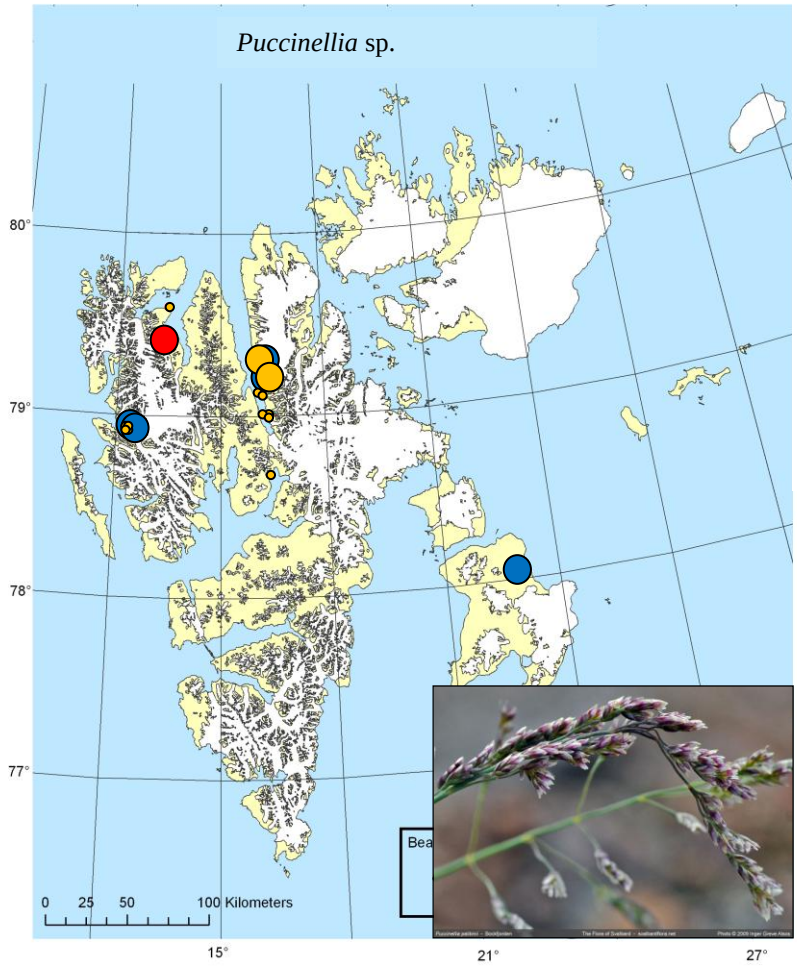

Figure 5 Location of the *Puccinellia* sp. Bockfjorden population (red); sampled (large circles) and unsampled known (small circles) populations of *Puccinellia svalbardensis* (yellow); and sampled populations of *Puccinellia angustata* ssp. *angustata* (blue) in Svalbard, modified after Alsos et al. (2012a). Photo of *Puccinellia* sp.: Inger Greve Alsos (Alsos et al. 2012a).

Study area

Spitsbergen is the largest island of the Svalbard archipelago, situated in the High Arctic at 74-81°N and 10-30°E. As part of this study, eight localities (excluding *P. svalbardenis* and *P. angustata*) were visited around Isfjorden (Dickson Land) and Kongsfjorden (Haakon VII Land) on the west coast of Spitsbergen, and in Bockfjorden (Haakon VII Land) and Wijdefjorden (Ny-Fries Land) on the northern coast of Spitsbergen. All localities are located within bioclimatic subzone C, the middle arctic tundra zone, which is the warmest bioclimatic subzone found in Svalbard, and corresponds to a mean July temperature of 4-6 °C and a growth season length of 2.5-3 months (Elvebakk 1999, 2005b, Jónsdóttir 2005).

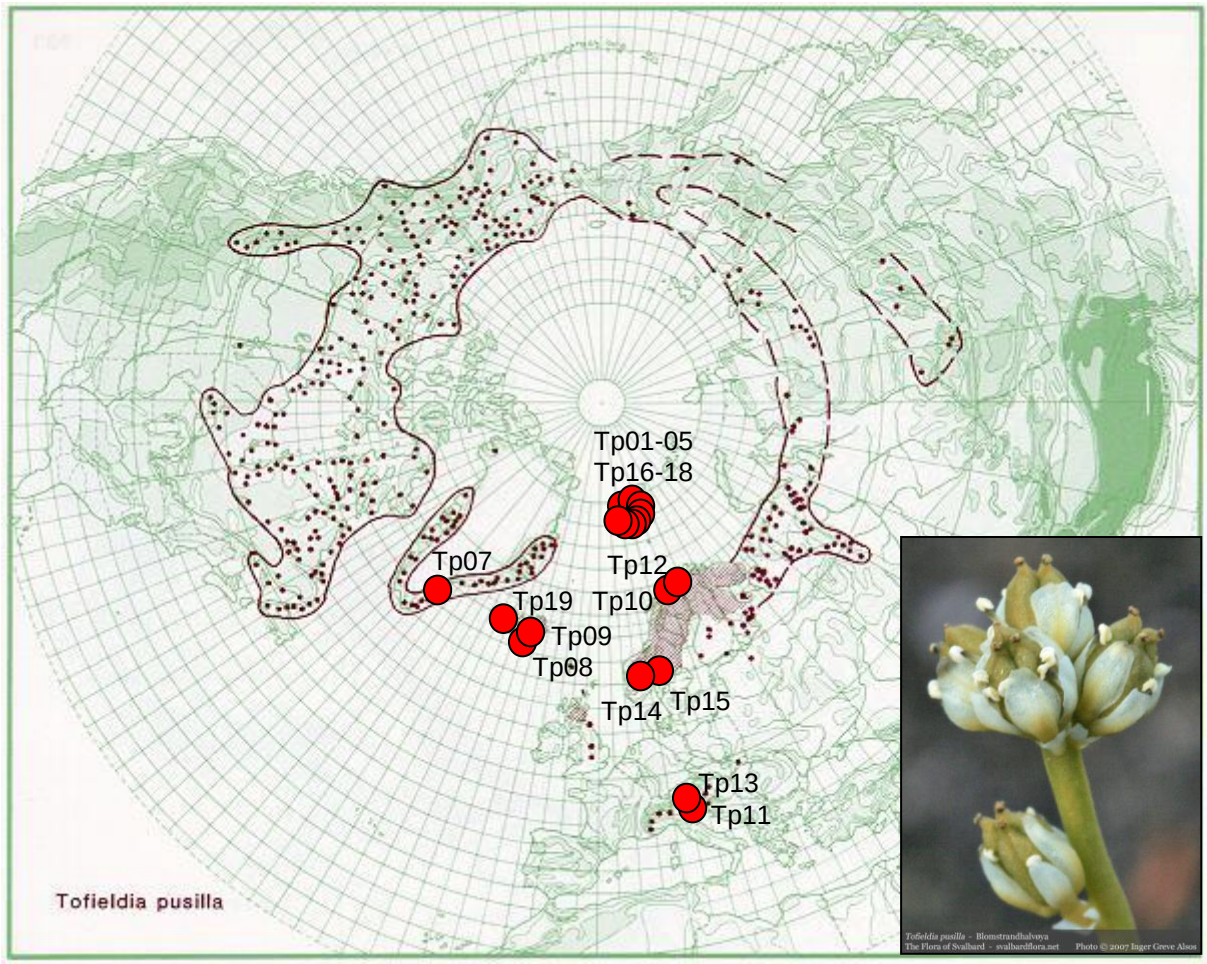

Figure 6 Geographical distribution (Hultén and Fries 1986) and sampled populations of *Tofieldia pusilla*. Population ID follows Table 1. Photo of *T. pusilla*: Inger Greve Alsos (Alsos et al. 2012a).

Mapping of distribution area and population size estimation

For each of the four focus species, distribution area (m^2) within the eight visited Svalbard localities was estimated, and GPS coordinates were taken (Table A1). Population size was estimated by counting individuals, or assessed subjectively if population size exceeded ~200 individuals. For the caespitose species (i.e. *C. capillaris*, *Puccinellia* sp., and *T. pusilla*) each tussock/cushion was counted as an individual if the distance to the nearest tussock/cushion was >5 cm.

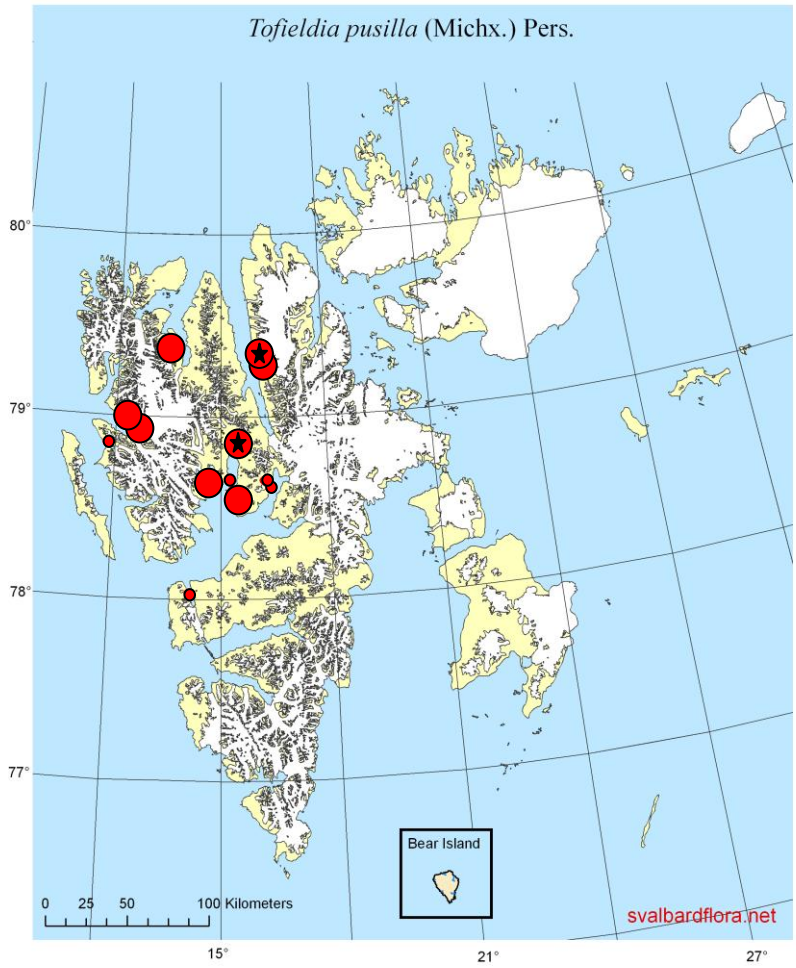

Figure 7 Sampled (large circles) and unsampled known (small circles) populations of *Tofieldia pusilla* in Svalbard, modified after Alsos et al. (2012a). The populations discovered for the first time by this study (Kapp Nathorst and Ringhorndalen) are indicated with a star.

Vegetation analysis and environmental variables

Vegetation analyses were carried out in totally 110 plots at six Svalbard localities, and eight sites (site here defined as the location of a focus species at a locality) (Table 1). At each site 50 x 50 cm plots were placed in the habitat in such a way that the focus species was present in the plot (hereafter referred to as red list plots). To examine if the species had potential for expanding within the site, plots not including the focus species (hereafter referred to as expanding plots) were placed 50 cm north, east, south or west of the red list plot. At the *C. capillaris* site, plots were included from two subsites, corresponding to two areas with a continuous distribution of the species in between. No expanding plots were included from subsite B, as *C. capillaris* was literally growing everywhere there. To examine if *T. pusilla* had potential to disperse outside its site, a similar habitat found at least 50 m away (i.e. without the species) was chosen, wherein randomly placed plots were analysed (hereafter referred to as reference plots).

The vegetation analysis included recording of vascular plant species according to the point intercept method (Bråthen and Hagberg 2004). Nomenclature follows Elven et al. (2011). All vascular plant species hit by a needle at 25 evenly distributed points across each plot were recorded. Based on the number of hits, a frequency value was assigned to each taxon (i.e. ranging from one to 25). Vascular plant species present in the plot but without hits were given a frequency value of 0.5 if present once in the plot or 0.75 if present twice or more. Percentage cover of vascular plants, bryophytes, cryptogamic crust, lichens, stones, and bare ground was estimated.

A set of abiotic factors was assessed in each plot. Temperature in plots was measured at 3 cm soil depth (three replicates per plot) and at 10 cm soil depth (four replicates per plot), using a digital thermometer (TFX410, Ebro®, Ingolstadt, Germany). Since soil temperature is highly influenced by local weather conditions, it was left out of all analysis which extended over more than one site or sampling day. Degree of slope and aspect of the plots were measured. Soil moisture was estimated in field as (1) dry, (2) moist, (3) wet, or (4) very wet by using "the finger method" as described by Raup (1969). Soil samples were collected (down to ca. 5 cm depth) from each plot. pH was measured in the laboratory using an electronic pH-meter (MX300® X-mate pro, Mettler Toledo, Greifensee, Switzerland), with an accuracy of ±0.1, in a mix of 4 g soil sample and 10 ml deionized water. Before measuring, the soil-water mix was shaken for one hour at180 strokes per minute in a reciprocating shaker (SSL2, Stuart®, Stone, UK), and left over night to settle.

Indications of disturbance due to trampling, grazing, frost, and human traffic was assessed at each site as one of four levels: no impact, low impact, moderate impact or high impact, while disturbance from wind was assessed as one of two levels: no impact or high impact.

Plant material

Plant material for AFLP fingerprinting was collected from all visited Svalbard localities (Table 1). In addition, reference material was sampled from other arctic-alpine populations within the species' geographical distribution ranges (Table 1). From each population, fresh and healthy leaves from (if possible) ten plants were collected with a distance of 2 m, and immediately stored in silica gel. *Carex capillaris* was sampled from one Svalbard and nine

Table 1 Population information, sampling information and AFLP diversity estimates. Focus species and outgroup species, including morphological determination of *Carex capillaris* into ssp. *fuscidula* (*fus*) and ssp. *capillaris* (*cap*); country*; population ID (pop. ID); UTM zone and coordinates; collectors**; number of individuals per population included in the AFLP analysis (no. AFLP); minimum to maximum number of AFLP multilocus phenotypes (min-max no. AFLP pheno.) and number of private AFLP markers (no. private markers); proportion of polymorphic markers (Poly. [%]); average genetic diversity (D); frequency down weighed marker values (DW); and number of plots (no. of plots) and plot types*** included in the vegetation/ecological analysis. For *C. capillaris*, letter A and B indicate subsites.

Species	Country*	Locality	Pop. ID	UTM zone	UTM N	UTM E	Collectors**	No. AFLP	Min-max no. AFLP pheno. (no. private markers)	Poly. [%]	D	DW	No. of plots (plot type***)
Carex capillaris L.													
fus	S (NO)	Haakon VII Land, Bockfjorden	Cc01	33X	8813474	467946	IGA, IS, RE, SB	10	8-10 (1)	13.3	0.044	1.022	20 (red A=7, B=8; exp A=5)
?	NO	Hedmark, Folldal	Cc09	32V	6912579	562546	IS, RE, SB	9	9 (3)	24.1	0.104	1.333	
fus	NO	Troms, Tromsø	Cc06	34W	7714000	428500	RE	3	3 (0)	18.1	0.120	1.015	
fus	NO	Troms, Nordreisa I	Cc07	34W	7722399	544900	RE	4	4 (0)	27.7	0.157	1.012	
fus	NO	Troms, Nordreisa II	Cc08	34W	7711000	512000	RE	4	4 (0)	36.1	0.199	1.308	
fus	GL (DK)	A. P. Olsen Land, Zackenberg	Cc11	34W	8212296	469234	OG	6	6 (6)	33.7	0.142	2.499	
fus	IS	Suðurnes, Grindavik	Cc05	27W	7079050	428300	RE	7	7 (0)	26.5	0.119	0.978	
fus	IS	Suðurland, Laugarvatn	Cc02	27W	7120614	510936	IS, SB	10	6-8 (1)	16.9	0.049	0.924	
cap	CH	Valais, Zermatt	Cc10	32T	5092967	406452	PK	7	7 (1)	28.9	0.109	1.082	
cap	IT	Valle d'Aosta, Walliser Alpen	Cc03	32T	5088415	395744	AT	8	7 (1)	34.9	0.139	0.978	
Carex krausei Boeck.													
	S (NO)	James I Land, Kapp Smith	Ck01	33X	8732500	502500	IGA	8					
Comastoma tenellum (Rottb.) Toyok**.**													
	S (NO)	Haakon VII Land, Ossian Sarsfjellet	Ct01	33X	8763178	445308	IGA, IS, RE, SB	7	2-3 (0)	7.1	0.024	1.036	3 (red=3)
	S (NO)	Ny-Fries Land, Flatøyrdalen	Ct03	33X	8802463	521882	AB, IGA, PBE, RE	8	1-4 (0)	2.4	0.011	1.032	
	S (NO)	Ny-Fries Land, Ringhorndalen	Ct04	33X	8807676	523307	AB, IGA	10	5-7 (0)	8.3	0.028	1.036	
	NO	Hedmark, Folldal	Ct05	32V	6895876	540492	AB, IS, RE, SB	10	2-4 (0)	6.0	0.018	1.036	
	NO	Troms, Tromsø	Ct02	34W	7742537	439667	TA	9	5-7 (0)	15.5	0.036	1.040	
	AT	Styria, Sölkpass	Ct09	33T	5235579	430410	Schönswetter et al. (2004)	5	5 (1)	16.7	0.088	1.038	
	CH	Valais, Zermatt	Ct06	32T	5092915	405763	PK	10	9 (3)	27.4	0.103	1.042	
	CH/IT	Splügenpass	Ct07	32T	5149656	525322	Schönswetter et al. (2004)	5	4-5 (3)	7.1	0.038	1.035	
	FR/IT	Col du Petit St. Bernard	Ct08	32T	5059590	334092	Schönswetter et al. (2004)	2	1-2(1)	-	-	-	
	RU	Polar Ural, Slantzevaga	Ct10	41W	7423499	619415	AT, IGA	10	4-9 (2)	10.7	0.042	1.035	
	US	Alaska, Seward Peninsula	Ct11	3W	7238106	436962	Schönswetter et al. (2004)	5	2-4 (5)	4.8	0.019	1.038	
Gentianella campestris L.													

	NO	Troms, Tromsø	Gc01	34W	7735700	426600	TA	5					
Puccinellia angustata (R. Br.) Rand & Redf													
	S (NO)	Edgeøya, Blåbukta	Pa10	35X	8668140	404937	PBE	7	1-7 (1)	10.6	0.043	-	
	S (NO)	Ny-Fries Land, Flatøyrdalen	Pa03	33X	8802033	520522	AKB,PBE	6	2-6 (0)	26.6	0.113	-	
	S (NO)	Ny-Fries Land, Flatøyrdalen	Pa07	33X	8802115	520853	AKB, IGA, PBE, RE	1	1 (0)	-	-	-	
	S (NO)	Ny-Fries Land, Ringhorndalen	Pa02	33X	8804020	519504	AKB, IGA, PBE, RE	5	1-5 (0)	13.8	0.068	-	
	S (NO)	Ny-Fries Land, Ringhorndalen	Pa05	33X	8803980	519613	AKB, IGA, PBE, RE	10	1-10 (0)	16.0	0.070	-	
	S (NO)	Ny-Fries Land, Ringhorndalen	Pa06	33X	8804483	520598	PBE, RE	9	2-9 (0)	20.2	0.087	-	
	S (NO)	Ny-Fries Land, Ringhorndalen	Pa08	33X	8806164	521394	AKB, IGA	2	2 (0)	-	-	-	
	S (NO)	Ny-Fries Land, Ringhorndalen	Pa09	33X	8805874	520770	AKB, IGA	7	2-7 (0)	25.5	0.084	-	
	S (NO)	Haakon VII Land, Bockfjorden	Pa11	33X	8813508	467981	AKB, RE	5	1-5 (1)	13.8	0.060	-	
	S (NO)	Haakon VII Land, Leirholmen	Pa15	33X	8762616	442727	IGA, LA, ML, UL	1	1 (0)	-	-	-	
	S (NO)	Haakon VII Land, Sigridholmen	Pa14	33X	8764010	442646	IGA, LA, ML, UL	7	1-7 (0)	21.3	0.091	-	
Puccinellia svalbardensis Rønning													
	S (NO)	Ny-Fries Land, Flatøyrdalen	Ps07	33X	8802115	520853	AKB, IGA, PBE, RE	2	2 (0)	-	-	-	
	S (NO)	Ny-Fries Land, Ringhorndalen	Ps08	33X	8806164	521394	AKB, IGA	5	5 (0)	55.0	0.278	-	
Puccinellia sp.													
	S (NO)	Haakon VII Land, Bockfjorden	Psp01	33X	8813508	467981	IGA, IS, RE, SB	10	7 (0)	58.5	0.219	-	20 (red=10; exp=10)
Puccinellia vahliana (Liebm.) Scribn. & Merr.													
	S (NO)	Ny-Fries Land, Ringhorndalen	Pv01	33X	8803980	519613	AKB, IGA, PBE, RE	9					
*Tofieldia pusilla (*Michx.) Pers.													
	S (NO)	Dickson Land, Blomesletta	Tp01	33X	8727478	496510	IGA, IS, SB	9	7-9 (0)	37.5	0.139	0.191	12 (red=7; exp=5)
	S (NO)	Dickson Land, Kapp Nathorst	Tp04	33X	8744574	509881	EM, IS, OM, SB	10	10 (0)	40.6	0.156	0.196	8 (red=4; ref=4)
	S (NO)	Dickson Land, Kapp Wijk	Tp03	33X	8725140	507303	IGA, KBW	10	6-9 (0)	34.4	0.133	0.203	24 (red=6; exp=6; ref=12)
	S (NO)	Haakon VII Land, Blomstrand	Tp02	33X	8768534	439822	IGA, IS, SB	15	5-8 (0)	25.0	0.079	0.220	17 (red=5; exp=7; ref=5)
	S (NO)	Haakon VII Land, Bockfjorden	Tp05	33X	8813884	467918	IGA, IS, RE, SB	6	6 (0)	40.6	0.173	0.196	6 (red=6)
	S (NO)	Haakon VII Land, Ossian Sarsfjellet	Tp18	33X	8764224	445153	IGA	5	5 (0)	21.9	0.094	0.214	
	S (NO)	Ny-Fries Land, Flatøyrdalen	Tp16	33X	8802208	521726	AB, IGA	8	6-8 (0)	37.5	0.144	0.188	
	S (NO)	Ny-Fries Land, Ringhorndalen	Tp17	33X	8807442	523294	AB, IGA	9	3-6 (0)	21.9	0.069	0.207	
	NO	Hedmark, Folldal	Tp15	32V	6890256	551591	IS	9	7-8 (0)	31.3	0.151	0.184	
	NO	Hordaland, Finse	Tp14	32V	6719832	420554	IS	9	4-6 (0)	21.9	0.078	0.229	
	NO	Troms, Nordreisa	Tp12	34W	7733191	508128	RE	5	3-5 (0)	28.1	0.119	0.220	
	NO	Troms, Tromsø	Tp10	34W	7742793	440180	TA	9	9 (0)	53.1	0.207	0.183	
	GL (DK)	Angmagssalik, Tasiilaq	Tp07	24W	7277122	563599	IS, SB	10	9-10 (1)	53.1	0.214	0.290	

IS	Suðurland, Geysir	Tp09	27W	7132216	533545	IS, SB	10	8-9 (0)	34.4	0.139	0.231
IS	Suðurland, Laugarvatn	Tp08	27W	7120567	510962	IS, SB	9	2-6 (0)	12.5	0.052	0.259
IS	Vestfirðir, Önundarfjördur	Tp19	27W	7320000	391900	RE	5	4-5 (0)	21.9	0.106	0.184
AT	Salzburg, Weisseck	Tp11	33T	5224320	377016	AT	2	1-2 (0)	-	-	-
DE	Berchtesgadener, Watzmann	Tp13	33T	5270397	344432	AT	5	5 (0)	40.6	0.213	0.197
Tofieldia calyculata (L.) Wahlenb											
AT	Salzburg, Lungau	Tca01	33T	5225822	376843	AT, IGA	4				
Tofieldia coccinea Richardson											
CA	Yukon, Yukon/Northwest Territories	Tco01	8W	7436258	447087	LG	8				

* Country: AT, Austria; CA, Canada; CH, Switzerland; DE, Germany; DK, Denmark; FR, France; GL, Greenland; IS, Iceland; IT, Italy; NO, Norway; RU, Russia; S, Svalbard; US, United States of America.

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***Plot type: red, red list plot (i.e. containing focus species); exp, expanding plot (i.e. not containing focus species and placed 50 cm away from a red list plot); ref, reference plot (i.e. not containing focus species and placed in a similar habitat at least 50 m away from the red list/expanding plots).

other populations; *C. tenellum* from three Svalbard and eight other populations; *Puccinellia* sp. from one, *P. svalbardensis* from two, and *P. angustata* from eleven Svalbard populations, respectively; and *T. pusilla* from eight Svalbard and ten other populations. In addition, for *C. capillaris*, *C. tenellum*, and *Puccinellia* sp. one population of a closely related species was sampled and used as outgroup in the neighbor-joining analysis (described later), while two outgroup taxa were include for *T. pusilla* (Table 1). Herbarium vouchers from most populations are deposited at the University of Oslo and the University of Tromsø.

DNA isolation

The silica dried leaves were powdered on a mixer mill (MM301, Retsch GmbH & Co., Haan, Germany). *Carex capillaris* individuals were ground for 5-8 minutes, *C. tenellum* and *Puccinellia* sp. for ca. 4 minutes, and *T. pusilla* for ca. 5 minutes, all at 20 Hz.

To obtain optimal purity and concentration of DNA, two to three different protocols were tested on two to three individuals of each species, and the best protocol was used further. DNA from individuals of *C. capillaris* was isolated from 10-20 mg dried leaves using the acidic DNA isolation protocol by Ziegenhagen et al. (1993). The following minor modifications were done: a washing step of the DNA pellet in 1 ml 70 % ethanol was added, and centrifugation periods were increased by 5 minutes and done at 13,500 rmp.

DNA from individuals of *C. tenellum* was isolated from 1-15 mg dried leaves, using the Qiagen DNeasy™ Kit, following the DNeasy Plant Mini Handbook (Qiagen, Hilden, Germany). To increase the final DNA concentration, the amount of AE buffer was reduced to 30-50 μl, the first eluate (i.e. DNA dissolved in AE buffer) was re-eluted in a second elution step, and incubation was done at 65°C.

DNA from *Puccinellia* sp. individuals from the Bockfjorden population and all *T. pusilla* individuals was isolated using the E.Z.N.A.™ SP Plant DNA Mini Kit, following the protocol for dry specimens (Omega Bio-Tek, Norcross, USA). 10 mg and 5-10 mg dried leaves were used from each *Puccinellia* sp. and *T. pusilla* individual, respectively. The protocol was modified by adding a freezing step (at -80°C for 10 minutes) prior to cell lysis. In addition, the first eluate was used in a second elution step and incubation was done at 65°C to increase DNA yield. For *T. pusilla* samples, the amount of Elution buffer was reduced to 30 μl to increase the final DNA concentration.

DNA isolation of *P. angustata*, *P. svalbardensis*, and the outgroup *Puccinellia vahliana* (Liebm.) Scribn. & Merr. was performed by Associate Professor P. Bronken Eidesen and coworkers at the University Centre in Svalbard, as part of a project on the genetics of *Puccinellia* species in Svalbard. A master project (A. Launis in prep.) will specifically look into the origin, infrageneric relations, and species delimitation of *P. svalbardensis*. DNA was isolated using a CTAB procedure, according to Schönswetter et al. (2002).

DNA concentration of the samples was measured using a spectrophotometer (NanoDrop™ 1000, Thermo Fisher Scientific, Wilmington, USA). Samples were, if DNA concentrations exceeded 100 ng/µl, diluted to a final concentration of ca. 50 ng/µl. Isolated DNA was stored at -20°C.

AFLP analysis

Amplified Fragment Length Polymorphism (AFLP) was used to generate dominant molecular markers from the sampled individuals (Vos et al. 1995). The AFLP procedure was modified slightly from Jørgensen et al. (2006): 2 µl DNA isolate was used in the restriction-ligation step, and the amount of AmpliTaq polymerase (Applied Biosystems, Foster City, USA) used in the preselective amplification of fragments was increased to 0.075 µl. PCR conditions during the elongation step were modified to 2 minutes and 1 minute at 72 °C for the preselective and selective amplification of fragments, respectively. All reactions were carried out on an Eppendorf Thermal Cycler (Mastercycler® ep gradient S, Hamburg, Germany).

To check for contamination, negative controls were included in all steps of the genotyping process. To check the reproducibility of fragments, a random selection of samples was duplicated/replicated for all species (ca. 10% of the total number of samples), as recommended by Bonin et al. (2004). In addition, samples with low quantity or quality of DNA (i.e. possibly resulting in markers with low reproducibility) were replicated. In total 24 %, 26 %, and 8 % of the individuals were duplicated/replicated for *C. capillaris*, *C. tenellum* and *T. pusilla*, respectively.

For *C. capillaris*, eight pairs of selective primers were tested on a subsample of seven individuals and the following four primer combinations were chosen based on quality of the profiles, number of markers, and levels of polymorphism: *Eco*RI ACT (6-FAM)-*Mse*I CTT, *Eco*RI ACC (6-FAM)-*Mse*I CTA, *Eco*RI AGG (VIC)-*Mse*I CA, and *Eco*RI AGA (PET)-*Mse*I

CAT. For *C. tenellum*, the same three primer pairs as used by Schönswetter et al. (2004) were chosen after tested on a subsample of eleven individuals: *Eco*RI ACC (6-FAM)-*Mse*I CAT, *Eco*RI AGG (NED)-*Mse*I CAC, and *Eco*RI ACA (VIC)-*Mse*I CAC. For *T. pusilla*, eighteen primer pairs were tested on a subsample of six individuals and the following four were chosen: *Eco*RI ACC (6-FAM)-*Mse*I CAG, *Eco*RI ACA (NED)-*Mse*I CAT, *Eco*RI AAG (VIC)-*Mse*I CTT, and *Eco*RI AGA (PET)-*Mse*I CT. The 6-FAM primer and all non-labelled primers and adaptors were ordered from MWG (Ebersberg, Germany) or IDT (Leuven, Belgium), the other labelled primers (NED, PET, VIC) from Applied Biosystems.

The fluorescently labeled AFLP fragments were detected on an ABI3730 DNA Analyser (Applied Biosystems). To ensure optimal fluorescence intensity, 3 µl (6-FAM, NED and PET) and 2 µl (VIC) labeled selective PCR products were mixed. Two µl of this mix was added in 11.7 µl Hi-Di formamide and 0.3 µl GeneScan 500 LIZ Size Standard (both Applied Biosystems).

AFLP profiles were visualised using GeneMapper ver. 4.0 (Applied Biosystems). Unambiguously scorable fragments in the size range of 50-500 bp were scored as absence/presence of peaks, following the method of Whitlock et al. (2008), and their R-based interactive scripting program AFLPscore ver. 1.4., using the filtering option for locus selection and relative threshold for phenotype calling. Error rate estimation (i.e. estimation of marker reproducibility) is a crucial step in this scoring method, and was calculated as the average percentage of differences between replicate pairs (i.e. mismatch error rate) (Bonin et al. 2004). For each primer combination, the thresholds for locus selection and phenotype calling that resulted in the highest number of highly reproducible markers were chosen. Fragments with a frequency lower than the error rate were re-checked, and removed if no clear peak was present. Fragments missing in only a few individuals were also re-checked, and corrected if miss-scored.

The AFLP analysis of all *Puccinellia* material was preformed by Associate Professor P. Bronken Eidesen and coworkers at the University Centre in Svalbard according to Gaudeul et al. (2000), using the following primer pairs: *Eco*RI ACC (FAM)-*Mse*I CTT, *Eco*RI AGT (VIC)-*Mse*I CAA, and *Eco*RI AGG (NED)-*Mse*I CTC.

Inspection of *Puccinellia* herbarium vouchers

Because *P. angustata*, *Puccinellia* sp., and *P. svalbardensis*, and to some extent *P. vahliana*, are morphologically very similar (i.e. may easily be confused in field), herbarium vouchers from all populations and of most individuals included in the analyses were carefully inspected by Professor R. Elven at the University of Oslo and the author prior to the AFLP data analyses (Table A2). Since a detailed identification key has not yet been made (but see Rønning 1961b, Elven 2005, Elvebakk and Nilsen 2011), identification was based on R. Elven's personal experience with identification of these species both in field and on basis of herbarium specimens. Characters useful to distinguish them include size of spikelets, numbers of flowers in the spikelets, size and shape of glumes, and shape of lemmas and paleas. To make an identification key was, however, beyond the scope of this study. For some of the individuals, the field determination differed from the identification based on inspection of vouchers. Prior to the AFLP data analyses, these individuals were renamed and organized into populations according to the inspection of vouchers, as listed in Table 1.

Vegetation and environmental data analyses

To summarize the main patterns of the species composition in the plots and their relation to the environmental variables, ordination of species data and environmental variables was carried out in R ver. 2.12.1 (R Development Core Team 2011). To make sure that the main gradient structure in the species data was found, two complementary ordination methods were used in parallel (Økland 1996): DCA (detrended correspondence analysis) (Hill and Gauch 1980) and GNMDS (global non-metric multi-dimensional scaling) (Minchin 1987). DCA is based on CA (correspondence analysis) (Hill 1974), which is a statistical ordination technique, whereas GNMS is a purely geometrical method. Prior to the analyses, the environmental variables were standardized by zero-skewness transformation (Økland et al. 2001) to improve homoscedasticity (i.e. homogeneity of the variance). Aspect was recalculated according to Økland (1990) to represent aspect favorability, in which southwest (202.5°) was considered the most favorable aspect. Species abundance data was weighted to increase the influence of rare species in the plots, so that weighted species frequency values ranged from one (species present in the plot but without hits) to five (species with 25 hits), using the following power function modified from Eilertsen et al. (1990):

$$y_{ij} = 1.33 * x_{ij}^{0.41}$$

where x is the original value of species i in plot j, while y is the weighted value. DCA was run with the command *decorona* in the package vegan ver. 1.17, using default settings (Oksanen et al. 2011). Kendall's non-parametric correlation coefficient τ (Kendall 1938) was used to test for correlation between the environmental variables and the ordination axes, as well as among the environmental variables. For the GNMDS ordination, the packages vegan (Oksanen et al. 2011), MASS (Venables and Ripley 2002), and stats (R Development Core Team 2010) were used. GNMDS was run with the commands *vegdist, initMDS, iso-MDS* and *postMDS*, using Bray-Curtis dissimilarity index for abundance data (Bray and Curtis 1957) and two dimensions (i.e. resulting in a diagram with two ordination axes). The best solution (i.e. the one with the lowest stress value) from 100 different starting points was chosen and used to make an ordination diagram. Corresponding DCA and GNMDS ordination axes were tested for correlation using Kendall's correlation coefficient τ. The ordination axes were trusted only if recognized by both methods, i.e. the corresponding DCA and GNMDS axes were strongly correlated (here $\tau > 0.4$). When ordination axes were strongly correlated and the two methods gave conforming results, only results from the DCA ordinations were are presented. To investigate (1) the ecology of the species and (2) their local expansion potential, the two ordination methods were run on each datasets twice: (1) allowing and (2) not allowing the focus species to have influence on the ordination pattern. To investigate the ecology and local expansion potential of *C. capillaris* and *Puccinellia* sp. in Bockfjorden, a data set (hereafter referred to as the Bockfjorden data set) including Bockfjorden plots of *C. capillaris*, *Puccinellia* sp., and *T. pusilla* (n=46, Table 1), as well as plots of another red listed vascular plant (*Sibbaldia procumbens* L.) (n=13), was used. The ecological requirements and local expansion potential of *S. procumbens* were addressed in a parallel master project by Birkeland (2012). However, when using the Bockfjorden data set to evaluate the local expansion potential of *C. capillaris* and *Puccinellia* sp. (i.e. excluding the focus species from the analysis), the corresponding DCA and GNMDS axes were not strongly correlated ($\tau < 0.4$). Therefore, instead of the Bockfjorden data set, a data set including 20 *C. capillaris* plots (Table 1) was used to evaluate the local expansion potential of *C. capillaris*, while a data set (hereafter referred to as the *Puccinellia* sp. data set) including 20 *Puccinellia* sp. plots (Table 1) was used to evaluate the local expansion potential of *Puccinellia* sp.. As the DCA and GNMDS analyses of the *Puccinellia* sp. data set failed to give conforming results regarding its local expansion potential, a PCA analysis was additionally carried out in Past ver. 2.12

(Hammer et al. 2001), using default settings, to indicate whether there were differences in the environmental variables between the red list and expanding plots (i.e. using the data set of the environmental variables instead of the species data). To investigate the ecology and local expansion potential of *T. pusilla*, a data set (hereafter referred to as the *Tofieldia pusilla* data set) of 67 plots from five localities was used (Table 1). To further investigate the species local expansion potential, the non-parametric Wilcoxon signed rank test for paired samples (Wilcoxon 1945) was used to test for differences in the environmental variables between the paired red list and expanding plots. The Wilcoxon rank sum test for unpaired samples (Wilcoxon 1945) was to test for differences between the *T. pusilla* red list and reference plots. Both tests were carried out in R ver. 2.12.1 (R Development Core Team 2011). Since only three red list plots of *C. tenellum* were analysed (Table 1), the results from the ordination analyses are not presented.

AFLP data analyses

The percentage of polymorphic AFLP markers was calculated both at species level and population level. Monomorphic markers at species level were excluded from further analyses. Within-population genetic diversity was estimated as the average proportion of pairwise differences between individuals (i.e. Nei's (1987) gene diversity (D); Kosman (2003)) for all populations with more than two sampled individuals. To enable comparisons with another study of *T. pusilla* (Line 2006), the overall population average of percentage of polymorphic markers and genetic diversity were additionally calculated including monomorphic markers. The minimum and maximum number of AFLP multilocus phenotypes was calculated for each population. When calculating the minimum number of AFLP multilocus phenotypes, only AFLP multilocus phenotypes which did not differ by any markers were considered identical, while the maximum number allowed for a certain number of pairwise differences, determined by the error rate and the total number of markers. To address distinctiveness of the populations, a rarity index, the frequency down weighed marker value (DW) by Schönswetter and Tribsch (2005), was calculated for each population (except those with less than three sampled individuals), based on the number of occurrences of each marker in the population, relative to the number of occurrences in the total data set. Private multi-locus AFLP markers, unique to a single population or group (geographic or revealed by ordination and clustering methods, see below), were also recorded. The R-script AFLPdat ver. 2010 (Ehrich 2006) was

used for calculations of genetic diversity, proportion of polymorphic markers, number of AFLP multilocus phenotypes, rarity index, private multi-locus AFLP markers, and for most data format conversions.

To investigate the genetic structure in the data, principal coordinates analysis (PCO) (Davis 1986) and neighbor-joining analysis (Saitou and Nei 1987) were performed with the complementary Dice similarity (Dice 1945) and Hamming distance (Hamming 1950) for binary data, using Past ver. 2.12 (Hammer et al. 2001). While the Dice similarity index puts most weight on shared presence of markers, Hamming distance puts equal weight on mismatches and shared presence of markers. As the two similarity/distance measures gave nearly identical results, only the results using Dice similarity are presented. To obtain confidence estimates for groups in the neighbor-joining tree, bootstrap analysis, using 10,000 replicates, was preformed. Due to the low level of differentiation in the *T. pusilla* data set, a neighbor-net (Bryant and Moulton 2004) was constructed instead of a neighbor-joining tree, using Splits Tree ver. 4.12 (Huson and Bryant 2006). Further, two model-based Bayesian clustering methods were performed. The clustering method implemented in Structure ver. 2.3.3 (Pritchard et al. 2000) was run at the University of Oslo Bioportal (www.bioportal.uio.no). Both the admixture (which allows individuals to have mixed ancestry) and the no-admixture model (which always assigns an individual to only one group) were tested, with no prior population information and using the uncorrelated allele frequency model. The data was coded as diploid multi-locus genotypes, using the recessive allele option for dominant markers (Falush et al. 2007). Structure allocates individuals to a fixed (user defined) number of groups (K). The number of groups from 1-18 was tested, with ten independent runs for each K. The run length was set to 10^{-6} iterations, after a burn-in period of 10^{-5} iterations. As structure sequentially derives posterior probability distributions for the independent runs, the results were summarized using the R-script Structure-sum ver. 2011 (Ehrich et al. 2007). The optimal K was chosen according to Evanno et al. (2005) (i.e. as the K with the highest value of delta K), but the posterior probabilities (Pritchard et al. 2000) and the similarity coefficient estimates (Nordborg et al. 2005) were also considered. To reveal hierarchical genetic structure in the data, separate structure analyses were run on the group(s) to which Svalbard individuals were grouped by the first Structure analysis. Finally, the clustering method implemented in Baps (bayesian analysis of population structure) ver. 5.4 (Corander et al. 2003), which in contrast to Structure first finds the optimal number of groups and then allocates individuals to these groups, was performed using the mixture analysis with

no prior population information. The maximum number of groups (K) was set to 18, with five replicate runs.

To determine the level of genetic differentiation among populations and among groups (geographic and genetic groups revealed by ordination and clustering), AMOVAs (analyses of molecular variance) were run in Arlequin ver. 3.5 (Excoffier et al. 2005), and the Φ_{ST} analog for F_{ST} was calculated (Excoffier et al. 1992), based on the number of pairwise differences between individuals.

Svalbard individuals were assigned to their most likely source region(s) by multi-locus assignment tests in AFLPOP ver. 1.1 (Duchesne and Bernatchez 2002). Geographic regions, as well as genetic groups revealed by the ordination and clustering methods were considered as potential source populations. Svalbard individuals were not allowed to be assigned to Svalbard. Markers with zero frequency were replaced by 1/ [sample size + 1]. A minimal log likelihood difference (MLD) of MLD=2 was first tested. If all individuals could not be assigned with MLD=2, MLD=1, and subsequently MLD=0 was used in addition. With MLD=2 and MLD=1, the likelihood for an AFLP phenotype to be found in its most likely source population had to be 10^2 and 10^1 higher, respectively, than for the second most likely source population. With MLD=0, all individuals were 'forced' to assign to the most probable of the potential source populations.

Results

Population size and status

Carex capillaris

At its only known locality in Svalbard, Bockfjorden, *C. capillaris* (Table 2) was found in an area of ca. 100 x 600 m, stretching from north of the thermal springs to the riverbank in south. It was among the most abundant species in the area, and the population was estimated to more than 2000 individuals. The plants seemed highly fertile, and most had flowering/fruiting spikes. However, smaller (probably younger) sterile plants were also observed. The population was moderately affected by grazing (mostly by geese), and on grazed plants, loss of fertile parts was frequent.

Comastoma tenellum

Of the three *C. tenellum* populations investigated in Svalbard (Table 2), a population of more than 50 individuals in Ringhorndalen was discovered for the first time. Together, the three populations numbered between 550 and 650 individuals within a total area of ca. 370 m^2. The site at Ossian Sarsfjellet was highly impacted by grazing (geese and reindeer) and moderately impacted by trampling (reindeer). A large number of withered flowers from the last year was observed in the two populations from Wijdefjorden (Flatøyrdalen and Ringhorndalen), indicating favorable conditions for reproduction.

Puccinellia sp.

Puccinellia sp. was found in Bockfjorden (Table 2) distributed in seven patches ranging from 6 m^2 to 4050 m^2. The size of the population was estimated to ca. 1000 individuals. The population seemed highly fertile, and although there were signs of grazing in the area, no grazed *Puccinellia* sp. plants were observed. However, the substrate of *Puccinellia* sp. was highly frost and wind disturbed.

Tofieldia pusilla

Of the eight *T. pusilla* populations investigated in Svalbard (Table 2), two were discovered for the first time: a population of ca. 1000 individuals in Kapp Nathorst (Dickson Land), and a population of ca. 100 individuals in Ringhorndalen (Ny-Fries Land). Population sizes were

highly variable. In total the populations numbered ca. 1500 individuals within a distribution area of ca. 3000 m^2. The populations seemed stable, and flowering plants were observed in six of them. However, frost boils were frequent at most sites.

Ecological requirements and local expansion potential

Carex capillaris

The DCA plot separated the *C. capillaris* plots from Bockfjorden mainly along the second ordination axis (DCA 2) (Figure 8), which was negatively correlated with temperature (at both 3 cm and 10 cm depth) and moisture, and slightly positively correlated with lichen cover and slope angle (Table A3). Along this gradient, the species had its highest concentration and optimum at the warmest and wettest end, which corresponds to the area around the warmest thermal spring (subsite B) (Figure 8). However, as the DCA plot shows, it was also thriving under more moderate conditions, corresponding to a seepage influenced area downstream of the springs (subsite A) (Figure 8). This corresponded to a moisture range of 2-3 (i.e. moist-wet) and a temperature range of 12.1-16.5 °C (at 10 cm depth; highly depending on daily weather conditions) (Table 3). Because moisture and temperature were inter-correlated (Table A4), it was not possible to disentangle their individual effect on the species composition. In total 39 vascular plant species were recorded from Bockfjorden, of which 22 were found in the 15 red list and 5 expanding plots from the *C. capillaris* site (not shown). *Carex capillaris* and *Festuca rubra* L. ssp. *richardsonii* (Hook.) Hultén were the dominant species in the red list plots, while *Bistorta vivipara* (L.) Delarbre, *Carex maritima* Gunn. coll., and *Salix polaris* Wahlenb. were also frequent. Summary statistics of all the measured environmental variables in the *C. capillaris* red list plots are listed in Table 3.

In the DCA plot, which aimed to indicate the local expansion potential of *C. capillaris* (i.e. excluding the focus species from the analysis), the expanding plots were not separated from the red list plots at subsite A (Figure 9). The species composition of the expanding plots thus indicated that *C. capillaris* has potential for local expansion within subsite A in Bockfjorden, which was supported by the lack of significant differences in the environmental variables between the red list and the expanding plots (Table A5).

Table 2 Information on the populations of the four focus species in Svalbard: distribution area and population size, and the total number of individuals (i.e. sum of all population sizes); presence of flowering individuals; estimates of disturbance from grazing, trampling, frost, human impact, and wind; and comments. If a species is patchily distributed at a locality, distribution area and number of individuals are given for each of the patches. Populations discovered for the first time by this study are marked in bold. N/A= data not available.

Species	Locality	Site/ pop. ID	Date visited	Distribution area (m²) at locality	No. of individuals estimated at locality	Flow-ering	Grazing*	Tramp-ling*	Frost*	Human impact*	Wind**	Comments
Carex capillaris												
	Haakon VII Land, Bockfjorden	Cc01	1/8-2009	60,000	>2000	Yes	2	0	1	0	0	
Comastoma tenellum												
	Haakon VII Land, Ossian Sarsfjellet	Ct01	20/7-2009	51	171	Yes	3	2	0	0	0	
	Ny-Fries Land, Flatøyrdalen	Ct03	24/8-2010	300	300-400	Yes	0	0	0	0	0	Large number of withered flowers from the last year.
	Ny-Fries Land, Ringhorndalen	Ct04	25/8-2010	20	>50	Yes	0	0	0	0	0	Large number of withered flowers from the last year.
				Sum:	ca. 550-650							
Puccinellia sp.												
	Haakon VII Land, Bockfjorden	Pp01	1/8-2009	6	37	Yes	0	0	3	0	1	
		Pp01	1/8-2009	4050	200	Yes	0	0	3	0	1	
		Pp01	1/8-2009	375	100	Yes	0	0	3	0	1	
		Pp01	1/8-2009	26	20	Yes	0	0	1	0	1	
		Pp01	1/8-2009	1000	>200	Yes	1	0	3	0	1	
		Pp01	1/8-2009	3000	>200	Yes	0	0	1	0	0	
		Pp01	1/8-2009	2000	>200	Yes	0	0	3	0	1	
				Sum:	ca. 1000							
Tofieldia pusilla												
	Dickson Land, Blomesletta	Tp01	6/7-2009	600	51	No	0	0	2	0	0	Too early for flowering? Many flowers from the last year.
	Dickson Land, Kapp Nathorst	Tp04	24/7-2009	403	ca. 1000	Yes	0	0	0	0	0	
	Dickson Land, Kapp Wijk	Tp03	24/7-2009	800	>146	Yes	2	0	1	0	0	
	Haakon VII Land, Blomstrand	Tp02	19/7-2009	63	24	Yes	1	0	2	0	0	>48 cushions with flowers were observed 24/7- 2009

	Tp02	19/7-2009	72	33	Yes	1	0	2	0	0
Haakon VII Land, Bockfjorden	Tp05	1/8-2009	6	100	Yes	0	0	1	0	0
	Tp05	2/8-2009	1	6	Yes	0	0	2	0	0
Haakon VII Land, Ossian Sarsfjellet	Tp18	5/8-2010	3	5	Yes	2	1	N/A	N/A	0
Ny-Fries Land, Flatøyrdalen	Tp16	24/8-2010	300	9	Yes	0	0	0	0	0
Ny-Fries Land, Ringhorndalen	Tp17	25/8-2010	1000	100	N/A	0	0	0	0	0
			Sum:	ca. 1500						

*0=no impact; 1=low impact; 2= moderate impact; 3=high impact. **0= no impact; 1= high impact.

Table 3 Summary statistics of the environmental variables in the red list plots (n) of the four focus species. Abbreviations of environmental variables used in the ordination plots are listed (Abbr.).

		Carex capillaris (n=15)		*Comastoma tenellum* (n=3)		*Puccinellia* sp. (n=10)		*Tofieldia pusilla* (n=24)	
Variable	Abbr.	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Temperature 3 cm depth [°C]	temp3	13.9	12.2-15.0	7.3	7.2-7.8	12.2	10.6-14.3	13.8	7.0-21.0
Temperature 10 cm depth	temp10	14.9	12.1-16.5	7.2	7.1-7.3	11.9	9.9-13.7	8.4	3.2-14.2
pH		7.2	6.3-8.1	7.4	7.3-7.5	8.7	6.8-9.3	7.2	6.5-7.6
Moisture*	moist	3	2-3	2	-	2	1-2	2	1-3
Slope angle [°]	slope	5.6	0-16	39	35-42	8.4	1-30	10.0	1-24
Aspect *		E	NE-S	SW	SW-W	E	NE-S	S	S-W
Vascular plants [% cover]	vasccov	50	10-90	68	50-85	10	2-40	48	5-100
Bryophytes [% cover]	brycov	42	0-100	38	4-95	1	0-5	10	0-30
Lichens [% cover]	lichcov	-	-	-	-	-	-	7	0-60
Cryptogamic crust [% cover]	crypcru	27	0-80	1	0-4	5	0 -20	43	0-90
Stones [% cover]		2	0-10	-	-	4	0-10	5	0-15
Bare ground [% cover]	bagrcov	-	-	6	2-10	86	60-95	2	0-20

* Median given instead of mean.

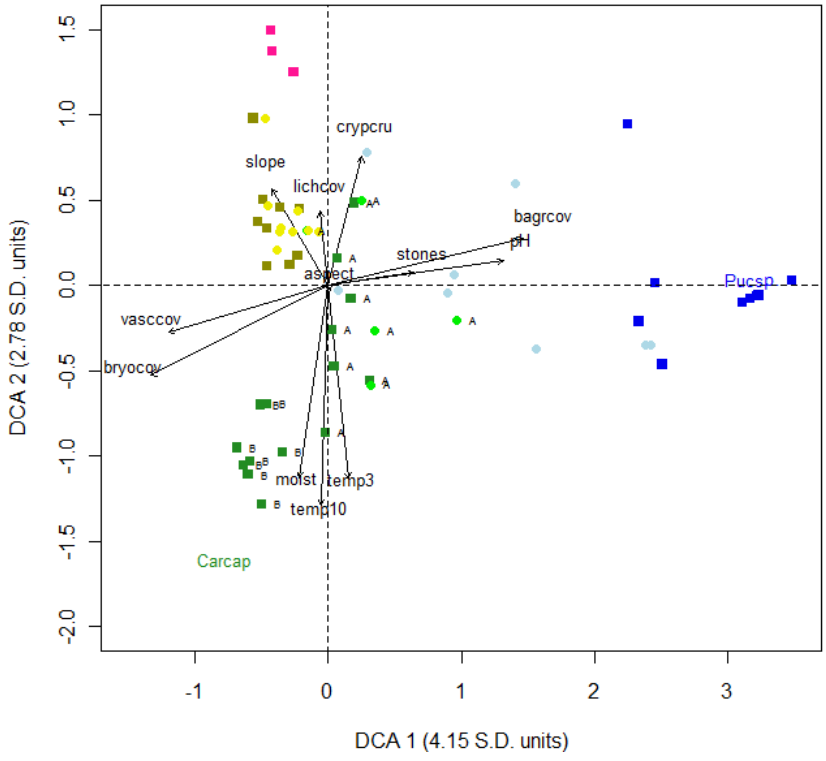

Figure 8 DCA (detrended correspondence analysis) of the species composition in 59 plots from Bockfjorden with overlaid environmental variables to describe the ecology of *Carex capillaris* and *Puccinellia* sp. (i.e. *C. capillaris* and *Puccinellia* sp. had impact on the ordination pattern). Four focus species are indicated by colors: blue, *Puccinellia* sp.; green, *C. capillaris*; pink**,** *Tofieldia pusilla* (see Figure 10); yellow, *Sibbaldia procumbens* (see Birkeland 2012). Symbols represent plot types: circle, expanding plot; square, red list plot. Species optima of *C. capillaris* and *Puccinellia sp*. are indicated on the plot by abbreviated names (Carcap and Pucsp). The two *Carex capillaris* subsites are indicated by the letters A and B. Names of environmental variables are abbreviated according to Table 3.

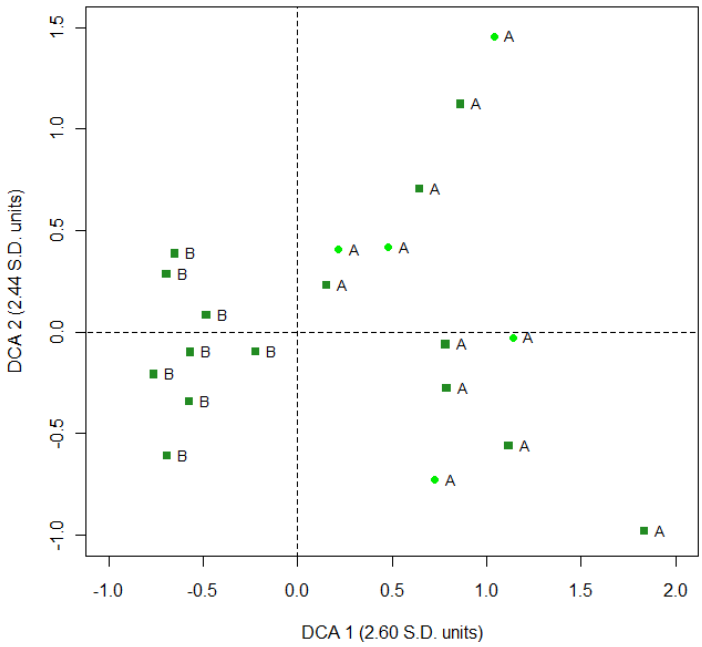

Figure 9 DCA (detrended correspondence analysis) of the species composition in 20 *Carex capillaris* plots from Bockfjorden to evaluate its local expansion potential (i.e. *C. capillaris* had no impact on the ordination pattern). Symbols represent plot types: circle, expanding plot; square, red list plot. The two *Carex capillaris* subsites are indicated by the letters A and B.

Comastoma tenellum

Only the population at Ossian Sarsfjellet was analysed in relation to ecology. There, *C. tenellum* was found in a bird cliff meadow on a very steep (mean slope angle 39°) southwest- to west-facing hillside (Table 3). The substrate was moist and slightly basic (mean pH ~7.4), with relatively high temperature (mean ~7.2 °C at 10 cm depth, but highly depending on daily weather conditions), and medium to highly vegetated (Table 3). Nineteen vascular plant species were recorded in the three red list plots (not shown). The bird cliff vegetation was luxuriant, hosting species like *Poa glauca* Vahl, *Potentilla insularis* Soják, *Ranunculus arcticus* Richardson, and *Taraxacum brachyceras* Dahlst. *Bistorta vivipara* and *Poa* sp. were the most frequent taxa in the red list plots. Also in Flatøyrdalen, *C. tenellum* was found in luxurious vegetation, growing together with *Campanula uniflora* L., *Cystopteris fragilis* (L.) Bernh., *Potentilla* cf. *insularis* Soják., *Ranuculus arcticus* Richardson, *Silene acaulis* (L.) Jacq., and *Trisetum spicatum* (L.) K. Richt.. In Ringhorndalen, *C. tenellum* was found in *Festuca rubra* L. dominated vegetation, on moist substrates. Summary statistics of all the measured environmental variables in the *C. tenellum* red list plots are listed in Table 3.

***Puccinellia* sp.**

The DCA plot separated the *Puccinellia* sp. plots from those of the other focus species in Bockfjorden along the first ordination axis (DCA 1) (Figure 8). The first axis was positively correlated with pH, cover of stones and bare ground, and negatively correlated with cover of vascular plants and bryophytes (Table A3). Along this pH/ground cover gradient, the species had its highest concentration and optimum at the most 'extreme' end, i.e. with the highest pH (mean ~8.7) and cover of stones/bare ground (mean 4 % and 86 %, respectively) (Figure 8, Table 3). However, as these variables were inter-correlated (Table A4), it was not possible to disentangle their individual effect on the species composition. Sixteen vascular plant species were recorded in the 20 plots (of which ten were red list plots). After *Puccinellia* sp., *Potentilla pulchella* R. Br. was the most dominant species in the red list plots. The relatively long gradient length (4.15 S.D. units) of the first axis indicates a high turnover in species composition and abundance between the *Puccinellia* sp. plots and the plots of the other focus species in Bockfjorden. Summary statistics of all the measured environmental variables in the *Puccinellia* sp. red list plots are listed in Table 3.

In the ordination analyses which aimed to evaluate the local expansion potential of *Puccinellia* sp. (i.e. excluding the focus species from the analysis), only the first axes of the DCA and GNMDS ordinations (i.e. DCA 1 and GNMDS 1) were acceptably correlated (τ= 0.4 and p=0.01). In the DCA plot, the red list and expanding plots were not separated (Figure A1), while the GNMDS plot separated the two plot types along the first axis (Figure A2). It was therefore not possible to conclude about the local expansion potential based on the species composition. The PCA of the environmental variables, indicated some level of difference between the red list and the expanding plots, but the separation was not complete (Figure A3). The Wilcoxon signed rank test (Table A5) did, however, detected a significant difference in pH between the red list and the expanding plots ($p<0.01$), indicating that the lower pH in the expanding plots might hinder local expansion.

Tofieldia pusilla

In the DCA plot, *Tofieldia pusilla* had its highest concentration and optimum at high DCA 1 and DCA 2 scores (Figure 10). The first ordination axis (DCA 1) was positively correlated with pH and moisture, and negatively correlated with three ground cover variables (vascular plants, lichen and stones), forming a complex ecological gradient (Table A3). The second ordination axis (DCA 2) was positively correlated with three ground cover variables (lichens,

stones and bare ground) as well as slope angle and aspect, and negatively correlated with pH, moisture and bryophyte cover, i.e. also forming a complex ecological gradient. Thus, no single environmental variable could be pinpointed as the most important for the abundance of *T. pusilla*. The generally high range in environmental variables (Table 3), show that *T. pusilla* was found in different habitats, but all characterized by a favorable aspect. The DCA plot (Figure 10) further indicates that *T. pusilla* may be associated with decreasing cover of vascular plants and increasing cover of cryptogamic crust, although both varied highly among the plots (Table 3). Plots from Blomesletta (site 1) Blomstrand (site 2), and Bockfjorden (site 5) were closest to the *T. pusilla* optimum in the DCA plot, while plots from the largest population, Kapp Nathorst (site 4), were found around origo. However, as the gradient length of the first and second axis was relatively short (2.51 and 2.24 S.D. units, respectively), the species composition was relatively similar among the different plots and sites. In total 28 vascular plant species were recorded from the five *T. pusilla* sites and 46 plots (of which 24 were red list plots). In addition to *T. pusilla*, *B. vivipara*, *Cassiope tetragona* (L.) D. Don., *Dryas octopetala* L., *S. polaris*, and *Saxifraga oppositifolia* L. were the most dominant species in the red list plots. Summary statistics of all the measured environmental variables in the *T. pusilla* red list plots are listed in Table 3.

In the DCA plot, which aimed to indicate the local expansion potential of *T. pusilla* (i.e. excluding the focus species from the analysis) (Figure 11), the red list plots were not separated form the expanding plots, and only separated from a few reference plots (mainly from Kapp Nathorst, site 4). The species composition of the expanding and reference plots thus indicated that *T. pusilla* has potential for local expansion, with the reference site at Kapp Nathorst (site 4) as an exception. The Wilcoxon signed rank test (Table A5) did, however, detect an overall significant difference in temperature (at 3 cm depth) between the red list and the expanding plots ($p<0.05$), indicating that the lower temperatures in the expanding plots might hinder local expansion. Significant differences between the red list and the reference plots (Table A6) were found in Blomstrand (site 2), where temperature (at 3 cm depth) was higher ($p<0.05$) and vascular plant cover lower ($p<0.05$) in the red list plots, and in Kapp Wijk (site 3), where both temperature (at 10 cm depth) ($p<0.01$) and bryophyte cover ($p<0.05$) was lower in the red list plots.

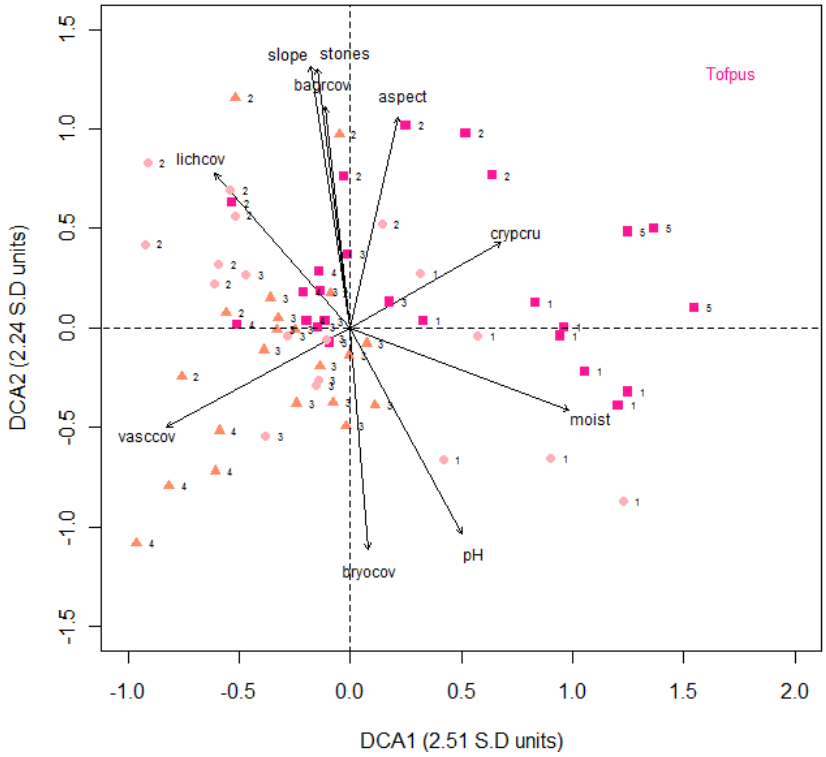

Figure 10 DCA (detrended correspondence analysis) of the species composition in 67 plots from five *Tofieldia pusilla* localities with overlaid environmental variables to describe its ecology (i.e. *T. pusilla* had impact on the ordination pattern). Symbols represent plot types: circle, expanding plot; square, red list plot; triangle, reference plot. Numbers represent sites: 1, Blomesletta; 2, Blomstrand; 3, Kapp Wijk; 4, Kapp Nathorst; 5, Bockfjorden. Species optimum of *T. pusilla* is indicated on the plot by abbreviated name (Tofpus). Names of environmental variables are abbreviated according to Table 3.

AFLP data

Carex capillaris

The AFLP analysis of the 76 individuals generated 151 markers (69.5 % polymorphic). Excluding the outgroup, 137 markers (60.6 % polymorphic) from 68 individuals were obtained. The mismatch error rate for the total data set was 1.9 %. The proportion of polymorphic markers (Table 1) varied among the studied populations, and was lowest in Bockfjorden (Svalbard) (13.3 %) and highest in Nordreisa II (Norway) (36.1 %). The proportion of polymorphic markers in Svalbard (Bockfjorden) was about half of the overall population average (26.0 %). Likewise, the level of genetic diversity measured by D-values (Table 1) varied greatly among populations, ranging from 0.044 to 1.999 in Bockfjorden and Nordreisa II, respectively. The genetic diversity in the Svalbard population was less than half

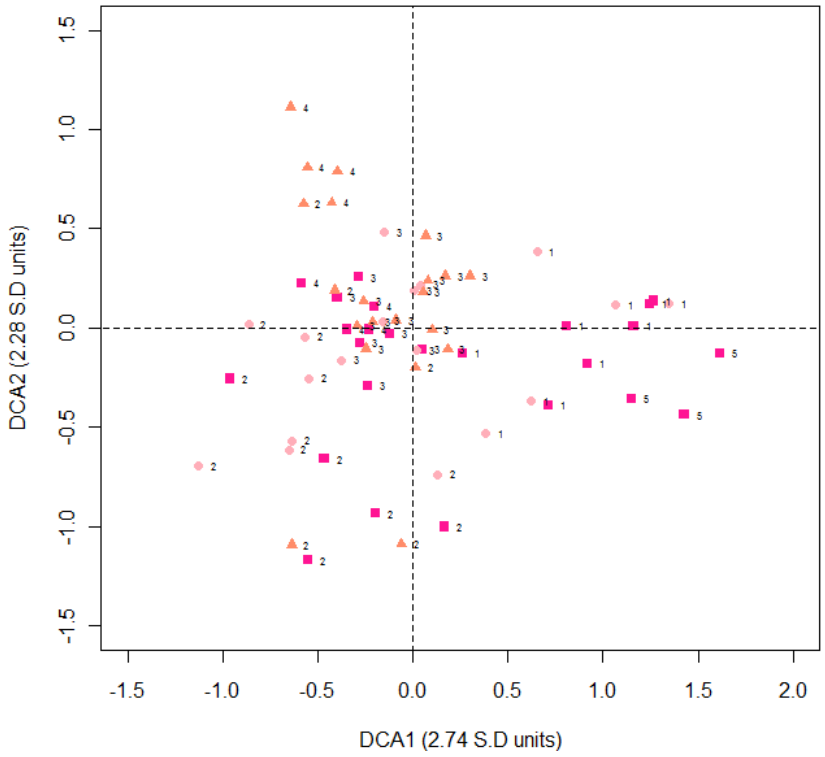

Figure 11 DCA (detrended correspondence analysis) of the species composition in 67 plots from five *Tofieldia pusilla* localities to evaluate its local expansion potential (i.e. *T. pusilla* had no impact on the ordination pattern). Symbols represent plot types: circle, expanding plot; square, red list plot; triangle, reference plot. Numbers represent sites: 1, Blomesletta; 2, Blomstrand; 3, Kapp Wijk; 4, Kapp Nathorst; 5, Bockfjorden.

of the overall population average (D=0.118), but comparable the population from Laugarvatn (Iceland) (D=0.049). In most populations, the minimum number of AFLP multilocus phenotypes (Table 1) was equal or similar to the number of individuals analysed. The rarity index (DW-values) (Table 1) ranged from 0.924 to 2.499 in Laugarvatn (Iceland) and Zackenberg (Greenland), respectively. The mean rarity of the Svalbard population (DW=1.022) was only slightly lower than the overall population average (DW=1.215). The highest number of private markers (Table 1) was found in the Greenlandic population, which had six private markers. Four populations, including the Svalbard population, had one private marker each, while four populations had no private markers.

In the PCO plot including the outgroup species *C. krausei*, the outgroup population was clearly separated from the *C. capillaris* populations along the first ordination axis (which explained 35. 1 % of the total variation) (Figure A4). The PCO plot including only the *C. capillaris* populations revealed three well separated groups, with the first and second axis explaining 30.0 % and 16.5 % of the total variation, respectively (Figure 12). The two

populations from the Alps and the Southern Norwegian (Folldal) population formed one group (ssp. *capillaris* group); a second group comprised of the Svalbard population, the two Icelandic populations, and the three Northern Norwegian populations (ssp. *fuscidula* group), while the single Greenlandic population (morphologically determined ssp. *fuscidula*) formed a third group. In the PCO plot including only the ssp. *fuscidula* group (i.e. excluding the Greenlandic population), the two first axes together explained 48.9 % of the total variation (Figure 13). The Svalbard population was separated as a group of its own whereas the populations from Northern Norway and Iceland were more or less overlapping, but with most of the individuals from one of the Icelandic populations (Laugarvatn) forming a distinct group.

The neighbor-joining tree revealed the same three main groups, with the Greenlandic population (99 % bootstrap support) as sister to the two other groups (72 % bootstrap support) (Figure 14). The ssp. *capillaris* group was, however, not supported (<50 % bootstrap support), while the ssp. *fuscidula* group had medium bootstrap support (64 %). The neighbor-joining analysis further revealed some supported subgroups, including the Svalbard population (92 % bootstrap support) and the Laugarvatn population (except one individual) (84 % bootstrap support) within the ssp. *fuscidula* group, and the population from Southern Norway (Folldal) (99 % bootstrap support) within the ssp. *capillaris* group.

In the Structure analysis using the "no admixture" model, the highest value of delta K (Figure A5) was obtained for two groups. The same ssp. *fuscidula* group was found, but the Greenlandic population clustered with the ssp. *capillaris* group. Also the "admixture" model suggested that the optimal number of groups was K=2 (Figure A6), but delta K was high and the similarity coefficient as high for K=3. With K=3 (Figure 1), the three groups corresponded to ssp. *capillaris*, ssp. *fuscidula*, and Greenland, respectively, thus supporting the results from the PCO and neighbor-joining analyses. There was no mixed ancestry in all but four individuals (from Northern Norway and Greenland). The hierarchical Structure analyses of the ssp. *fuscidula* group suggested that the optimal number of groups was K=3 (Figure A7, Figure A8) for both the "no admixture" and the "admixture" model (although the similarity coefficient was higher for K=2 in the "no admixture" model). The Svalbard population and the Laugarvatn (Iceland) population (except one individual) formed two separate groups, while the third group comprised of the remaining populations (three from Northern Norway and one from Iceland (Grindavik)) and one Laugarvatn individual (Figure 1), confirming the grouping found in the PCO plot of the ssp. *fuscidula* group and in the neighbor-joining tree

(Figure 13, Figure 14). However, both populations from Iceland and two of the three Northern Norwegian populations (Tromsø and Nordreisa II) were not assigned to the same group in all runs by the "no admixture" model, and the "admixture" model detected individuals with mixed ancestry in all populations, except from Svalbard (not shown).

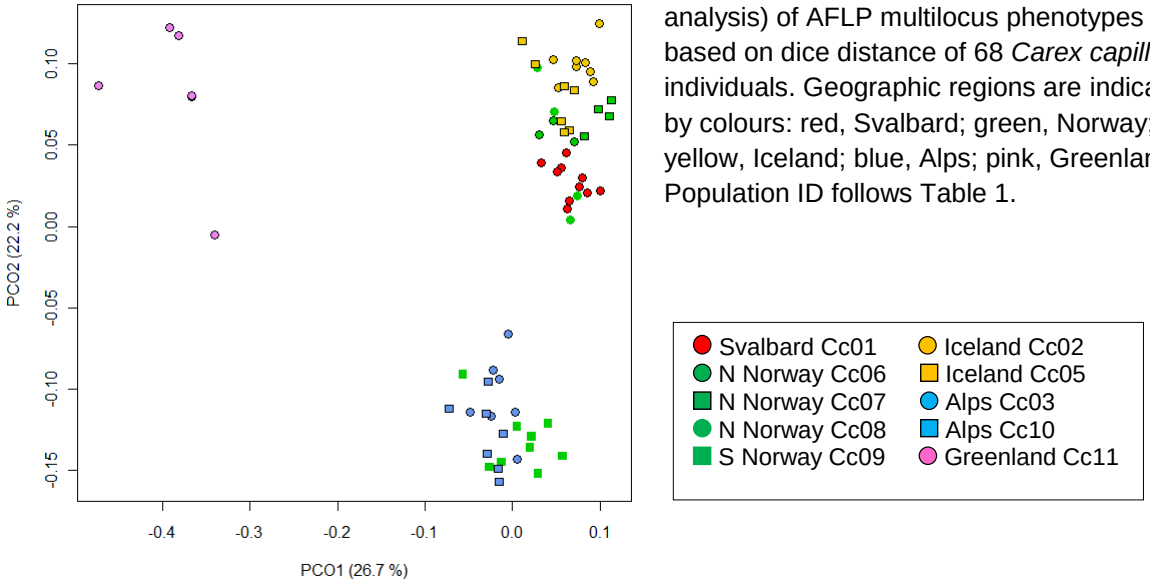

Figure 12 PCO (principal coordinates analysis) of AFLP multilocus phenotypes based on dice distance of 68 *Carex capillaris* individuals. Geographic regions are indicated by colours: red, Svalbard; green, Norway; yellow, Iceland; blue, Alps; pink, Greenland. Population ID follows Table 1.

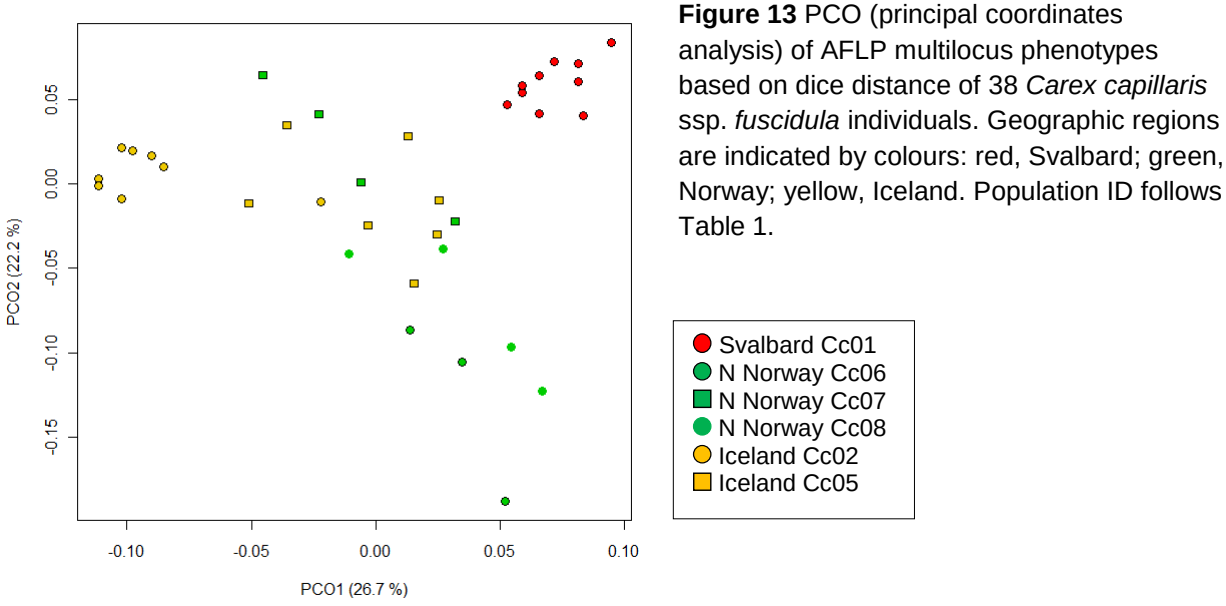

Figure 13 PCO (principal coordinates analysis) of AFLP multilocus phenotypes based on dice distance of 38 *Carex capillaris* ssp. *fuscidula* individuals. Geographic regions are indicated by colours: red, Svalbard; green, Norway; yellow, Iceland. Population ID follows Table 1.

In the clustering analysis using Baps, the highest log marginal likelihood (-1795.7) was obtained for six groups. Baps detected subgroups revealed by the PCO, neighbor-joining,

and structure analyses: (1) Svalbard, (2) Laugarvatn (Iceland), (3) Northern Norway, Grindavik (Iceland) and one Laugarvatn individual, (4) Southern Norway, (5) Alps, and (6) Greenland. Thus, (1), (2) and (3) are subgroups within the ssp. *fuscidula* main group; (4) and (5) are subgroups within the ssp. *capillaris* main group; and (6) correspond to the Greenland main group (Figure 1).

The AMOVA analysis of all populations partitioned most of the variation (65.94 %) among populations (Table 4). When grouping the populations according to the two assumed subspecies (Greenland excluded), 27.97 % of the variation was found among ssp. *capillaris* and ssp. *fuscidula*. When using the three main groups (ssp. *capillaris*, ssp. *fuscidula*, Greenland) the among-group variation increased to 38.61 %, and further to 47.41 % when using the six subgroups (listed above). In the hierarchical AMOVA of the ssp. *fuscidula* populations (excluding Greenland), the variation was split almost evenly among (52.95 %) and within (47.05 %) populations. The among-group variation was higher when using the three ssp. *fuscidula* subgroups than grouping according to geographic regions (Svalbard, Northern Norway, Iceland) (31.10 % and 17.08 %, respectively).

In the assignment test using geographical regions (Greenland, Northern Norway, Southern Norway, Iceland, Alps) to assign the ten individuals from Svalbard, three individuals were assigned to Northern Norway when the minimal log likelihood difference (MLD) threshold was set to MLD=2 (Table A7). Two more were assigned with MLD=1, and all ten individuals assigned to Northern Norway with MLD=0 (Figure 1). When using the ssp. *fuscidula* subgroups as putative source regions, all individuals assigned to Northern Norway/Grindavik/one Laugarvatn individual, even with MLD=2 (Table A8).

Comastoma tenellum

The AFLP analysis of the 86 individuals generated 123 markers (97.6 % polymorphic). Excluding the outgroup, 101 markers (83.2 % polymorphic) from 81 individuals were obtained. The mismatch error rate for the total data set was 2.2 %. The proportion of polymorphic markers (Table 1) was generally low in the studied populations, ranging from 2.4 % to 27.4 % in Flatøyrdalen (Svalbard) and Zermatt (Alps), respectively. The average proportion of polymorphic markers in Svalbard populations (5.9 %) was low compared to the overall population average (10.6 %). Similarly, genetic diversity measured by D-values (Table 1) was low within most of the studied populations, ranging from 0.011 to 0.103, also in

Flatøyrdalen and Zermatt, respectively. The mean genetic diversity within the Svalbard populations (D=0.021) was comparable to some of the other populations, but low compared to

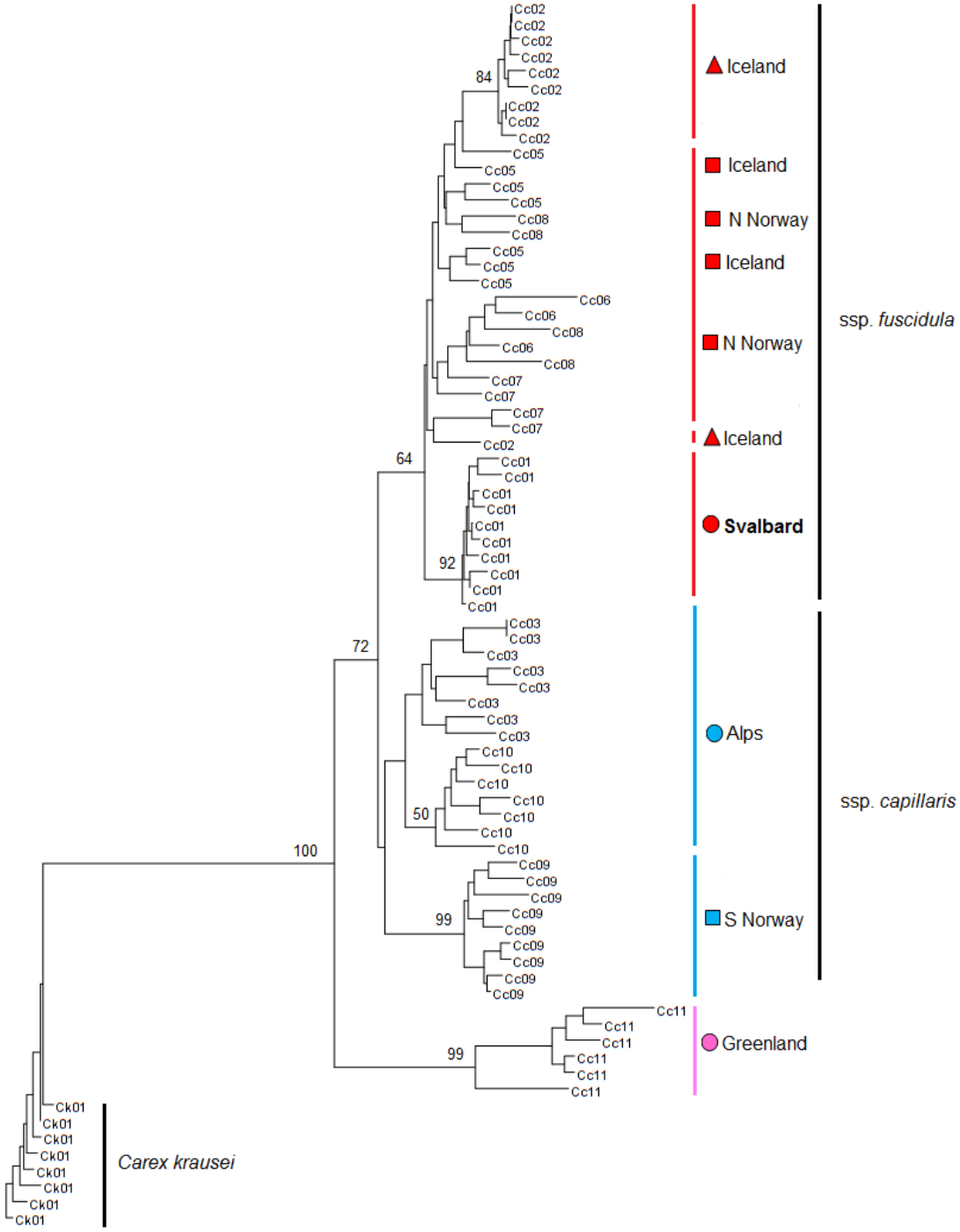

Figure 14 Neighbor-joining tree of AFLP multilocus phenotypes based on dice similarity of 68 *Carex capillaris* individuals. The tree is rooted with *Carex krausei*. Bootstrap support values higher than 50 % are given for major branches. Population ID follows Table 1. Symbols and colors follow Figure 1.

the overall population average (D=0.041). The minimum number of AFLP multilocus phenotypes was lower than the number of individuals analysed in all populations except the Sölkpass population (Alps), and the maximum number was rarely as high as the number of individuals analysed (Table 1). Within the Flatøyrdalen and Ossian Sarsfjellet populations, a minimum number of only one and two AFLP multilocus phenotypes were found, respectively, while 5-7 different AFLP multilocus phenotypes were found in Ringhorndalen. The rarity index (Table 1) was similar among populations, with DW-values ranging from 1.032 to 1.042, again in Flatøyrdalen and Zermatt, respectively. The mean rarity of the Svalbard populations (DW=1.035) was comparable to the overall population average (DW=1.037). The highest number of private markers (Table 1) was found in the Alaskan population, which had five private markers. The four Alps populations had one to three private markers each, while none of the Svalbard or Norwegian populations had any private markers.

Table 4 AMOVAs (analyses of molecular variance) of AFLP multilocus phenotypes in *Carex capillaris*.

Source of variation	d.f.	Sum of squares	Variance components	% Variation	Fixation index (Φ_{ST})*
Among all populations	9	542.668	8.34847	65.94	
Within all populations	58	250.127	4.31253	34.06	0.66
Among two assumed subspecies (ssp. *fuscidula*, ssp. *capillaris*) excluding Greenland	1	144.460	3.47961	27.97	
Among populations within assumed subspecies	7	251.123	4.79602	38.56	
Within populations	53	220.627	4.16277	33.47	0.67
Among three main groups (Svalbard/Iceland/N Norway, S Norway/Alps, Greenland)	2	291.544	5.71348	38.61	
Among populations within PCO/neighbor-joining groups	7	251.123	4.77337	32.25	
Within populations	58	250.127	4.31253	29.14	0.71
Among six subgroups (Svalbard, Laugarvatn (Iceland), N Norway/Grindavik (Iceland) /one Laugarvatn individual, S Norway, Alps, Greenland)	5	470.089	6.26200	47.41	
Among populations within Baps groups	5	79.423	2.67943	20.28	
Within populations	57	243.282	4.26811	32.31	0.67
Among all ssp. *fuscidula* (i.e. Svalbard/Iceland/Norway)	5	140.259	4.02916	52.95	
Within populations	32	114.557	3.57991	47.05	0.67
Among three geographical regions (Svalbard, Iceland, N Norway)	2	83.895	1.34332	17.08	
Among populations within regions	3	82.029	3.19167	37.56	
Within populations	32	114.557	3.57991	42.13	
Among three ssp. *fuscidula* subgroups (Svalbard, Laugarvatn (Iceland), N Norway/Grindavik (Iceland)/one Laugarvatn individual)	2	100.539	2.58340	31.10	
Among populations within	3	34.266	1.79479	21.61	
Within populations	32	125.695	3.92796	47.29	0.53

* All p<0.0001

The PCO plot of all *C. tenellum* individuals revealed four well separated main groups, with the first two axes together explaining as much as 62.5 % of the total variation (Figure 15). The Svalbard populations and the population from Polar Ural comprised one group (the Svalbard/Polar Ural group); a second group was formed by the Norwegian populations and the Sölkpass population (Ct09) from the Alps (the Norway/Alps group); the rest of the Alps formed a third group (the Alps group), and the single population from North America (Alaska) formed the last group (the N American group). The third axis (which explained 14.5 % of the total variation), separated the Alaska from the rest (not shown). Six markers were private to the Svalbard/Polar Ural group. Further, two markers were private to Svalbard (found in all individuals). Also, two markers were private to Polar Ural. Three, four and five private markers were found in the Norway/Alps group, the Alps group, and the Alaska group, respectively (not shown).

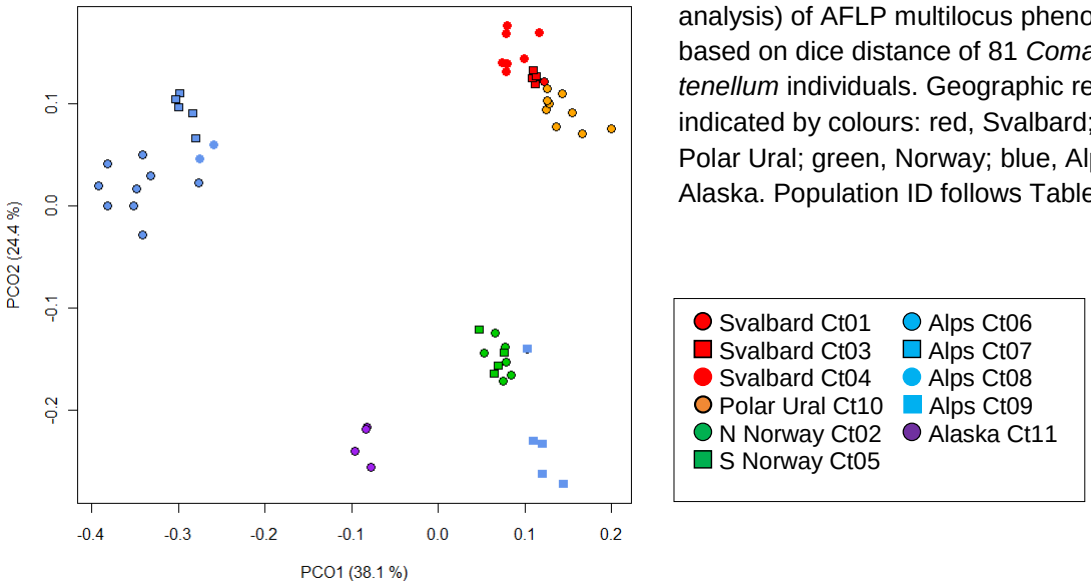

Figure 15 PCO (principal coordinates analysis) of AFLP multilocus phenotypes based on dice distance of 81 *Comastoma tenellum* individuals. Geographic regions are indicated by colours: red, Svalbard; orange, Polar Ural; green, Norway; blue, Alps; purple, Alaska. Population ID follows Table 1.

The same four main groups (with Alaska as sister to the remaining groups) were found by the neighbor-joining analysis, mostly with high bootstrap support values (Figure 16). The neighbor-joining analysis further revealed several subgroups, including the three Svalbard populations, which together were highly supported as a separate group (92 % bootstrap support). However, no clear grouping appeared within Svalbard. Other subgroups generally corresponded to sampled populations, like within the Alps group where each of the three sampled populations was supported as individual subgroups.

In the Structure analysis using the "no admixture" model, the highest value of deltaK was obtained for K=3 (Figure A9). Mainly the same structure was found, except that the

population from Alaska clustered with Norway/Alps (Figure 3). For the "admixture" model, K=2 had the highest value of delta K (Figure A10). However, using two groups resulted in mixed ancestry for all individuals and no clear structure. Instead, K=3 was chosen because it provided more biologically interpretable results and gave the second highest value of delta K. With three groups, the same grouping as for the admixture model was found (not shown). None of the Svalbard/Polar Ural individuals showed mixed ancestry, while mixed ancestry was evident in all other individuals (not shown). The hierarchical Structure analyses of the Svalbard/Polar Ural group clearly suggested that the number of groups was K=2, for both the "no admixture" and the "admixture" model (Figure A11, Figure A12). The individuals from the Svalbard populations formed one group (the Svalbard group), while Polar Ural formed the other, supporting the result from the neighbor-joining analysis (Figure 3). Low levels of mixed ancestry (<5 % in all individuals) were detected by the "admixture" model (not shown).

In the clustering analysis using Baps, the highest log marginal likelihood (-1460.8) was obtained for six groups. Baps detected subgroups revealed by the PCO, neighbor-joining and Structure analyses: (1) Svalbard, (2) Polar Ural, (3) Norway/Alps, (4) Alps, (5) Splügenpass (Alps), and (6) Alaska (Figure 3). Thus, (1) and (2) are subgroups within the Svalbard/Polar Ural main group; (3) correspond to the Norway/Alps main group; (4) and (5) are subgroups within the Alps main group; while (6) correspond to the Alaska main group.

The AMOVA analysis of all populations partitioned nearly all of the variation (86.21 %) among populations (Table 5). The among-group variation was higher when grouping the populations according to the four main groups (Svalbard/Polar Ural, Norway/Alps, Alps, Alaska) than when using five geographic regions (Svalbard, Polar Ural, Norway, Alps, Alaska) (69.00 % and 55.59 %, respectively). When using the six subgroups (listed above), the among-group variation increased further to 76.16 %. Also in the hierarchical AMOVA of Svalbard and Polar Ural, most of the variation (64.17 %) was among groups.

In the assignment test, all individuals from Svalbard assigned to Polar Ural, even when the minimal log likelihood difference threshold was set to MLD=2 (Figure 3, Table A9).

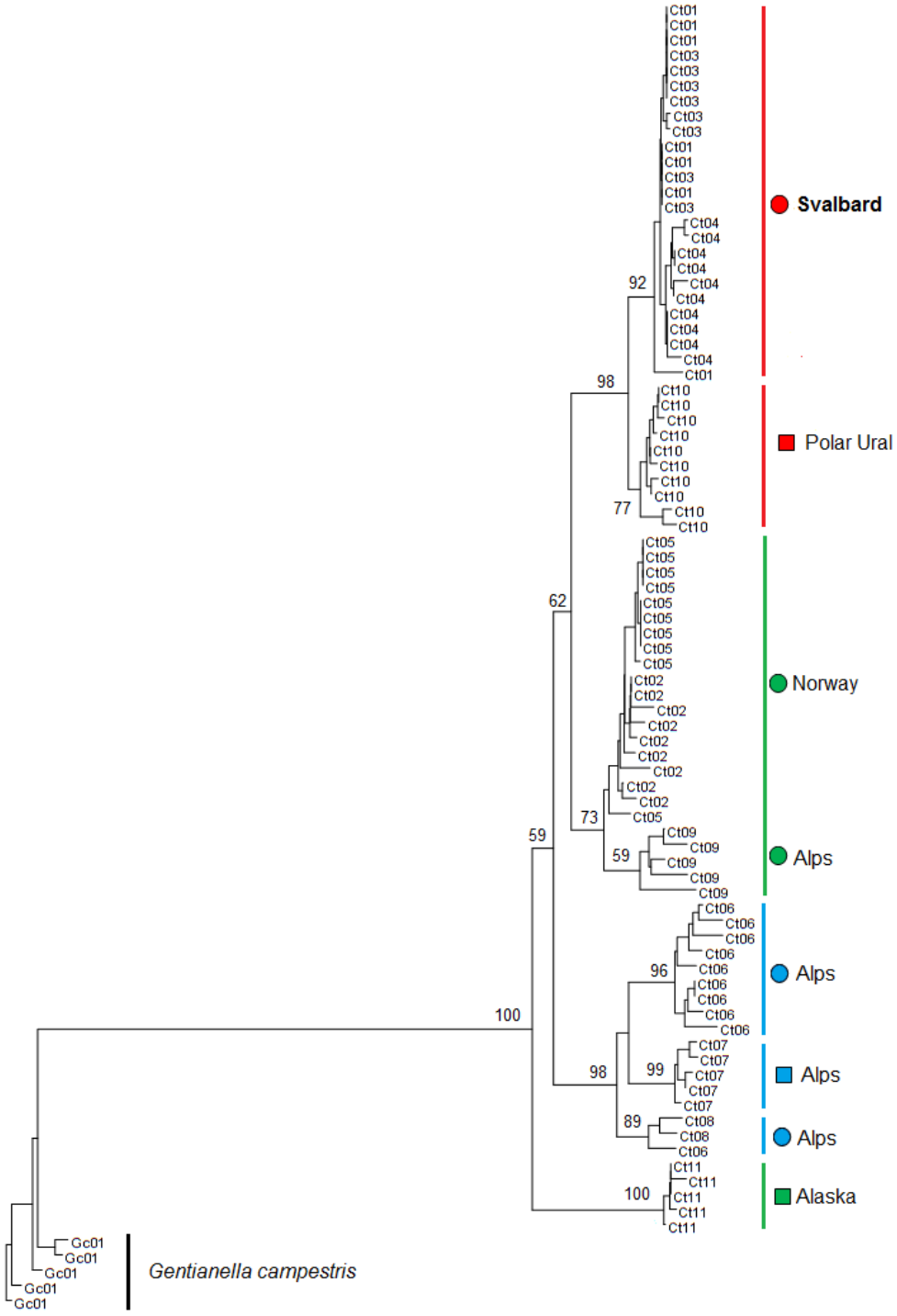

Figure 16 Neighbor-joining tree of AFLP multilocus phenotypes based on dice similarity of 81 *Comastoma tenellum* individuals. The tree is rooted with *Gentianella campestris*. Bootstrap support values higher than 50 % are given for major branches. Population ID follows Table 1. Symbols and colors follow Figure 3.

Table 5 AMOVAs (analyses of molecular variance) of AFLP multilocus phenotypes in C*omastoma tenellum*.

Source of variation	d.f.	Sum of squares	Variance components	% Variation	Fixation index (Φ_{ST})*
Among all populations	10	799.429	10.76077	86.21	
Within all populations	70	120.497	1.72139	13.79	0.86
Among five geographic regions (Svalbard, Polar Ural, Norway, Alps, Alaska)	4	610.922	7.60015	55.59	
Among populations within regions	6	188.507	4.35072	31.82	
Within populations	70	120.497	1.72139	12.59	0.87
Among four main groups (Svalbard/Polar Ural, Norway/Alps, Alps, Alaska)	3	638.040	10.36422	69.00	
Among populations within PCO/neighbour-joining groups	7	161.389	2.93480	19.54	
Within populations	70	120.497	1.72139	11.46	0.89
Among six subgroups (Svalbard, Polar Ural, Norway/Alps, Alps, Splügenpass (Alps), Alaska)	5	734.148	10.63708	76.16	
Among populations within Baps groups	5	65.281	1.60869	11.52	
Within populations	70	120.497	1.72139	12.32	0.88
Among Svalbard and Polar Ural	1	44.680	2.74333	64.17	
Among populations within Svalbard and Polar Ural	2	9.745	0.46145	10.79	
Within populations	31	33.175	1.07016	25.03	0.74

* All p<0.0001

Puccinellia sp.

The individuals of the focus population from Bockfjorden, previously considered as *P. angustata* ssp. *palibinii*, were all determined as *P. svalbardensis* after the herbarium voucher inspection (Table A2). In addition to Bockfjorden, *P. svalbardensis* individuals were identified in two populations (both from Wijdefjorden). These two populations were, however, heterogeneous (i.e. also containing *P. angustata* individuals) (Table A2). Further, a population from Bockfjorden (Pa11, Table 1), determined *P. angustata* ssp. *palibinii* in field, was determined *P. angustata* after inspection of the herbarium vouchers, meaning that *P. svalbardensis* and *P. angustata* were co-occurring also in Bockfjorden.

The AFLP analysis of the 86 *Puccinellia* individuals resulted in 118 markers (100% polymorphic). Excluding the outgroup *P. vahliana*, 98 markers (95.9 % polymorphic) from 77 individuals were obtained. In addition to the ten individuals from the focus population from Bockfjorden, 60 *P. angustata* and seven *P. svalbardensis* individuals were analysed, respectively. The mismatch error rate for the total data set was as high as 9.3 %.

In the PCO plot (Figure 17), the outgroup *P. vahliana* was clearly separated from *P. angustata*, *Puccinellia* sp., and *P. svalbardensis* along the second axis (PCO 2), which

explained 26.5 % of the total variation. Along the first axis, which explained as much as 33.4% of the total variation, *P. angustata* formed a separate group. Most *Puccinellia* sp. and *P. svalbardensis* individuals (with all three populations represented) formed a group which was well separated from *P. angustata*, while five individuals (also with all three populations represented) formed an intermediate group, which was as close to *P. angustata* as to the other *Puccinellia* sp./*P. svalbardensis* individuals. The PCO thereby supported the conclusion from the inspection of herbarium vouchers that *Puccinellia* sp. from Bockfjorden belongs to *P. svalbardensis*.

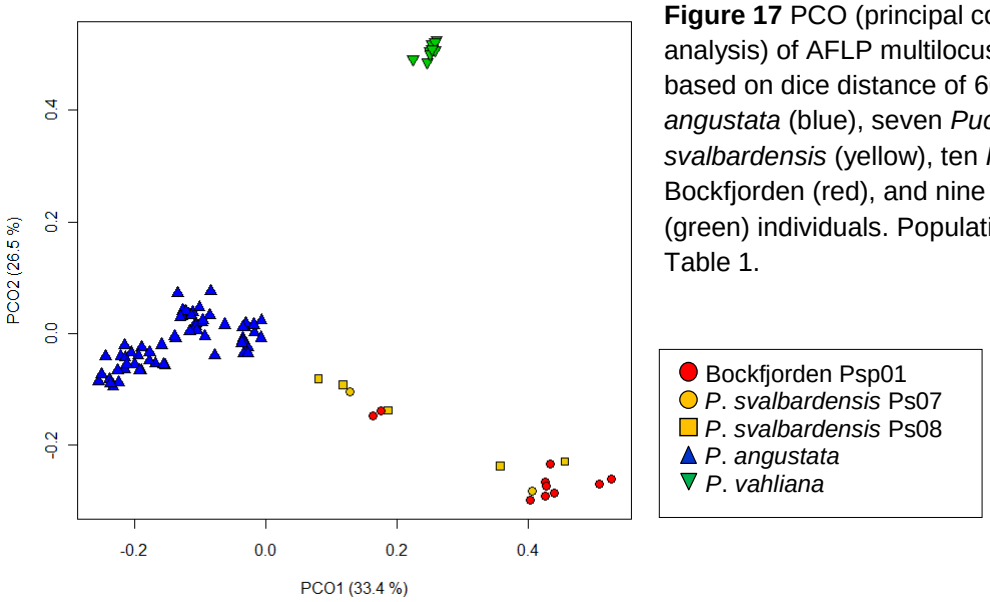

Figure 17 PCO (principal coordinates analysis) of AFLP multilocus phenotypes based on dice distance of 60 *Puccinellia angustata* (blue), seven *Puccinellia svalbardensis* (yellow), ten *Puccinellia* sp. Bockfjorden (red), and nine *P. vahliana* (green) individuals. Population ID follows Table 1.

In the neighbor-joining tree (Figure 18) (using *P. vahliana* as outgroup), *P. angustata* and *Puccinellia* sp./*P. svalbardensis* formed two separate groups, although they were not supported (<50 % bootstrap support) and poorly supported (51 % bootstrap support), respectively. Thus, the neighbor-joining tree also revealed that *P. svalbardensis* is found in Bockfjorden. *Puccinellia* sp. is therefore hereafter called, and included with, *P. svalbardensis*. Within the *P. svalbardensis* group (i.e. including *Puccinellia* sp.), some individuals formed a well supported (99 % bootstrap support) group, corresponding to the pattern seen in the PCO plot (Figure 17).

The proportion of polymorphic markers (Table 1) varied greatly among the sampled populations, ranging from 10.6 % to 58.5 % in *P. angustata* from Edgeøya and *P. svalbardensis* from Bockfjorden, respectively. The mean proportion of polymorphic markers was considerably higher in *P. svalbardensis* (overall population average 56.8 %) than in *P.*

angustata (overall population average 18.5 %). Similarly, the level of genetic diversity measured by D-values (Table 1) was high in the *P. svalbardensis* populations (Bockfjorden, D=0.219; Ringhorndalen, D=0.278) compared to *P. angustata* (overall population mean D=0.077). The genetic diversity was lowest in *P. angustata* from Edgeøya (D=0.043) and highest in the *P. svalbardensis* population from Ringhorndalen (D=0.278). The minimum number of AFLP multilocus phenotypes (Table 1) was generally much lower than the number of individuals analysed in *P. angustata* populations, while it was similar or equal to the number of individuals analysed in the *P. svalbardensis* populations. Four markers were private to the three *P. svalbardensis* populations, while one marker was found in all *P. angustata* populations, but not in *P. svalbardensis* (not shown).

Tofieldia pusilla

The AFLP analysis of the 157 individuals generated 127 markers (97.6 % polymorphic). Excluding the two outgroup taxa, only 68 markers (47.1 % polymorphic) from 145 individuals were obtained. The mismatch error rate for the total data set was 1.5 %. The proportion of polymorphic markers (Table 1) varied among the studied populations, ranging from 12.5 % to 53.1 % in Laugarvatn (Iceland) and Nordreisa (Troms)/Tasiilaq (Greenland), respectively. The average proportion of polymorphic markers in the Svalbard populations (32.4 %) was similar to the overall population average (32.7 %). Similarly, the level of genetic diversity measured by D-values (Table 1) varied among the studied populations, and was lowest in Laugarvatn (D=0.052) and highest in Tasiilaq (D=0.214) (Table 1). D-values within the populations from Svalbard ranged from 0.069 to 0.173 in Ringhorndalen and Bockfjorden, respectively. The mean genetic diversity within the Svalbard populations (D=0.123) was comparable to the overall population average (D=0.133). Including the monomorphic markers, the overall population average of proportion of polymorphic markers and genetic diversity were 15.4 % and 0.063, respectively. In most populations, even the minimum number of AFLP multilocus phenotypes (Table 1) was equal or similar to the number of individuals analysed. The rarity index (Table 1) ranged from 0.183 to 0.290 in Tromsø (Norway) and Tasiilaq (Greenland), respectively. The mean rarity of the Svalbard populations (DW=0.202) was similar to the overall population average (DW=0.211). One marker was private to Greenlandic population (Table 1). None of the other populations had any private markers, however, three markers were not found in the population from Greenland, but in all other populations (not shown).

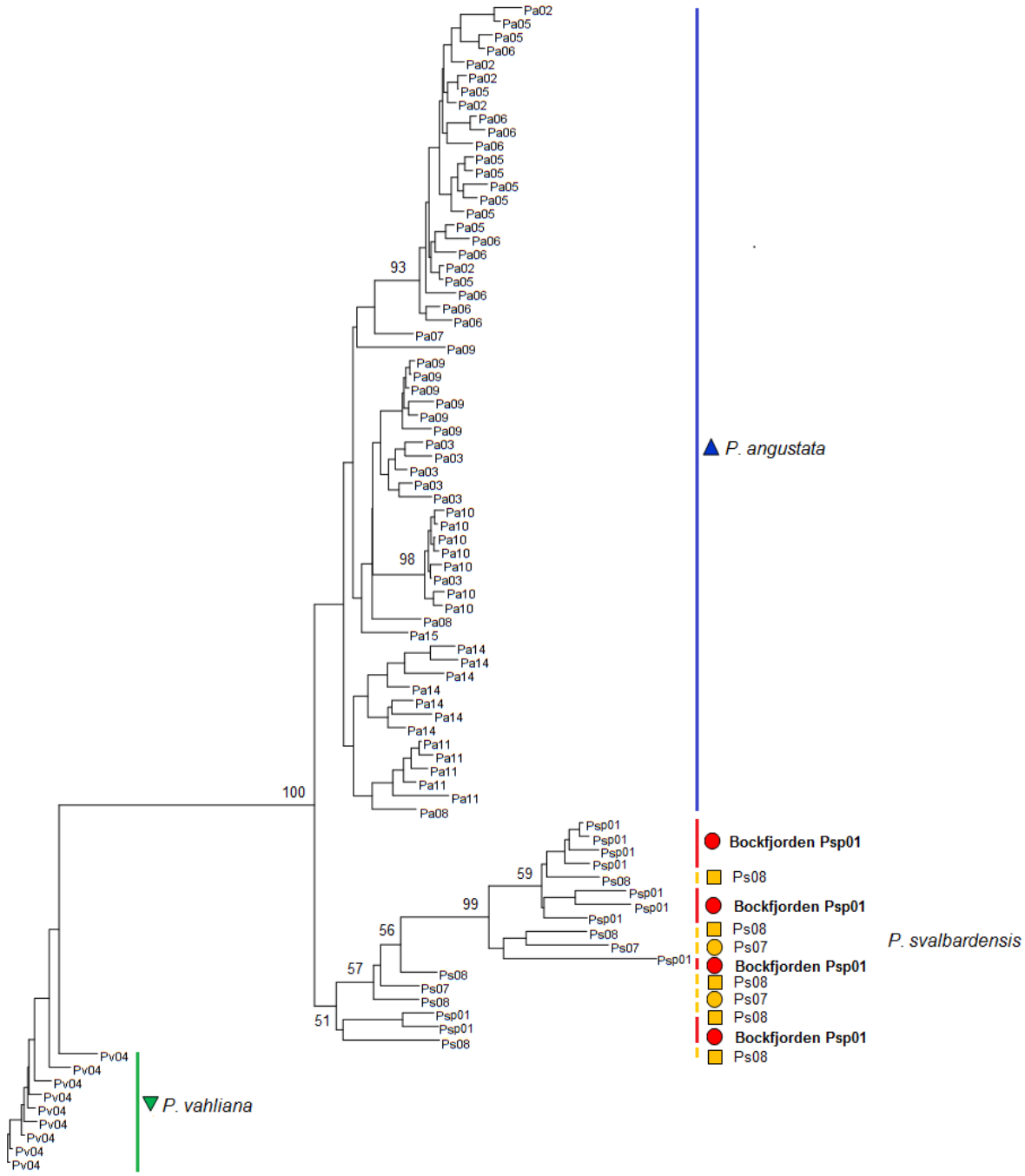

Figure 18 Neighbor-joining tree of AFLP multilocus phenotypes based on dice similarity of 60 *Puccinellia angustata*, seven *P. svalbardensis*, and ten *Puccinellia* sp. Bockfjorden individuals, respectively. The tree is rooted with *P. vahliana*. Bootstrap support values higher than 50 % are given for major branches. Population ID follows Table 1. Symbols and colors follow Figure 17.

The PCO plot of all *T. pusilla* individuals indicated two groups along the first axis, explaining 18.9 % of the total variation, in which the population from Greenland was slightly separated from the rest (Figure 19). No further structure was apparent.

The same separation was found in the neighbor-net, where the major split in the network was found between Greenland and the other populations. The remaining structure within the network was not evidently related to geographic regions or individual populations (Figure A13).

The Structure analysis using the "no admixture" model suggested that the optimal number of groups was K=4, although the similarity coefficient was highest for K=2 (Figure A14). Using K=4, the Greenlandic population comprised one group, while the three remaining groups were made up by a mix of individuals from different populations and geographical regions (Table A10). The "admixture" model suggested that the optimal number of groups was K=3 (Figure A15).This model resulted in the same main structure, with Greenland as separate group (not shown). The "admixture model" found relatively low levels of mixed ancestry (<10 %) in most individuals (not shown).

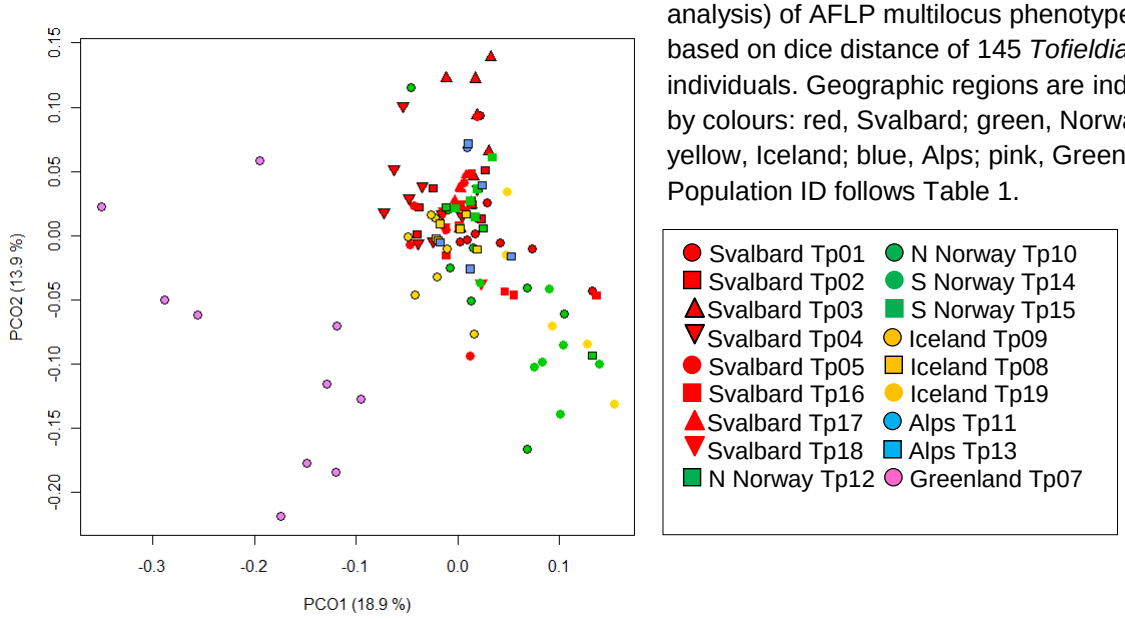

Figure 19 PCO (principal coordinates analysis) of AFLP multilocus phenotypes based on dice distance of 145 *Tofieldia pusilla* individuals. Geographic regions are indicated by colours: red, Svalbard; green, Norway; yellow, Iceland; blue, Alps; pink, Greenland. Population ID follows Table 1.

In the clustering analysis using Baps, the highest log marginal likelihood (-1220.0) was obtained for seven groups. Here, the Greenlandic population comprised two of the groups. Further, the same lack of population and geographical structure as for the other clustering methods was found (Table A10).

The AMOVA analysis of all populations partitioned most of the variation (64.59 %) within populations (Table 6). Using five geographic regions (Svalbard, Greenland, Norway, Iceland, Alps), only 19.41 % of the total variation was found between these regions. When

using the two PCO/neighbor-net group (Greenland, 'the rest') the among-group variation increased to 49.00 %, while the among-population variation was only 13.72 %. Also in the hierarchical AMOVA of the eight Svalbard populations, most of the variation (76.94 %) was within populations.

In the assignment test using the geographical regions to assign Svalbard individuals, none of the individuals could not be assigned to any geographical region when the minimal log likelihood difference threshold was set to MLD=2, and only three (to Norway) when set to MLD=1(Table A11). However, with MLD=0 all individuals were forced to assign to one of the four regions (Greenland, Norway, Iceland, Alps). Most individuals then assigned either to Norway (41.7 %) or Iceland (45.8 %), and none to Greenland. To which region individuals were assigned to, varied both within and among the Svalbard populations. When using the two PCO/neighbor-net groups (Greenland, the rest), only two individuals could not be assigned with MLD=2, and all individuals assigned to 'the rest' with MLD=1 (Table A12).

Table 6 AMOVAs (analyses of molecular variance) of AFLP multilocus phenotypes in *Tofieldia pusilla*.

Source of variation	d.f.	Sum of squares	Variance components	% Variation	Fixation index (Φ_{ST})*
Among all populations	17	189.644	1.13599	35.41	0.35
Within all populations	127	263.169	2.07220	64.59	
Among five geographic regions (Svalbard, Greenland, Norway, Iceland, Alps)	4	93.564	0.65910	19.41	
Among populations within regions	13	96.080	0.66476	19.57	
Within populations	127	263.169	2.07220	61.02	0.39
Among two PCO/neighbour-net groups (Greenland, the rest)	1	60.369	2.72392	49.00	
Among populations within PCO/neighbour-net groups	16	129.275	0.76286	13.72	
Within populations	127	263.169	2.07220	37.28	0.62
Among Svalbard populations	7	48.797	0.57094	23.06	
Within populations	64	121.925	1.90508	76.94	0.23

* All p<0.0001

Discussion

Carex capillaris

Population status

The population of *Carex capillaris* in Bockfjorden was considerably larger (>2000 individuals) than assumed in the 2006 Norwegian Red List (maximum 100 individuals) (Elven et al. 2006), and the population size has thus been underestimated. Since the discovery in 1960 (Rønning 1961a), the population has been observed at least twice: in 1881 by Elvebakk and Spjelkavik (1981) and in 1991 by Tannheiser and co-workers (Svalbard Herbarium database 2006), but past population sizes have not been reported. It is therefore uncertain whether the population size has increased since 1960. However, the large population size and high number of fertile plants suggest that *C. capillaris*, despite some grazing impact, is currently thriving in Bockfjorden, and the results moreover suggest that the species has local expansion potential in Bockfjorden. This is further supported by the observation of smaller infertile plants, which indicates population recruitment, and the local dominance of *C. capillaris*, which indicates that it is not restricted by competition from other species. At last, the moderate grazing levels does not seem to notably harm the species at the moment, but if geese populations continue to grow in Svalbard (Norwegian Polar Institute 2012), the increased grazing pressure could represent a future threat to the population. However, other *Carex* species tolerate grazing well (Cargill and Jefferies 1984, Jónsdóttir 1991), and this may also apply to *C. capillaris*. Thus, there does not seem to be any immediate environmental threats to the population, but the fact that the Bockfjorden population is the only population of the species in Svalbard makes it vulnerable to stochastic, catastrophic events.

Ecological requirements and expansion potential

The results suggest that temperature and moisture are the two ecological factors most important to *C. capillaris* in Bockfjorden. The species prefers the immediate surroundings of the warmest spring in Bockfjorden, where the substrate temperature and moisture is the highest. This preference is shared with another red listed vascular plant, *Botrychium lunaria* (L.) Sw. (Birkeland 2012), but in contrast to this species, *C. capillaris* is also found downstream of the springs in areas where the conditions are more moderate. *Carex capillaris*

seem to prefer wet habitats also in other parts of its distribution range (Hegi 1939, Schütz and Rave 1999, Lunterbusch and Daniels 2004, Elven 2005), but is found in drier habitats as well (Hegi 1939, Aiken et al. 2003), and Raup (1969) reported that the species exhibits a wide moisture tolerance in North East Greenland. Thus, although the relative effect of temperature and moisture on the abundance of the species in Bockfjorden could not be disentangled, the dependence of a mean July temperature of more than 6 °C (Karlsen and Elvebakk 2003), which is not found in Svalbard at a regional scale (Elvebakk 1999), suggests temperature to be the limiting factor in Svalbard. Due to the geothermal heat, Bockfjorden is among the areas in Svalbard with the highest concentration of thermophilous plants (Elvebakk 1989), and could be the only place with currently favorable enough conditions to support *C. capillaris*. Thus, although the species has local expansion potential, it is probably restricted to the warmer parts around the thermal springs. Furthermore, *C. capillaris* can be assumed to increase in abundance with a warmer climate, which may be facilitated a responsive flowering phenology (Molau et al. 2005).

Carex capillaris seems to be rather tolerant to cover of vascular plants, bryophytes, and cryptogamic crust. A wide amplitude and high tolerance to vascular cover was also recognized by Raup (1969). Further, the low levels of frost disturbance observed are probably not of concern, as several studies suggest that *C. capillaris* tolerates it well (Raup 1969, Jonasson and Skold 1983, Jonasson 1986, Jonasson and Callaghan 1992).

Genetic structure and diversity, and taxonomic implications

The genetic diversity (population mean D=0.049) in Bockfjorden was less than half of the overall population mean (D=0.118). This result indicates that the Bockfjorden population is genetically depleted and its evolutionary potential may be restricted compared to other populations of the species. The low genetic diversity in this northernmost and highly isolated population is, however, not surprising and is probably a result of a strong founder effect, which is evident also in other thermophilous species in Svalbard (Alsos et al. 2007, Birkeland 2012).

The results show that *C. capillaris* in general exhibits moderate levels of within-population genetic diversity (overall population mean D=0.118). Further, within the three main genetic groups, the proportion of within-population variation (29.14 %) is similar to that among populations (32.25 %). Although levels of genetic diversity are species specific and therefore not directly comparable (Thiel-Egenter et al. 2009), the levels of genetic diversity in

C. capillaris is notably higher than inferred from AFLPs in the presumably predominantly autogamous *Carex atrofusca* Schkuhr (Schönswetter et al. 2006a), and also somewhat higher than in the predominantly allogamous *Carex bigelowii* Torr. (Schönswetter et al. 2008). Further, the population differentiation within the main genetic groups of *C. capillaris* is weaker than in *C. atrofusca* (Schönswetter et al. 2006a), but stronger than in *C. bigelowii* (Schönswetter et al. 2008). Together, this indicates that *C. capillaris* may be a mixed mater, rather than mainly autogamous as suggested from its caespitose growth (Ford et al. 1991, Jonsson et al. 1996) and also assumed by Brochmann and Steen (1999). A mixed mating system is in fact not very surprising, as it seems to be very common in arctic plants (Murray 1987), despite being associated with strong inbreeding depression (Goodwillie et al. 2005). However, as the proportion of heterozygotes cannot be disentangled by the dominant AFLP markers, the level of inbreeding cannot be precisely estimated. Still, some level of inbreeding depression in the Bockfjorden population is likely.

The AFLP results support the current treatment by PAF (Elven et al. 2011) of two species, *Carex capillaris* and *C. krausei*. The results further revealed three main genetic groups of *C. capillaris*, of which two correspond to the proposed subspecies *C. capillaris* ssp. *capillaris* and ssp. *fuscidula* (Elven et al. 2011). The populations from Svalbard, Iceland, and Northern Norway correspond to ssp. *fuscidula*. Thus, there is support for the classification of the Bockfjorden population as ssp. *fuscidula* by Elven et al. (2001), and further that ssp. *fuscidula* is the predominant subspecies/variety in Iceland, and present in Northern Norway, as suggested by PAF (Elven et al. 2011). The populations from the Alps and Southern Norway (Folldal) correspond to ssp. *capillaris*. The former is expected (Elven et al. 2011), while the presence of ssp. *capillaris* in Folldal suggests that Elven and Solstad (Solstad et al. 2010, Elven et al. 2011) were probably mistaken when they recently proposed that ssp. *fuscidula* is replacing ssp. *capillaris* in southern mountain ranges of Scandinavia. Further, PAF (Elven et al. 2011) suggested that ssp. *capillaris* is present at the northern, arctic coast of Scandinavia, but the three populations from the northern coast of Norway all belong to ssp. *fuscidula*. The population from North East Greenland (Zackenberg) formed a separate group. This result is surprising, as it conflicts the morphology-based determination, and because ssp. *fuscidula* is expected to be the only subspecies/race in Northern Greenland (Elven et al. 2011). Although it may reflect the complexity of this species complex, more material should be examined, as the individuals from this particular population had somewhat lower quality of the AFLP profiles compared to the other populations. Thus, except for the material from

North East Greenland, European material of *C. capillaris* seems to fit nicely into two subspecies: the mainly temperate-boreal ssp. *capillaris* and the mainly arctic ssp. *fuscidula*, of which the Svalbard population belongs to the latter.

The Svalbard population (with one private marker) formed one of three slightly separated subgroups of ssp. *fuscidula* (i.e. excluding Greenland). The genetic subgroup most similar to Svalbard was found in both Northern Norway and Iceland, but the assignment test indicated that Northern Norway is the most likely source region of the Bockfjorden population. Colonization of Svalbard from Northern Norway and/or North West Russia is also inferred from the thermophilous *Salix herbacea* (Alsos et al. 2007, Alsos et al. 2009). However, as no populations from Northern Russia were included in this study, it is not possible to distinguish between these two possible source regions. The slight distinctiveness of the Svalbard population, and the fact that it was not much more differentiated from the remaining ssp. *fuscidula* populations than the two Icelandic populations were from each other, indicate that glacial survival of *C. capillaris* in Bockfjorden, as proposed by Rønning (1963), is unlikely. Based on these results, it is more likely that the population in Bockfjorden has existed since the warmer Holocene periods (i.e. about 9500-4000 years before present) and is a relict of a former wider distribution in Svalbard, as Rønning (1961a, 1972) further proposed. However, that Bockfjorden is the only locality of the species in Svalbard, which is frequently visited by geese, suggests that a bird-mediated introduction during the last hundred or thousand of years is another possible scenario.

Comastoma tenellum

Population status

A new and third population of *C. tenellum* (Ringhorndalen) in Svalbard was discovered during this study and the estimated number individuals in Svalbard (minimum 550) is more than twice the number assumed by the 2006 Norwegian Red List (maximum 200 individuals) (Elven et al. 2006). However, since *C. tenellum* is annual/biennial, population sizes may vary considerably from year to year. While 300-400 individuals were observed in Flatøyrdalen during this study (2010), Elvebakk and Nilsen (2002) reported only six individuals at the assumed same locality (Table A1). The better reproductive success in 2010 might be due to the 1°C higher mean summer temperatures in 2009-2010, compared to 2001-2002 (May-July, data from Svalbard airport, eklima@met.no). No population size estimates exist for evaluating the population trend at Ossian Sarsfjellet, despite that the site has been frequently

visited by botanists (Svalbard Herbarium database 2006, I. G. Alsos pers. obs. 2003, 2006). Also, the species has been observed at an additional site at Ossian Sarsfjellet (ca. 100 m away) in 2003 (I. G. Alsos pers. com.), but no individuals were found there in 2006 (I. G. Alsos pers. obs.) or in 2009 (this study). If *C. tenellum* has persistent seed banks, recruitment from them would buffer population fluctuations and extinctions. Other thermophilous species in Svalbard lack seed banks because production of ripe seeds fails (Alsos et al. 2003, Cooper et al. 2004). In contrast, *C. tenellum* certainly does produce ripe and viable seeds. However, data on their longevity is lacking, and the only record (not from Svalbard) indicates that the species has a transient, rather than persistent, seed bank (Thompson et al. 1997). If this observation applies to Svalbard, populations may go extinct during two seasons with unfavorable conditions. In conclusion, the imprecise recordings of localities and populations sizes, together with fluctuating sizes of the populations, make it difficult to infer whether there has been a positive trend for *C. tenellum* in Svalbard since the first report in1963 (Svalbard Herbarium database 2006).

Ecological requirements and expansion potential

Comastoma tenellum is found in luxuriant bird cliff meadow in a steep southwest- to west-facing slope at Ossian Sarsfjellet, and is associated with bird cliff vegetation also in Flatøyrdalen and Ringhorndalen. Bird cliff meadows are the only true meadows in Svalbard (Elvebakk 1994), and the habitat is rare and disjunctly distributed within the archipelago (Elvebakk 2005b). *Comastoma tenellum* is a habitat specialist (Elven and Elvebakk 1996, Sætersdal and Birks 1997), and is found in meadows and slopes, often on calcareous substrates, also in other parts of its distribution range (Hegi 1925, Aiken et al. 2003, Elven 2005). Thus, both the specialised ecology of *C. tenellum* and the scarcity of its habitat probably contribute to the rarity of the species in Svalbard.

The site at Ossian Sarsfjellet was highly impacted by grazing and moderately impacted by trampling. As an annual/biennial herb, *C. tenellum* exhibits a ruderal strategy (Grime 1977), which implies that the species is highly disturbance tolerant. In fact, loss of grazed habitats has caused decline of *C. tenellum* in mainland Norway (Solstad et al. 2010). Further, evidence for high tolerance to moderate and low levels of grazing is found in studies of the related *Gentianella amarella* (L.) Börner and *Gentianella campestris* (L.) Börner, which are also associated with grazed habitats (Lennartsson et al. 1997, Lennartsson et al. 1998, Huhta et al. 2000, Huhta et al. 2003). Consequently, some level of grazing and

trampling is likely beneficial to *C. tenellum*, as it keeps the vegetation open and thus allows for re-establishment of the species.

The impact of temperature on the local abundance and distribution of *C. tenellum* was not evaluated. However, Ossian Sarsfjellet and Flatøyrdalen are known to have particularly high local temperatures, and consequently a high concentration of thermophilous plants (Elvebakk 1989, Elvebakk and Nilsen 2002, Joly et al. 2010). Further, because of the extrazonally warm conditions and thermophilous biodiversity elements of these two sites, both are recognized as 'arctic hotspots'(Elvebakk 2005a). Although Ringhorndalen is less studied, also this area is known to hosts thermophilous species, like e.g. *T. pusilla* (this study). As an indicator species for areas with mean July temperature above 6 °C (Karlsen and Elvebakk 2003), but with its optimum at 9.5 °C and relatively narrow temperature tolerance (Sætersdal and Birks 1997), it is not surprising that *C. tenellum*, under the current climatic conditions, is found only at these three localities in Svalbard. However, *C. tenellum* can be expected to respond particularly quickly to climate warming due to its flexible flowering phenology (Molau et al. 2005) and short generation time.

Genetic structure and diversity

The low levels of within-population genetic diversity found in *C. tenellum* (overall population mean D=0.041) are expected for an autogamous species (Hamrick and Godt 1996, Nybom and Bartish 2000, Nybom 2004, Thiel-Egenter et al. 2009). It may additionally be explained by the short life span and fluctuating populations of *C. tenellum*, which make the species more prone to genetic drift, and thus loss of genetic diversity (Hamrick et al. 1979).

The genetic diversity in Svalbard (population mean D=0.021) was low compared to the overall population mean (D=0.041). Further, a minimum of only one, two, and five AFLP multilocus phenotypes were found in Flatøyrdalen (n=7), Ossian Sarsfjellet (n=8), and Ringhorndalen (n=10), respectively, which was also low compared to most other populations. These results indicate that the Svalbard populations are somewhat genetically depleted and that their evolutionary potential may be restricted compared to other populations of the species. Further, as *C. tenellum* is mainly autogamous, high levels of inbreeding could represent a threat to the three Svalbard populations. However, a study of the closely related and autogamous *Comastoma pulmonarium* (Turcz.) Toyok. found signs of reduced inbreeding depression (i.e. no early-acting inbreeding depression was evident) (Zhang et al. 2011). Also in general, there is evidence (although not conclusive) for reduced inbreeding depression in

naturally inbreeding species, resulting from purging of deleterious recessive alleles (Husband and Schemske 1996, Byers and Waller 1999, Keller and Waller 2002, Leimu et al. 2006, Frankham et al. 2010).

The population differentiation (86.21 % among-population variation) was very strong, but expected for an annual, autogamous species with gravity dispersed seeds (Hamrick and Godt 1996, Nybom and Bartish 2000, Nybom 2004, Thiel-Egenter et al. 2009). The further strong geographical structuring into four main groups and six subgroups (revealed by the ordination and clustering analyses, AMOVAs, and the high number of private markers) probably corresponds to at least four different glacial refugia: (1) The population from Alaska exhibited the highest number of private markers (but probably partly a sampling effect) and may represent a Beringian refugium, as inferred for many other arctic-alpine plants (Abbott et al. 2000, Abbott and Brochmann 2003, Hewitt 2004); (2) The Alps group (including most of the Alp populations) was clearly distinct, and may correspond to at least one glacial refugium located in the South West Alps, as suggested by Schönswetter et al. (2004), and inferred for other arctic-alpine plants (Schönswetter et al. 2005); (3) The Norway/Alps group partly corresponds to a group of populations identified by Schönswetter et al. (2004), including also populations from the Carpathians, which is recognized as a glacial refugium (Després et al. 2002, Ronikier et al. 2008); (4) The Svalbard/Polar Ural group suggests a close relationship of the Svalbard populations with Polar Ural indicating a shared glacial refugium, which may have been located in the Urals, where large areas remained unglaciated during the last glaciation (Abbott and Brochmann 2003). Thus, no support was found for the proposal by Hadač (1963) of *in situ* glacial survival of *C. tenellum* in Svalbard. The genetic similarity of the three Svalbard populations further suggests that Svalbard was colonized only once, and the comparably low genetic diversity in the Svalbard populations may be explained by a strong founder effect. The assignment test clearly supported that Svalbard was colonized from the Polar Urals, but the distinctiveness of the Svalbard populations (separate genetic subgroup with two private markers) indicates that the colonization event was not very recent. A likely scenario is that the colonization of Svalbard took place during the warmer periods of the Holocene (i.e. about 9500-4000 years before present), and that the present few and isolated populations represent relicts of a former wider distribution. A similar scenario was recently suggested for the thermophilous and annual *Euphrasia wettsteinii* Gussarova (G. Gussarova et al. in prep.). However, the possibility that *C. tenellum* more recently colonized Svalbard from a not sampled source in northern Russia, Greenland or Iceland can not be excluded.

Nevertheless, if *C. tenellum* colonized Svalbard from North West Russia during the warmer Holocene, its history is shared with several of Svalbard's thermophilous species (Engelskjøn et al. 2003), as already inferred for *Betula nana* L., *Vaccinium uliginosum* L. (Alsos et al. 2002, Alsos et al. 2007), *Minuartia biflora* (L.) Schintz & Thellung (Schönswetter et al. 2006b) (but only weakly thermophilous (Elvebakk 1989)), and *Rubus chamaemorus* L. (Alsos et al. 2007), in addition to *E. wettsteinii* (Gussarova et al. in prep.).

Puccinellia svalbardensis, including *Puccinellia* sp. from Bockfjorden

Population status

The estimated size of the Bockfjorden population (ca. 1000 individuals) is ten times larger than the maximum size suggested by the 2006 Norwegian Red List (Elven et al. 2006), and the population size has thus been underestimated. However, whether the population has increased in size since Elvebakk and Spjelkavik (1981) discovered it is not known, as neither they nor Tannheiser, who visited the population in 1991 (Svalbard Herbarium database 2006), reported the population size. However, in addition to Bockfjorden, *P. svalbardensis* is known from at least 15 sites in Wijdefjorden (Elvebakk and Nilsen 2002, Eidesen et al. 2011, Elvebakk and Nilsen 2011), where the species is thriving an numbering about 50,000 individuals (Elvebakk and Nilsen 2011). Thus, although goose grazing may have caused the extinction of this Svalbard endemic from Lovénøyene in Kongsfjorden (Eidesen et al. 2011), *P. svalbardensis* is still abundant in Svalbard.

Ecological requirements and expansion potential

The results show that *P. svalbardensis* in Bockfjorden is associated with open, saline, relatively dry, and frost/wind disturbed substrates with very high pH, growing together with *Potentilla pulchella*. Thus, the species has very specific ecological requirements, and a high ecological indicator value, as recognized by Elven and Elvebakk (1996). This is also evident from the other localities the species is known from. At the type-locality in Kongsfjorden it is/was associated with open clayey ground (Rønning 1961b) and Elvebakk and Nilsen (2002, 2011) reported the same ecology as in this study also in Wijdefjorden, where the species is abundant in high-arctic *Potentilla pulchella, Puccinellia angustata*, and *Puccinellia svalbardensis* steppe vegetation. This vegetation type is extremely rare in Svalbard, and is therefore itself of conservation importance (Elvebakk 2005b). Although *P. angustata* and *P.*

svalbardensis have a similar ecology, Elvebakk and Nilsen (2002) noted that *P. svalbardensis* has a narrower ecological niche than *P. angustata*. Further, Launis (in prep.) studied the ecological requirement of the two species at sites where they co-occur, and found that the two species in particular differ in their pH preference and amplitude. While the pH amplitude of *P. angustata* is wide, that of *P. svalbardensis* is narrower and more extreme (A. Launis pers. comm.). Because the ecological niche of *P. svalbardensis* has only been studied where the two species grow together, it is not known whether *P. svalbardensis* is a poor competitor, and that its realized niche is found where substrate pH is too high for other species (including *P. angustata*), or if the species also has a very narrow fundamental niche. Nevertheless, *P. svalbardensis* is probably among the vascular plants in Svalbard with the most specialized ecology.

Based on the species composition, it was not possible to conclude on the local expansion potential of *P. svalbardensis*, as the two ordination methods gave conflicting results. However, because the ecological amplitude of *P. svalbardensis* probably is much narrower than for most other species, species composition may be an inappropriate measure of local expansion potential. Further, that pH was significantly higher in the red list plots and that the PCA of all the environmental variables indicated some extent of difference between the red list and expanding plots indicate that the local expansion potential of *P. svalbardensis* in Bockfjorden might be limited.

A warmer climate will probably not be of great benefit to *P. svalbardensis*, as it is a high arctic species and not highly dependent on temperature (Rønning 1971). On the contrary, climatic change may in the long run have a negative impact on the species, as the projected increase in annual precipitation in the Arctic (Christensen et al. 2007) might represent a threat to the arid high-arctic steppe vegetation which *P. svalbardensis* is part of.

Genetic structure and diversity, and taxonomic implications

Both the morphological inspection of herbarium vouchers and the AFLP results suggest that the taxon *Puccinellia* sp. in Bockfjorden, previously determined as *P. angustata* ssp. *palibinii* (Elvebakk et al. 1994), belongs to *P. svalbardensis*, as Elvebakk and Spjelkavik (1981) first assumed when they discovered the population in 1981. Consequently, the taxon *P. angustata* ssp. *palibinii* is not found in Bockfjorden. Further, *P. svalbardensis* was only slightly genetically separated from *P. angustata* ssp. *angustata*, which indicates that the two species are closely related.

The results further indicate that *P. svalbardensis* exhibits high within-population genetic diversity (Bockfjorden, D=0.219; Ringhorndalen, D=0.278) compared to *P. angustata* (overall population mean D=0.077). This result is certainly surprising, as the restricted geographical distribution of *P. svalbardensis* suggests that it should exhibit less genetic diversity than the far more widespread *P. angustata* (Loveless and Hamrick 1984, Hamrick and Godt 1989). One possible hypothesis is that *P. svalbardensis* is of hybrid origin, with *P. angustata* as one of the parents, as inferred for another Svalbard endemic, *Saxifraga svalbardensis* Øvstedal (Brochmann et al. 1998). However, this will be more thoroughly discussed by Launis (in prep.). Although some of the variation in the data set can be attributed to the high AFLP error rate (9.3 %), it is clear that *P. svalbardensis* is not genetically depleted. The species was assumed autogamous by Brochmann and Steen (1999), but the high within-population genetic diversity and lack of population structure is consistent with allogamy by wind (Hamrick and Godt 1989, Nybom and Bartish 2000, Nybom 2004, Thiel-Egenter et al. 2009). And even if *P. svalbardensis* is autogamous to some extent, inbreeding depression is probably not a concern due to the possibly high level of fixed heterozygosity in this hexaploid species (Brochmann and Steen 1999, Frankham et al. 2010). In conclusion, there does not seem to be any genetic concerns regarding *P. svalbardensis*.

Tofieldia pusilla

Population status

Six previously reported populations of *T. pusilla* in Svalbard were successfully rediscovered during this study. Further, two previously not known populations were discovered, of which one is the largest known in Svalbard (Kapp Nathorst, ca. 1000 individuals). The species numbers ca. 1500 individuals in the eight visited populations, and its rarity has been overrated in the 2006 Norwegian Red List (Elven et al. 2006). Numbers on population sizes from previous years are in general lacking, but one exception is the population in Flatøyrdalen, where a similar number of individuals was observed in 2002 (Elvebakk and Nilsen 2002) (Table A1). The in general high number of AFLP multilocus phenotypes indicates that vegetative reproduction by rhizomes is not the main reproduction mode. Further, while flowering individuals have previously rarely been observed (Rønning 1996, Elven et al. 2006), at least six of the eight populations visited had plants in flower. The levels of genetic diversity moreover indicate that sexual reproduction has occurred, even though ripe seeds

have never been observed (Solstad et al. 2010). Is not clear from the results whether *T. pusilla* is mainly autogamous or allogamous in Svalbard (discussed below), which makes it difficult to infer about inbreeding depression. However, if we assume that *T. pusilla* is mainly allogamous as in northern Canada (Line 2006), inbreeding depression would represent a threat mainly to the populations with the smallest size, due to increased biparental inbreeding in small populations (Ellstrand and Elam 1993).

Ecological requirements and expansion potential

The results did not identify one or a few environmental variables as most important to *T. pusilla*, and showed that the species possesses a moderate to wide ecological amplitude regarding several of them. As *T. pusilla* can be considered a stress-tolerant species (Eckstein and Karlsson 2001), according to Grime (1977), it is indeed expected that the species is tolerant to suboptimal conditions of e.g. moisture and pH. This is also in accordance with the ecological amplitude of *T. pusilla* in other areas, as it seems to prefer mesic-wet, calcareous substrates (Hegi 1939, Lunterbusch and Daniels 2004, Elven 2005, Raynolds et al. 2005), but it is not confined to such conditions (Raup 1969, Aiken et al. 2003). Further, the habitats of *T. pusilla* in Svalbard, well-drained ridges to mesic plains/slopes (on limestone to circum-neutral substrates) and the associated vegetation types, *Dr*yas *octopetala* and *Cassiope tetragona* tundra, are rather common within the bioclimatic subzone C (Elvebakk 1994, 2005b). Thus, *T. pusilla* is probably not lacking potential habitats in Svalbard.

The results suggested that *T. pusilla* exhibits a relatively wide tolerance of, but overall negative association with, cover of vascular plants. A moderate vegetation cover tolerance was reported by Raup (1969), but the negative association with increased vascular plant cover found here might be explained by *T. pusilla* being a poor competitor that prefers somewhat open habitats. Further, the species was often found in frost boils, but not otherwise disturbed habitats. Like other stress-tolerant species, *T. pusilla* is expected to exhibit reduced competitive ability and possess low tolerance for disturbance (Grime 1977). This is due to the species low stature, relatively long-lived, and evergreen mode, which indicate that it responds slowly to changes in the environment. Consequently, low non-frost disturbance tolerance is expected (Raup 1969). The occurrence of *T. pusilla* in frost boils is, however, widely recognized (Raup 1969, Jonasson and Skold 1983, Jonasson 1986, Jonasson and Callaghan 1992, Fredskild 1996, Aiken et al. 2003), and is probably related to its mechanically elastic roots (Jonasson and Callaghan 1992), and that the species is a fibrous rooted perennial, which

generally does well in frost disturbed habitats (Jonasson 1986). Because frost disturbance reduces competition (Jonasson 1986), it may in fact be of great advantage for a poor competitor, like *T. pusilla,* which can take advantage of the reduced competition in frost boils. Further, its otherwise low disturbance tolerance indicates that the species is sensitive to any increase in impact from herbivores and/or humans.

Because substrate temperature could not be compared between the sites, its potential effect on the relative abundance of *T. pusilla* was not demonstrated. A temperature effect was, however, indicated by the association with favorable aspect (south-west). The result that substrate temperature (at 3 cm depth) was higher in the red list plots and that *T. pusilla*, despite similar species composition, was not found in the expanding plots further indicates that temperature may limit the species distribution at a local scale. Thus, the temperature niche of *T. pusilla* may be assumed filled within the borders of the current population distribution areas. Similarly, temperature was shown to be the main limiting factor for local growth of the less warmth demanding *Cassiope tetragona* in Svalbard (Havström et al. 1993). *Tofieldia pusilla* has its northern distribution range limit in Svalbard, and is an indicator for areas with mean July temperature above 6 °C (Karlsen and Elvebakk 2003), which are not found in Svalbard at a regional scale (Elvebakk 1999). Consequently, soil temperature probably is a limiting factor to the distribution of *T. pusilla* in Svalbard, at both local and regional scales.

This further implies that the species has expansion potential if the temperature increases in Svalbard. In a study from subarctic Sweden, temperature alone did seem to have a positive effect on the abundance of *T. pusilla* (Tiiva et al. 2008), and its flowering phenology suggests relatively high responsiveness to climate warming (Molau et al. 2005). On the contrary, two studies from an alpine and a subarctic site found that the species responded negatively if temperature increase was combined with increase in nutrients (Eckstein and Karlsson 2001, Klanderud 2008). The probable cause was increased competition from more responsive species; mainly grasses and high stature forbs (Klanderud 2008). However, as the dominant species in the habitat of *T. pusilla* in Svalbard are mostly low stature dwarf-shrubs (*Cassiope tetragona*, *Dryas octopetala,* and *Salix polaris*) or low stature forbs (*Saxifraga oppositifolia*) with presumably similar responsiveness as *T. pusilla*, an increase in competition will probably be less pronounced in Svalbard than in alpine and subarctic areas. Still, the positive effect of climatic change on the abundance of *T. pusilla* in Svalbard may not be as strong as expected from temperature increase alone.

Genetic structure and diversity

The levels of genetic diversity detected in *T. pusilla* were moderate (overall population mean D=0.133), while the overall number and proportion of polymorphic markers in the species was low (32 and 47.1 %, respectively). A low proportion of polymorphic markers (35.7 %) was also reported in an allozyme study of *T. pusilla* from northern Canada (Line 2006). When including the monomorphic markers in the calculations, as was done by Line (2006), the levels of genetic diversity and average proportion of polymorphic markers within populations (D=0.063 and 15.4 %, respectively) were low and similar to results from northern Canada (D=0.067 and 19.5 %, respectively) (Line 2006). The genetic diversity in *T. pusilla* is notably lower than in the related *Triantha racemosa* (Walter) Small (syn. *Tofieldia racemosa* Walter), which is restricted to North East America (Godt et al. 1997). This is surprising because widespread species, like *T. pusilla*, are expected to exhibit higher levels of genetic diversity than those with a restricted distribution range (Loveless and Hamrick 1984, Hamrick and Godt 1989).

Most Svalbard populations (population mean D=0.123) had levels of genetic diversity similar to that of *T. pusilla* populations outside Svalbard. Genetic depletion was indicated in the newly discovered Ringhorndalen population (D=0.069), and relatively low levels of genetic diversity were also found in Blomstrand (D=0.079) and Ossian Sarsfjellet (D=0.094), which for the two latter could be a result of small population sizes. However, in general, the eight Svalbard populations were not notably genetically depleted compared to other arctic-alpine populations of the species, indicating that their evolutionary potential is not particularly restricted. Further, the genetic diversity estimates for the Svalbard populations of *T. pusilla* was higher than those reported from other thermophilous plants in Svalbard (also based on AFLPs), including *Botrychium lunaria* (autogamous, rarer), *Empetrum nigrum* L. (autogamous, more common), *Rubus chamaemorus* (allogamous, rarer), *Salix herbacea* (allogamous, rarer), *Sibbaldia procumbens* (mixed mater, rarer), *Vaccinium uliginosum* (autogamous, rarer), and, to a lesser extent, *Betula nana* (mixed mater, similar rarity or slightly rarer) (Brochmann and Steen 1999, Engelskjøn et al. 2003, Alsos et al. 2007, Birkeland 2012). In contrast to *T. pusilla*, these species are all notably genetically depleted compared to populations from their respective main source regions (Alsos et al. 2007), indicating that *T. pusilla* is doing comparably better in Svalbard.

The AFLP markers revealed relatively weak population differentiation (35.41 % among population variation), also within Svalbard (23.06 % among-population variation).

Weak population differentiation was also found in northern Canada (Line 2006). These results contrasts with the expectations if *T. pusilla* is mainly autogamous, as suggested by Brochmann and Steen (1999), since autogamy and gravity dispersed seeds are usually associated with strong population differentiation due to restricted gene flow (Loveless and Hamrick 1984, Hamrick and Godt 1996, Thiel-Egenter et al. 2009). Further, these results also contrasts with the expectations if *T. pusilla* is predominantly allogamous (Line 2006), as pollination by small insects is expected to promote population differentiation (Loveless and Hamrick 1984). Thus, although *T. pusilla* is early-flowering (Molau 1993) and presumably relatively long-lived (Lesica and Steele 1996), which could increase the within-population variation component (Molau 1993, Nybom and Bartish 2000, Nybom 2004), it is most likely that additional historical processes have contributed to the structuring of the genetic diversity in this species.

In addition to weak population differentiation, the AFLP markers also revealed poor geographic structuring of the *T. pusilla* populations. Several, but not mutually exclusive, historical processes, operating at different time scales, could contribute to explain the weak genetic structure. First, the evolutionary age of *T. pusilla* may come into play. The family has a crown node age of about 100 million years (Janssen and Bremer 2004), and some old taxa, e.g. ferns, exhibit slow evolutionary rates (Soltis et al. 2002) in combination with poor structuring of genetic diversity (Soltis and Soltis 1990, Birkeland 2012). It is, however, not known whether there is a causal relationship between poor genetic structuring and slow evolution. Second, the overall low levels of polymorphic markers in *T. pusilla* may be a result of a strong pre-Wisconsinan/Weichselian bottleneck event, as also hypothesized by Line (2006). Such a bottleneck could be dated back to the origin of the species or might have occurred when *T. pusilla* emigrated from the diversity centre of the genus in central-Asia. A low number of informative markers, possibly in combination with slow evolution, could then contribute to the lack of genetic structuring. Also in other plant species, which exhibit poor geographic structuring (*Carex rufina* Drejer (Westergaard et al. 2011a) and *Saxifraga rivularis* L. (Westergaard et al. 2010)), few polymorphic AFLP markers were obtained. Third, the poor genetic structure found in North European populations of *T. pusilla* could be due to a strong genetic bottleneck during colonization from a glacial refugia in the Alps, as inferred for other species (e.g. *Arabis alpina* L. (Ehrich et al. 2007), *Ranunculus glacialis* L. (Schönswetter et al. 2003), *Ranunculus pygmaeus* Wahlenb. (Schönswetter et al. 2006b), and *Saxifraga stellaris* L. (Westergaard et al. 2008)). Similarly, the poor genetic structuring found

in *T. pusilla* in northern Canada was hypothesized to be partly due to rapid colonization from a few glacial refugia (Line 2006). Last, poor genetic structuring may be an indication of gene flow. Long-distance dispersal after the last glaciation has happened frequently in many arctic plants, even in species without any long-distance dispersal adaptations (Brochmann et al. 2003, Alsos et al. 2007), and is therefore likely to have occurred also in *T. pusilla*. In conclusion, a pre-Wisconsinan/Weichselian bottleneck event could have caused the overall low levels of variable markers in *T. pusilla*, which combined with slow evolution may have counteracted genetic differentiation. The poor genetic structuring could further have been maintained by survival in a few glacial refugia, followed by rapid expansion, and some degree of post-glacial gene flow through long-distance dispersal.

The AFLP results indicated a differentiation between the western (Greenland) and the eastern *T. pusilla* populations (Svalbard, Norway, Iceland, and Alps) (49.00 % among-group variation), which may represent two different refugia of the species during the last glaciation. Due to the poor genetic structuring, the most likely source of the Svalbard populations within the eastern group (Norway, Iceland, and Alps) can not be identified. However, in light of the historical scenario outlined above, the Svalbard populations may have been isolated for a longer time than the partitioning of genetic diversity indicates. Although a more recent colonization of Svalbard can not be excluded, an early or mid Holocene introduction of the species in Svalbard (e.g. 9500-6000 years ago) is possible, like inferred from other thermophilous species in Svalbard (e.g. *B. nana*, *Campanula rotundifolia* L., and *V. uliginosum* (Alsos et al. 2002), *Euphrasia wettsteinii* Gussarova (Gussarova et al. in prep.), *Salix herbacea* (Alsos et al. 2007)). Support for early-mid Holocene history of *T. pusilla* in Svalbard is found in the relatively high number of geographically disjunct populations, and the similar genetic diversity and rarity in Svalbard compared to the other eastern populations. With a early-mid Holocene introduction of *T. pusilla* to Svalbard, local adaptations may have taken place at this northernmost range limit, which were not captured by the selectively neutral AFLP markers, as they may change at a slower rate than selectively adaptive ones (McKay and Latta 2002, Leinonen et al. 2008).

Implications for conservation

Although part of the Kingdom of Norway, Svalbard is geographically well separated from mainland Norway. Even if many species of vascular plants are shared between the two areas, the history of the Svalbard populations are not necessarily shared with those from mainland Norway (Alsos et al. 2007), as exemplified by some of the species studied here. It is therefore reasonable to treat Svalbard as a separate conservation area, as done in the Norwegian Red List (Kålås et al. 2010). Even for species which have most likely colonized Svalbard from mainland Norway, the Svalbard populations may have been isolated for thousands of years, become genetically distinct, and local adaptations have likely taken place. Further, even if the genetic differentiation inferred from selectively neutral molecular markers like AFLPs, is weak, local adaptations may still have taken place (McKay and Latta 2002, Leinonen et al. 2008).

***Carex capillaris*.** Based on the results from this study, *C. capillaris* was downgraded two categories from the 2006 (Elven et al. 2006) to the 2010 (Solstad et al. 2010) Norwegian Red List: from critically endangered (on the basis of the assumed restricted extent of occurrence and small population size, criteria B1(ii)b(iii)); D1) to vulnerable (on the basis of the restricted number of locations, criterion D2)). Thus, although the population is of less concern than previously assumed, *C. capillaris* is still considered threatened in Svalbard, and therefore requires conservation attention. Further, the genetic distinctiveness of the population, although slight, strengthens its conservation value.

More important is, however, that *C. capillaris* is part of an extraordinary flora in Bockfjorden, including several other thermophilous red listed vascular plants (see Alsos et al. 2011, Birkeland 2012). This geothermal area additionally holds species of other organism groups, including fungi (Elvebakk and Spjelkavik 1981), bryophytes (Frisvoll 1978), and algae (Langangen 1979, 2000), which are not found elsewhere in Svalbard. The invertebrate fauna is not yet studied (S. Coulson pers. comm.), but we might expected it to contain such rare elements as well. The area is also of high geological value, and Trollkjeldene form, together with two other spring collections, the world's northernmost thermal springs (Salvigsen and Hogvard 1998, Banks et al. 1999). Further, the rare botanical element and the travertine terraces of the springs are very vulnerable to trampling, and human traffic should therefore be restricted. To elaborate on the statement by Langangen (2000): 'Growing tourism in Svalbard threatens to the springs; more active protection must be evaluated.', I suggest that

the area around the thermal springs Trollkjeldene in Bockfjorden should be given status as a protected biotope/geotope (Svalbard Environmental Protection Act 2001), and thereby get more active protection than it has as part of the North West Spitsbergen National Park.

***Comastoma tenellum*.** Based on the results from this study, *C. tenellum* was downgraded one category from the 2006 (Elven et al. 2006) to the 2010 (Solstad et al. 2010) Norwegian Red List: from critically endangered (on the basis of the assumed restricted extent of occurrence and small population size, criteria B1b(iii)c(iv))); D1) to endangered (on the basis of the few and fluctuating populations, criterion C2b). Thus, the species is still threatened in Svalbard. The clear genetic distinctiveness of the three Svalbard populations and their possibly early-middle Holocene introduction to Svalbard increase their conservation value. Furthermore, although the three Svalbard populations are genetically similar, conservation of more than one population is important, because of the possibility for strong bottlenecks, and even local extinctions, due to the fluctuating population sizes. However, this species can be expected to respond rapidly to a warmer climate in Svalbard, and may become more common there in the future than it is today.

***Puccinellia svalbardensis*.** The case of the *Puccinellia* sp. taxon in Bockfjorden exemplifies how resolution of taxonomic uncertainties is important to conservation. As the taxon belongs to *P. svalbardensis*, the Bockfjorden population should be evaluated together with the other known populations of the species in the next revision of the Norwegian Red List. Despite that *P. angustata* ssp. *palibinii* is not found in Bockfjorden, it should probably not be taken out of the Red List, as there have been identified other Svalbard specimens which probably belong to the subspecies (Elven et al. 2011). Although there are no immediate threats to *P. svalbardensis*, and no special conservation management is required at the moment, the species is of Norwegian responsibility because of its endemic status (Solstad et al. 2010), and should therefore be monitored.

***Tofieldia pusilla*.** Because of the relatively high number of individuals and populations, and lack of threats, *T. pusilla* does not meet the criteria for red listing and was therefore taken out of the 2010 Norwegian Red List (i.e. considered of least concern), while it was listed as near threatened in 2006 (on basis of the assumed small population sizes, criterion D1) (Elven et al. 2006). Consequently, the species is not of conservation priority. However, *T. pusilla* could be used as an indicator on how climate warming may impact the local and regional distribution of thermophilous species in Svalbard.

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Appendix

Figures

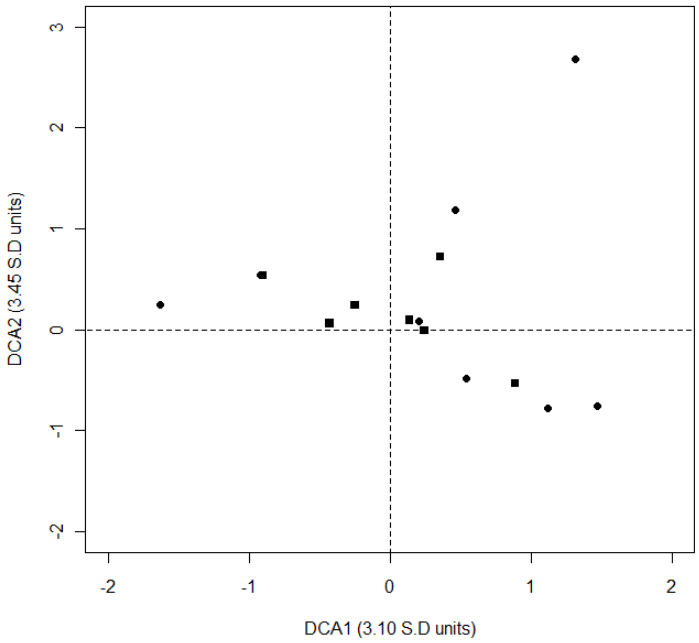

Figure A1 DCA (detrended correspondence analysis) of the species composition in 20 *Puccinellia* sp. plots from Bockfjorden to evaluate its local expansion potential (i.e. *Puccinellia* sp. had no impact on the ordination pattern). Symbols represent plot types: circle, expanding plot; square, red list plot.

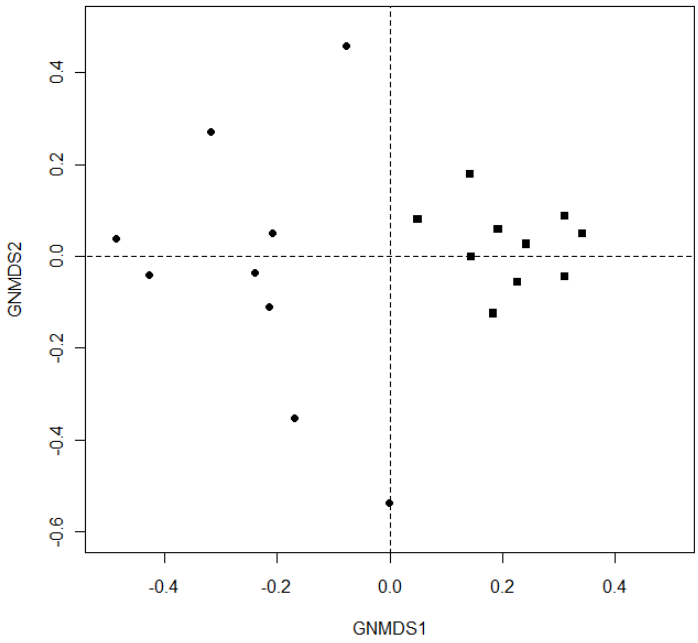

Figure A2 GNMDS (global non-metric multi-dimensional scaling) of the species composition in 20 *Puccinellia* sp. plots from Bockfjorden to evaluate its local expansion potential (i.e. *Puccinellia* sp. had no impact on the ordination pattern). Symbols represent plot types: circle, expanding plot; square, red list plot.

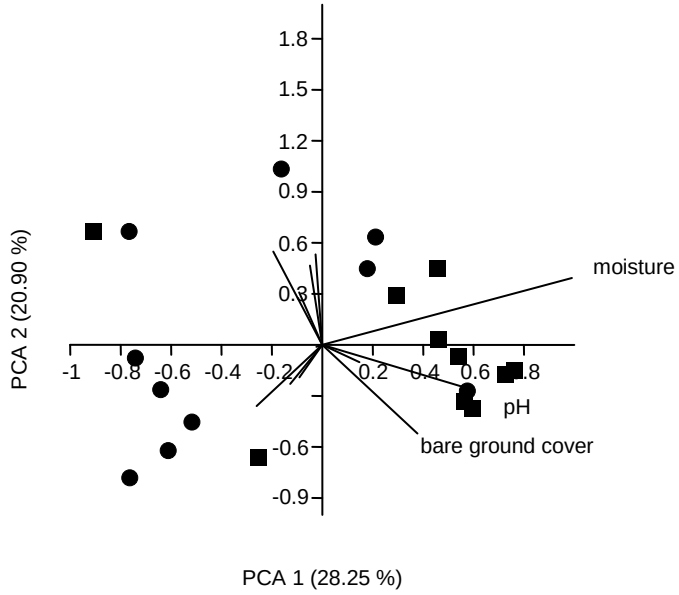

Figure A3 PCA (principal component analysis) of the environmental variables in 20 *Puccinellia* sp. plots from Bockfjorden to describe its local expansion potential. Symbols represent plot types: circle, expanding plot; square, red list plot.

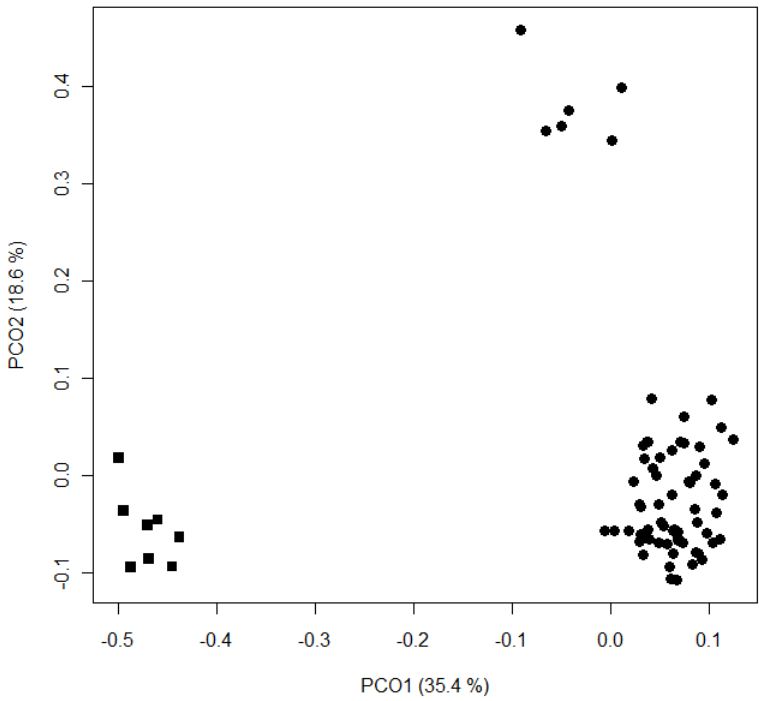

Figure A4 PCO (principal coordinates analysis) of AFLP multilocus phenotypes based on dice distance of 68 *Carex capillaris* (circle) and eight *Carex krausei* (square) individuals.

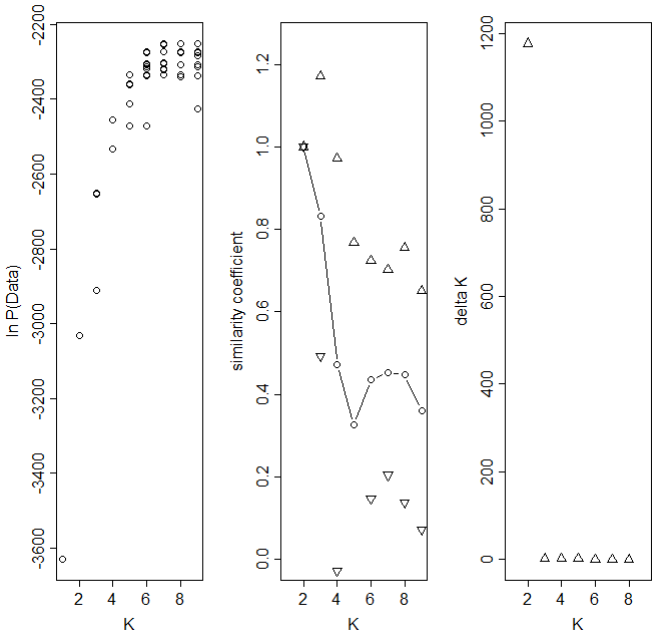

Figure A5 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Carex capillaris*, using the no admixture model.

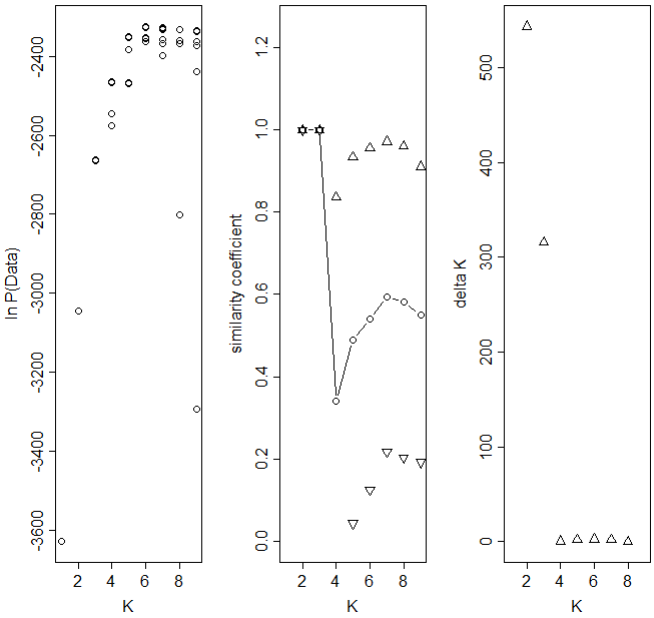

Figure A6 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Carex capillaris*, using the admixture model.

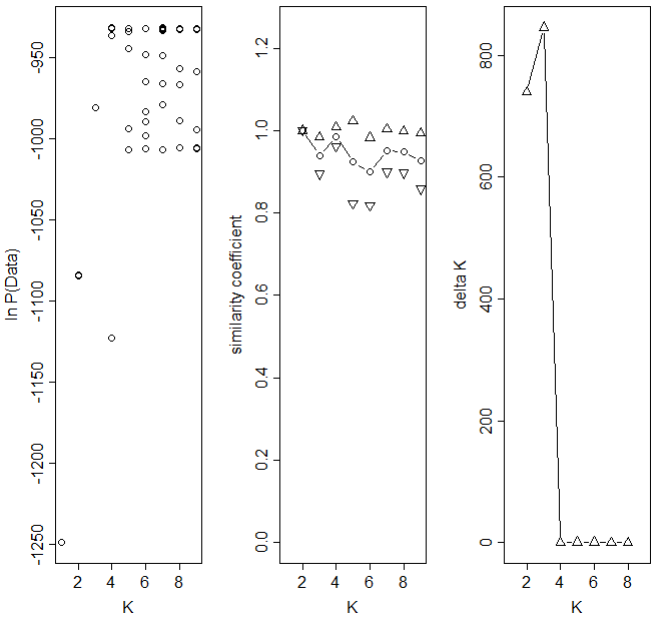

Figure A7 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Carex capillaris* individuals of the ssp. *fuscidula* group, using the no admixture model.

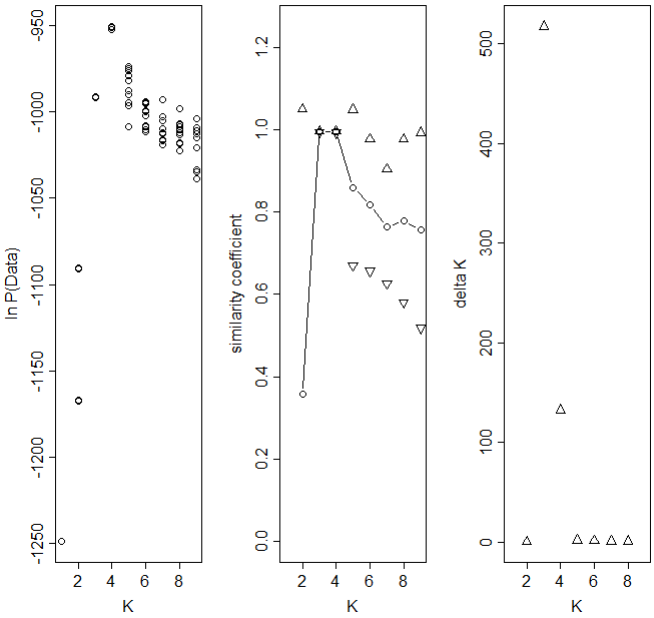

Figure A8 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Carex capillaris* individuals of the ssp. *fuscidula* group, using the admixture model.

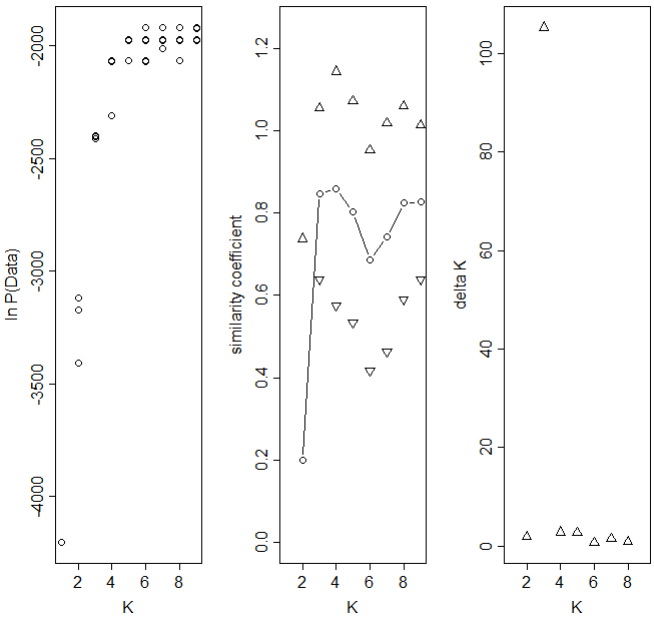

Figure A9 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Comastoma tenellum*, using the no admixture model.

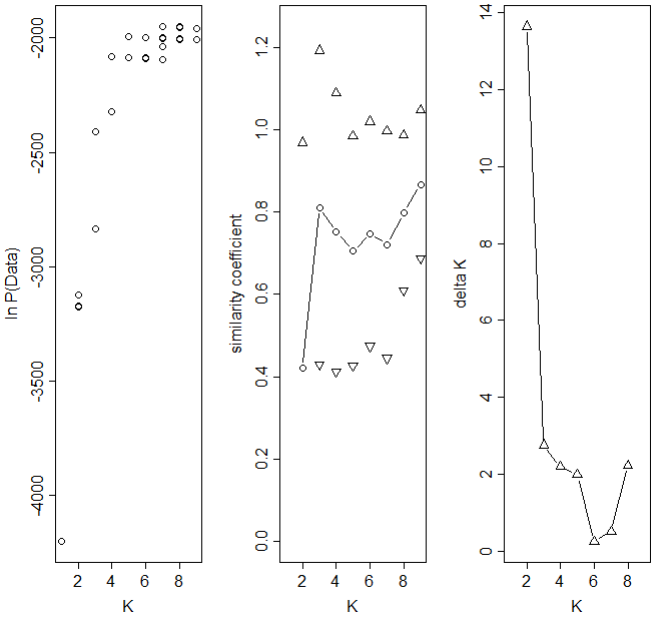

Figure A10 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Comastoma tenellum*, using the admixture model.

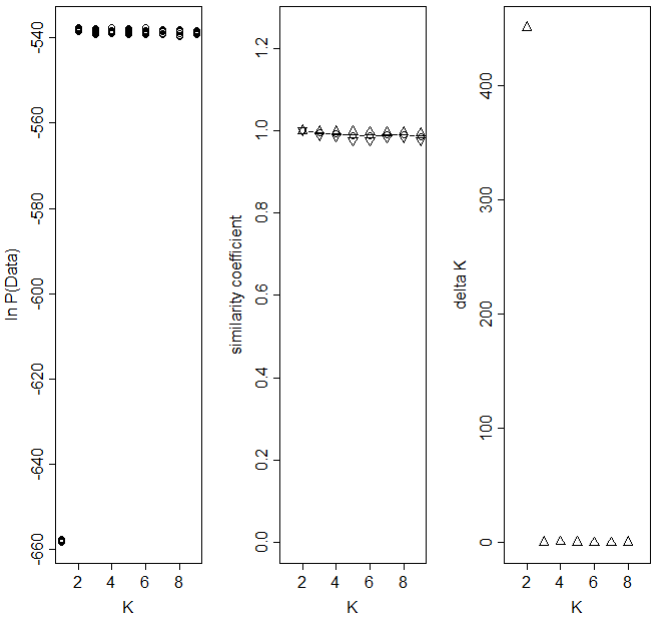

Figure A11 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Comastoma tenellum* individuals of the Svalbard/Polar Ural group, using the no admixture model.

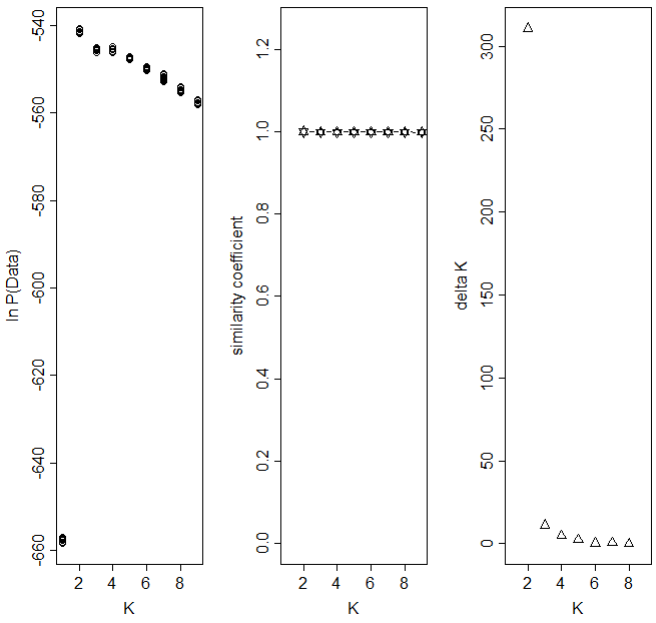

Figure A12 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Comastoma tenellum* individuals of the Svalbard/Polar Ural group, using the admixture model.

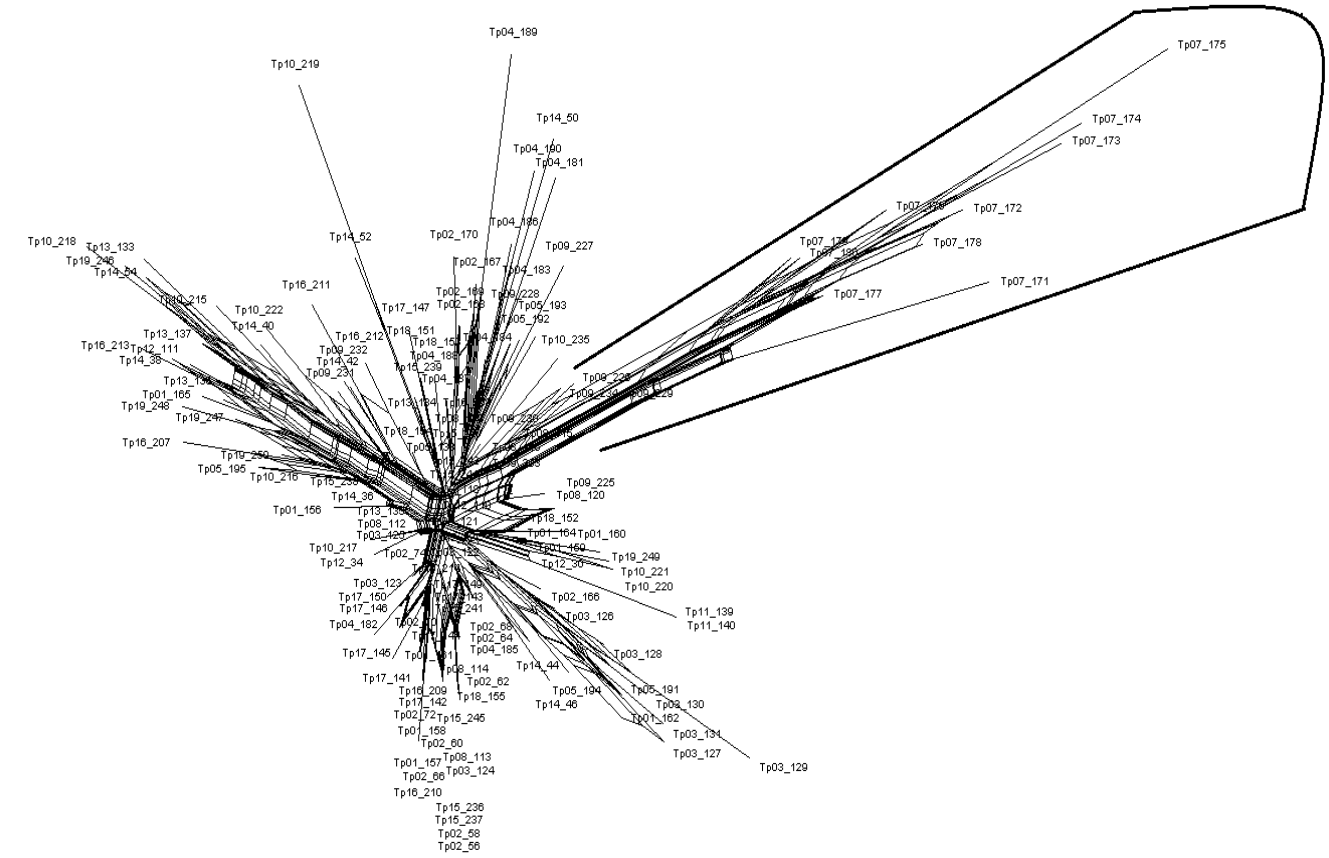

Figure A13 Neighbor-net of AFLP multilocus phenotypes based on dice similarity of 145 *Tofieldia pusilla* individuals. Population ID follows Table 1. The branch of the Greenland individuals is indicated on the figure.

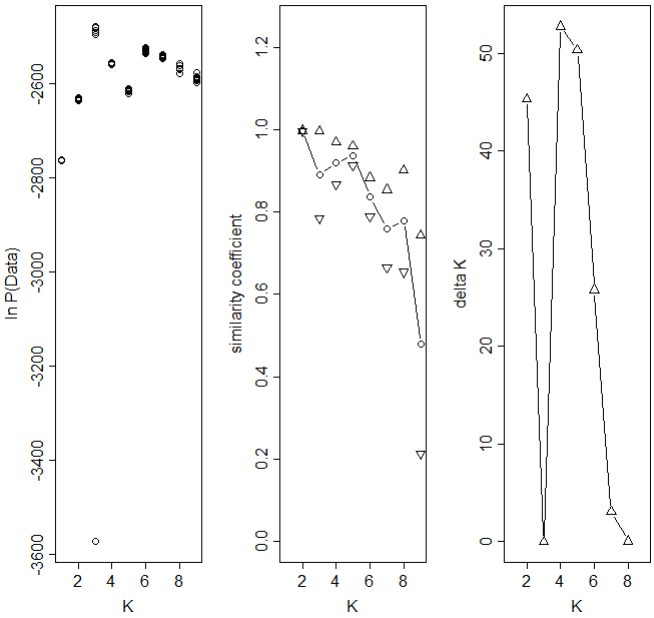

Figure A14 number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Tofieldia pusilla*, using the no admixture model.

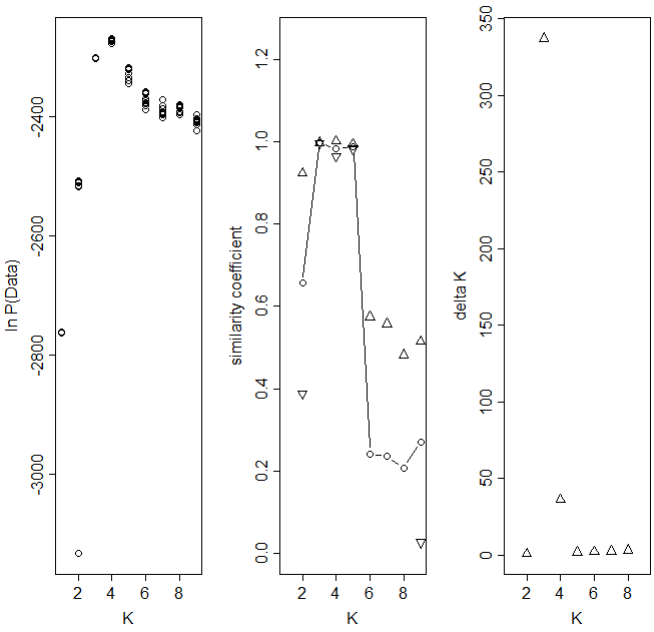

Figure A15 K number of groups from 1-9, based on ten replicate runs for each K, plotted against log probability of the data [lnP(Data)], similarity coefficient, and deltaK obtained by Structure analyses of AFLP multilocus phenotypes in *Tofieldia pusilla*, using the admixture model.

Tables

Table A1 All known localities of the focus species in Svalbard. Due to imprecise UTM coordinates and descriptions of localities, only one locality is given for spatially close populations of *Tofieldia pusilla*. The UTM zone is 33X at all localities. Source: this study and Svalbard Herbarium database (2006).

Species	Locality	UTM N	UTM E	Last visited	Visitors	Comments
Carex capillaris						
	Haakon VII Land, Bockfjorden, Trollkjeldene	8813474	467946	2009	This study	
Comastoma tenellum						
	Haakon VII Land, Kongsfjorden, Ossian Sarsfjellet	8763178	445308	2009	This study	
	Ny-Fries Land, Wijdefjorden, Flatøyrdalen	8802463	521882	2010	This study	Probably same as Elvebakk and Nilsen (2002)/ Neilson
	Ny-Fries Land, Wijdefjorden, Flatøyrdalen	8802050	520650	2002	Elvebakk and Nilsen (2002)	Population size: six individuals.
	Ny-Fries Land, Flatøyrdalen	8802000	524000	1963	Neilson	
	Ny-Fries Land, Wijdefjorden,	8807676	523307	2010	This study	
Tofieldia pusilla						
	Dickson Land, Isfjorden, Idodalen	8722500	509500	1997	Elven and Fjellheim	
	Dickson Land, Isfjorden, Kapp Nathorst	8744574	509881	2009	This study	
	Dickson Land, Isfjorden, Kapp Wijk	8725140	507303	2009	This study	
	Dickson Land, Isfjorden, Fiskeneset	8751500	508500	1973	Brattbakk and Frisvoll	
	Dickson Land, Isfjorden, Blomesletta	8727478	496510	2009	This study	
	Dickson Land, Isfjorden, Mimerdalen	8732500	528500	1939	Høeg	
	Haakon VII Land, Kongsfjorden, Blomstrand	8768534	439822	2009	This study	
	Haakon VII Land, Kongsfjorden, Ny-London	8767500	437500	1933	Sæther	
	Haakon VII Land, Bockfjorden, Trollkjeldene	8813884	467918	2009	This study	
	Haakon VII Land, Kongsfjorden, Ossian Sarsfjellet	8764224	445153	2009	This study	
	James I Land, Isfjorden, Kapp Smith	8731500	503500	1936	Dahl	
	Ny-Fries Land, Wijdefjorden, Flatøyrdalen	8802208	521726	2010	This study	Probably same as one of the two colonies observed by Elvebakk and Nilsen (2002), each with ten individuals.
	Ny-Fries Land, Wijdefjorden, Flatøyrdalen	8802050	520650	2002	Elvebakk and Nilsen (2002)	
	Ny-Fries Land, Wijdefjorden, Ringhorndalen	8807442	523294	2010	This study	
Puccinellia sp.						
	Haakon VII Land, Bockfjorden, Trollkjeldene	8813508	467981	2010	Eidesen et al. (2011)	

Table A2 Determination of *Puccinellia* individuals included in this study according to: field determination, re-investigation of herbarium vouchers, and AFLP phenotypes. Population ID used in this study (Table 1) and original population ID (from P. Bronken Eidesen) are included. The focus population Psp01 from Bockfjorden is marked in bold.

Pop. ID this study	Original pop. ID	n	Field	Herbarium vouchers	AFLP
Pa02	PEA_2	5	*P. vahliana*	*P. angustata*	*P. angustata*
Pa03	PEA_3	6	*P. svalbardensis*	*P. angustata*	*P. angustata*
Pa05	PEA_5	10	*Puccinellia* sp.	*P. angustata*	*P. angustata*
Pa06	PEA_6	9	*Puccinellia* sp.	*P. angustata*	*P. angustata*
Pa07/Ps07	PEA_7A	3	*P. svalbardensis*	*P. angustata* (n=1) *P. svalbardensis* (n=2)	*P. angustata* (n=1) *P. svalbardensis* (n=2)
Pa08/Ps08	PEA_8/ Pea-8	7	*P. svalbardensis*	*P. angustata* (n=2) *P. svalbardensis* (n=5)	*P. angustata* (n=2) *P. svalbardensis* (n=5)
Pa09	PEA_9	7	*P. angustata*	*P. angustata*	*P. angustata*
Pa10	P10	7	*P. vahliana*	*P. angustata*	*P. angustata*
Pa11	PEA_11	5	*P. angustata* ssp. *palibinii*	*P. angustata*	*P. angustata*
Pa14	PEA_14	7	*P. angustata*/*P. svalbardensis*	*P. angustata*	*P. angustata*
Pa15	PEA_15	1	*P. svalbardensis*	*P. angustata*	*P. angustata*
Psp01	**Pp01**	**10**	***P. angustata* ssp. *palibinii***	***P. svalbardensis***	***P. svalbardensis***
Pv01	PEA_4	9	*P. vahliana*	*P. vahliana*	*P. vahliana*

Table A3 Correlations between the environmental variables and DCA axes (Kendall's τ) are given for the Bockfjorden and *Tofieldia pusilla* data sets, respectively. Significant correlations are marked in bold.

Variable	Abbreviations	Bockfjorden data set (n=59)		*Tofieldia pusilla* dataset (n=67)	
		DCA 1	DCA 2	DCA 1	DCA 2
Temperature 3 cm depth [°C]	temp3	0.1320	**-0.4020*** **	NA	NA
Temperature 10 cm depth [°C]	temp10	-0.0317	**-0.5054*** **	NA	NA
pH		**0.5804*** **	-0.0261	**0.2944** **	**-0.2833** **
Moisture	moist	-1.143	**-0.3938*** **	**0.3739*** **	**-0.2149***
Slope angle [°]	slope	-0.2936	**0.2276***	-0.0607	**0.5138*** **
Aspect		0.0419	0.0296	-0.0548	**0.2976** **
Vascular plants [% cover]	vasccov	**-0.4679*** **	0.0445	**-0.1826***	-0.0868
Bryophytes [% cover]	brycov	**-0.6185*** **	0.0201	0.1673	-**0.3728*** **
Lichens [% cover]	lichcov	-0.0830	**0.2639***	**-0.1812***	**0.2593 ** **
Cryptogamic crust [% cover]	crypcru	0.0747	0.1677	0.1295	0.0382
Stones [% cover]		**0.3738*** **	-0.0630	**-0.2051***	**0.4917 *** **
Bare ground [% cover]	bagrcov	**0.5111*** **	-0.0970	-0.1442	**0.4933*** **

* p<0.05 **p<0.01 *** p<0.001

Table A4 Correlations among the environmental variables (Kendall's τ) are given for the Bockfjorden (upper right part of the table) and *Tofieldia pusilla* (lower left part of the table) data sets, respectively. Significant relationships are marked in bold. Environmental variables are abbreviated according toTable A3.

Variable	Temp 3	Temp 10	pH	Moist	Slope	Aspect	Vasccov	Bryocov	Lichcov	Crypcru	Stones	Baregrcov
Temp 3	-	**0.6996*** **	0.0505	**0.3546*** **	-0.2531**	-0.0501	-0.0869	-0.0336	-0.0448	-0.0565	**0.2447***	-0.0401
Temp 10	-	-	-0.0367	**0.4300*** **	-0.1565	-0.1168	-0.0681	0.1130	-0.0173	-0.0632	0.1800	-0.0875
pH	-	-	-	-0.0227	**-0.2451** **	0.0573	**-0.4591*** **	**-0.4739*** **	-0.0631	0.1386	**0.3657*** **	**0.4978*** **
Moist	-	-	**0.4592*** **	-	**-0.2210***	-0.0917	0.0086	0.2847	-0.0258	0.0343	0.0192	**-0.3500** **
Slope	-	-	**-0.5118*** **	**-0.3313** **	-	0.1044	**0.2402***	**0.2634** **	0.1551	-0.1169	-0.1953	**-0.2210***
Aspect	-	-	**-0.3194** **	**-0.2386***	**0.3232*** **	-	0.1432	-0.1387	-0.0104	0.1129	0.0205	-0.0636
Vasccov	-	-	0.1494	-0.0932	**-0.1822***	-0.2772	-	0.3108**	-0.0611	-0.1637	**-0.4767*** **	**-0.5080*** **
Bryocov	-	-	**0.2816** **	0.1285	-0.3501	**-0.4107*** **	0.1377	-	**0.2466***	-0.1193	**-0.3287** **	**-0.4858*** **
Lichcov	-	-	-0.1606	**-0.3342** **	**0.2336***	-0.0590	0.1049	-0.2251	-	-0.0246	-0.0837	-0.1002
Crypcru	-	-	-0.0873	0.1144	0.1066	**0.3272*** **	**-0.5907*** **	-0.1372	**-0.1972***	-	**0.2153***	-0.1706
Stones	-	-	**-0.5981*** **	**-0.4264*** **	**0.5692*** **	**0.5287*** **	**-0.3028** **	**-0.4973*** **	**0.2986** **	**0.2862** **	-	**-0.4858*** **
Baregrcov	-	-	**-0.5026*** **	**-0.3571** **	**0.4990*** **	**0.4393*** **	**-0.2813** **	**-0.4318*** **	**0.2362***	0.1423	**0.7695*** **	-

*p<0.05 **p<0.01 *** p<0.001

Table A5 Wilcoxon signed rank test (for paired observations) to test for differences in the environmental variables in red list (red) vs. expanding (exp) plots of the focus species. n is the total number of plots included in the test. Population/site ID follows Table 1.

	Carex capillaris Bockfjorden Cc01 (n=10)		*Puccinellia* sp. Bockfjorden Psp01 (n=22)		*Tofieldia pusilla* All sites Tp01-03 (n=34)		*Tofieldia pusilla* Blomesletta Tp01 (n=12)		*Tofieldia pusilla* Blomstrand Tp02 (n=10)		*Tofieldia pusilla* Kapp Wijk Tp03 (n=12)	
Variable	p-value	Direction of difference	p-value	Direction of difference	p-value	Direction of difference	p-value	Direction of difference	p-value	Direction of difference	p-value	Direction of difference
Temperature 3 cm depth [°C]	0.223		0.888		**0.000**	red>exp	**0.031**	red>exp	0.188		0.063	
Temperature 10 cm depth [°C]	0.188		0.160		0.563		NA		0.188		0.400	
pH	0.438		**0.009**	red>exp	0.282		0.414		0.586		0.181	
Moisture	1.000		0.072		1.000		1.000		1.000		1.000	
Slope angle [°]	0.789		1.000		0.950		0.916		0.850		1.000	
Aspect	0.583		0.100		1.000		1.000		1.000		1.000	
Vascular plants [% cover]	0.062		0.636		0.798		0.856		0.125		0.171	
Bryophytes [% cover]	0.713		0.204		0.126		0.710		0.174		1.000	
Lichens [% cover]	-		-		0.233		-		0.423		0.590	
Cryptogamic crust [% cover]	0.684		0.075		0.864		0.710		0.125		0.172	
Stones [% cover]	0.063		0.397		0.095		-		0.098		-	
Bare ground [% cover]	-		0.052		0.177		-		0.201		1.000	

Table A6 Wilcoxon rank sum test (for unpaired observations) to test for differences in the environmental variables in red list (red) vs. reference (ref) plots from three *Tofieldia pusilla* localities. n is the total number of plots included in the test. Population/site ID follows Table 1.

Variable	Blomstrand Tp02 (n=10)		Kapp Nathorst Tp04 (n=8)		Kapp Wijk Tp03 (n=12)	
	p-value	Direction of difference	p-value	Direction of difference	p-value	Direction of difference
Temperature 3 cm depth [°C]	**0.032**	red>ref	0.400		0.297	
Temperature 10 cm depth [°C]	0.056		0.825		**0.006**	red<ref
pH	0.805		NA		0.673	
Moisture	1.000		1.000		1.000	
Slope angle [°C]	0.594		0.505		0.359	
Aspect	0.439		NA		0.267	
Vascular plants [% cover]	**0.036**	red<ref	0.825		0.090	
Bryophytes [% cover]	0.334		1.000		**0.016**	red<ref
Lichens [% cover]	0.751		0.814		0.458	
Cryptogamic crust [% cover]	0.344		0.507		0.595	
Stones [% cover]	0.289		-		**-**	
Bare ground [% cover]	0.340		-		0.400	

Table A7 Assignment of *Carex capillaris* individuals from Svalbard to five geographic source regions (Alps; Iceland; Northern Norway; Southern Norway; Greenland), using a minimal log likelihood difference MLD of 0-2.

MLD threshold	Source population	Bockfjorden Cc01 (n=10)
2	Alps	0
	Iceland	0
	N Norway	3
	S Norway	0
	Greenland	0
	None	7
1	Alps	0
	Iceland	0
	N Norway	5
	S Norway	0
	Greenland	0
	None	5
0	Alps	0
	Iceland	0
	N Norway	10
	S Norway	0
	Greenland	0
	None	0

Table A8 Assignment of *Carex capillaris* individuals from Svalbard to two ssp. *fuscidula* genetic subgroups (Laugarvatn (Iceland); Northern Norway, Grindavik (Iceland)), using a minimal log likelihood difference MLD=2.

MLD threshold	Source population	Bockfjorden Cc01 (n=10)
2	Laugarvatn (Iceland)	0
	N Norway /Grindavik (Iceland)	10
	None	0

Table A9 Assignment of *Comastoma tenellum* individuals from Svalbard to four groups (Alaska; Alps; Alps, Norway; Polar Ural), using a minimal log likelihood difference MLD=2.

MLD threshold	Source population	Flatøyrdalen Ct03 (n=8)	Ossian Sarsfjellet Ct01 (n=7)	Ringhorndalen Ct04 (n=10)
2	Alaska	0	0	0
	Alps	0	0	0
	Alps/Norw	0	0	0
	Polar Ural	8	7	10
	None	0	0	0

Table A10 Percentage allocation of the *Tofieldia pusilla* populations to the groups revealed by the Baps and Structure (no admixture model) analyses, respectively.

Population	Baps							Structure			
	k=1	k=2	k=3	k=4	k=5	k=6	k=7	k=1	k=2	k=3	k=4
Dickson Land, Blomesletta			56	11			33		30	36	34
Dickson Land, Kapp Nathorst	20					60	20			57	43
Dickson Land, Kapp Wijk	40						60			51	49
Haakon VII Land, Blomstrand	73					27				44	56
Haakon VII Land, Bockfjorden	17		17			33	33		17	47	36
Haakon VII Land, Ossian Sarsfjellet	40		20				40		18	39	43
Ny-Fries Land, Flatøyrdalen	38		38	12			12		38	29	33
Ny-Fries Land, Ringhorndalen	89						11			44	56
Hedmark, Folldal	100									42	57
Hordaland, Finse			33	33		17	17		53	26	21
Troms, Nordreisa	60			20			20		22	34	43
Troms, Tromsø	11		44	22		11	11		46	31	22
Angmagssalik, Tasiilaq		20			80			100			
Suðurland, Geysir	20		30			30	20		16	46	38
Suðurland, Laugarvatn	100								2	40	58
Vestfirðir, Önundarfjördur			40	40			20		47	26	27
Salzburg, Weisseck							100			44	56
Berchtesgadener, Watzmann	20			80					60	17	23

Table A11 Assignment of *Tofieldia pusilla* individuals from Svalbard to four geographic regions (Alps; Iceland; Norway; Greenland), using a minimal log likelihood difference MLD of 0-2.

MLD threshold	Source population	Blomesletta Tp01 (n=9)	Blomstrand Tp02 (n=15)	Bockfjorden Tp06 (n=6)	Flatøyrdalen Tp16 (n=8)	Kapp Nathorst Tp04 (n=10)	Kapp Wijk Tp03 (n=10)	Ossian Sarsfjellet Tp18 (n=5)	Ringhorndalen Tp17(n=9)
2	Alps	0	0	0	0	0	0	0	0
	Iceland	0	0	0	0	0	0	0	0
	Norway	0	0	0	0	0	0	0	0
	Greenland	0	0	0	0	0	0	0	0
	None	9	15	6	8	10	10	5	9
1	Alps	0	0	0	0	0	0	0	0
	Iceland	0	0	0	0	0	0	0	0
	Norway	1	0	1	1	0	0	0	0
	Greenland	0	0	0	0	0	0	0	0
	None	8	15	5	7	10	10	5	9
0	Alps	1	0	1	0	4	3	0	0
	Iceland	7	7	1	3	2	6	3	4
	Norway	1	8	4	5	4	1	2	5
	Greenland	0	0	0	0	0	0	0	0
	None	0	0	0	0	0	0	0	0

Table A12 Assignment of *Tofieldia pusilla* individuals from Svalbard to two Neighbor-net/PCO groups (Greenland; 'the rest'), using a minimal log likelihood difference MLD of 1-2.

MLD threshold	Source population	Blomesletta Tp01 (n=9)	Blomstrand Tp02 (n=15)	Bockfjorden Tp06 (n=6)	Flatøyrdalen Tp16 (n=8)	Kapp Nathorst Tp04 (n=10)	Kapp Wijk Tp03 (n=10)	Ossian Sarsfjellet Tp18 (n=5)	Ringhorndalen Tp17(n=9)
2	Greenland	0	0	0	0	0	0	0	0
	'The rest'	9	15	6	8	9	9	5	9
	None	0	0	0	0	1	1	0	0
1	Greenland	0	0	0	0	0	0	0	0
	'The rest'	9	15	6	8	10	10	5	9
	None	0	0	0	0	0	0	0	0