

Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities

In ecology, expert knowledge on habitat characteristics is often used to define sampling units such as study sites. Ecologists are especially prone to such approaches when prior sampling frames are not accessible. Here we ask to what extent can different approaches to the definition of sampling units influence the conclusions that are drawn from an ecological study? We do this by comparing a formal versus a subjective definition of sampling units within a study design which is based on well-articulated objectives and proper methodology. Both approaches are applied to tundra plant communities in mesic and snowbed habitats. For the formal approach, sampling units were first defined for each habitat in concave terrain of suitable slope using GIS. In the field, these units were only accepted as the targeted habitats if additional criteria for vegetation cover were fulfilled. For the subjective approach, sampling units were defined visually in the field, based on typical plant communities of mesic and snowbed habitats. For each approach, we collected information about plant community characteristics within a total of 11 mesic and seven snowbed units distributed between two herding districts of contrasting reindeer density. Results from the two approaches differed significantly in several plant community characteristics in both mesic and snowbed habitats. Furthermore, differences between the two approaches were not consistent because their magnitude and direction differed both between the two habitats and the two reindeer herding districts. Consequently, we could draw different conclusions on how plant diversity and relative abundance of functional groups are differentiated between the two habitats depending on the approach used. We therefore challenge ecologists to formalize the expert knowledge applied to define sampling units through a set of well-articulated rules, rather than applying it subjectively. We see this as instrumental for progress in ecology as only rules based on expert knowledge are transparent and lead to results reproducible by other ecologists.

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15 Introduction



16 Sampling in ecology can be challenging. Ecological systems are characterized by a myriad of
17 complexity (Loehle, 2004) to which there is a paucity of information (Carpenter, 2002). Hence,
18 ecological sampling is often accompanied by unknown characteristics that may unintentionally
19 cause estimates to be dependent on the sampling designs, even to the extent that they “beget
20 conclusions”, as was shown for the impact of the Exxon Valdez oil spill (Peterson et al., 2001;
21 Peterson et al., 2002). The basis for achieving unbiased estimates are study- or sampling designs
22 that include well-articulated objectives along with proper methodology (Olsen et al., 1999;
23 Yoccoz et al., 2001; Albert et al., 2010). In addition, sampling designs need to be transparent,
24 enabling others to repeat the study. Accordingly, ecologists have been encouraged to use formal
25 approaches (Legendre et al., 2002; Edwards et al. 2005, Edwards et al., 2006; Albert et al., 2010).
26 However, whilst sources of bias and a call for formal rules in sampling designs have received
27 attention, the seemingly simple task of defining a sampling unit such as study sites, also merits
28 thorough consideration, especially in community ecology. Indeed, the definition of sampling
29 units is often a task which demands expert knowledge; however, sampling units are often not
30 formally defined before data collection is initiated (Whittaker et al., 1973; Kenkel et al., 1989;
31 Franklin et al., 2002; Loehle, 2004).

32 In situations where sampling units are not clearly defined, the availability of relevant
33 sampling units is not known before entering the field, i.e. there is no well-defined sampling frame
34 and in its vacancy, expert knowledge is applied in order to guide sampling to ecological units that
35 are decided to be suitable in the field. This situation is particularly common in ecological studies
36 where the spatial resolution of geographical and environmental data is at a scale too coarse to
37 reflect the spatial extent or grain of the sampling units of interest (Roleček et al., 2007). Only a
38 few formalized approaches exist to using expert knowledge for defining sampling units under

such circumstances (e.g. Ravolainen et al., 2010). More frequently, definition of sampling units is subjective and solely based on expert opinion (McBride & Burgman, 2012). In principle, the selection of any subjectively defined sampling unit may not be sufficiently articulated as to enable other researchers to repeat the study, or to allow generalizations of results to a specific target population (in a statistical sense) (Olsen et al., 1999; Schreuder, Gregoire & Weyer, 2001). Moreover, in phyto-sociological studies it has been documented that individual preferences in selecting sampling units that were defined subjectively can lead to biased estimates (Chytrý, 2001; Botta-Dukát et al., 2007; Hédli, 2007). The criticism of applying subjective expert knowledge is both theoretically and empirically based, but it may merely reflect a study-specific bias between subjective and more formal approaches.

Habitats are perhaps some of the most difficult sampling units to define (Whittaker et al., 1973; Franklin et al., 2002), but are central to many conservation programs such as the “European council directive on the conservation of natural habitats and of wild fauna and flora” (FFH) (Anon, 1992) or the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2013). Despite their acknowledged importance, definitions differ greatly among conservation programs worldwide. As is the case with selection of sampling units more generally, whereas some conservation initiatives rely on formal definitions of habitat criteria (Jeffers, 1998; Jongman et al., 2006), others rely on subjective expert opinion in the field (Jennings et al., 2009). In this paper, we focus on habitats as the sampling unit in order to address the question of whether subjective or formal application of expert knowledge in defining sampling units leads to different estimates of habitat properties. We therefore compared a formal approach, where the selection of these sampling units involved an *a priori* explicit definition of habitats, to an approach involving only subjective expert judgment (*sensu* Gilbert, 1987).

For both approaches we aimed at defining sampling units that reflect two habitats typical for tundra. These habitats are characterized by their difference in growing conditions and are found in sloping, concave terrain. Here, intermediate slopes provide intermediate moisture conditions (mesic habitats) and gentle slopes have moist conditions combined with a long lasting snow cover (snowbed habitats) (Fremstad, 1997). For both approaches we used existing environmental data to ensure balanced sampling with respect to major ecological gradients. For the formal approach, we used our knowledge of the aforementioned habitat terrain and a terrain model in order to extract a list of potential sampling units. Because we expected that some of these would not be suitable for sampling (e.g. because of boulder fields), we pre-defined additional habitat criteria to be applied in the field. This approach is therefore based on the selection of sampling units by formal rules. For the subjective approach, the sampling units were selected by applying expert judgment directly in the field.

The research question, i.e. what are the plant community characteristics that describe mesic and snowbed habitats, and the measurement of plant community characteristics, were the same in both approaches. For all sampling units, estimates of standing crop of the most abundant plant species and plant functional groups were assessed as well as within plant community diversity. Finally, to evaluate whether different approaches to defining sampling units lead to different estimates of habitat properties, we tested the effect of using formal *versus* subjective definition of sampling units on the estimates of these plant community characteristics.

Materials and Methods

Ecosystem Characteristics

The field sampling for the current study was conducted during peak growing season between 20th and 30th of July 2011 on Varanger Peninsula, the north-eastern part of Finnmark County in northern Norway (Fig. 1). The Varanger Peninsula is delineated by the Barents Sea towards the north and birch forests towards the south. Sandstone, sandstone intermingled with schist, and sandstone intermingled with schist and calcareous bedrock are among the most common geological parental materials (The Geological survey of Norway; www.ngu.no). The topography is characterized by a mixture of plateaus and gently sloping hills (maximum height of approximately 500 m) that are intersected by river valleys. The plateaus build a border with steep slopes towards the Barents Sea. During the growing season (July to August) average (monthly) precipitation varies between 38 and 55 mm and temperatures range from 6.2 to 10.5°C (30 year averages from 1960 to 1990, Norwegian Meteorological Institute, www.met.no).

We conducted our study in the low alpine zone. The vegetation of the low alpine zone in this region is generally classified as low shrub tundra (Walker et al., 2005) with mountain birch (*Betula pubescens* Ehrh.) forming the tree line (Oksanen & Virtanen, 1995). Topography affecting snow accumulation and moisture conditions creates habitats that are differentiated into exposed ridges, and steep and gentle parts of slopes, creating a sequence from xeric to mesic and very moist conditions with increasing duration of snow cover (Fremstad, 1997). These habitat characteristics give rise to distinct vegetation types such as ridge, mesic and snowbed vegetation (Fremstad, 1997). In this study we targeted mesic and snowbed habitats. Commonly occurring plant species in mesic habitat types on the Varanger Peninsula include tall stature forbs (e.g. *Alchemilla* sp., *Geranium sylvaticum* L., *Ranunculus acris* L., *Rhodiola rosea* L.) in combination with grasses (e.g. *Phleum alpinum* L., *Poa pratense* ssp. *alpigena* (Fr.) Hiit., *Festuca rubra* L.). Snowbed habitats are characterized by prostrate *Salix* species (*Salix herbacea* L.) in combination with other grasses (e.g. *Festuca rubra* L., *Poa alpina* L.) and forbs (e.g. *Cerastium* sp.) of lower stature. Mosses such as *Dicranum* sp. or *Polytrichum* sp. are also prevalent here.

Semi domesticated reindeer (*Rangifer tarandus* L.) which are managed by indigenous Sami people are the most common large herbivores in eastern Finnmark. In summer, reindeer herds are kept in the coastal mountains in large districts, which range in area from about 300 to 4000 km², with most reindeer migrating inland during winter. Densities of reindeer have increased during the past two decades in some of these summer grazing districts, whilst remaining constant in others (see Table 2 in Ravolainen et al., 2010). This was evident on Varanger Peninsula during the period of our study, with contrasting reindeer densities observed in the two neighboring districts (Fig. 1). Other large herbivores present on Varanger peninsula are moose (*Alces alces* L.) and locally occurring domestic sheep (*Ovis aries* L.). Ptarmigans (*Lagopus lagopus* L. and *Lagopus muta* Montin), Norwegian lemming (*Lemmus lemmus* L.), root vole (*Microtus oeconomus* Pallas) and grey-sided vole (*Myodes rufocanus* Sund.) are also found in the area (Henden et al., 2011).

Sampling design

We employed a hierarchical, nested sampling design. Our protocol for selecting sampling units that corresponded to the habitats of interest involved several levels of selection (Fig. 1). Using the Varanger Peninsula as the sampling region we covered both districts of contrasting reindeer density. We used information retrieved from a digital elevation model (DEM) to locate landscape areas that had potential sampling units representing the habitats of interest: Using GIS (ESRI ArcGIS with ArcMap. Version 8.3.0) we placed a raster of 2 x 2 km landscape areas over a 25 x 25 m pixel DEM covering the entire peninsula (Fig. 1). Potential sampling units needed to have at least two 25 x 25 m neighboring pixels of concave topography with a mean slope between 5° and 30°. We restricted sampling to units that were a minimum distance of 500 m from birch forests and to an altitude of below 350 m above sea level in order to stay within the low alpine tundra. Finally we avoided lakes, glaciers, major roads and power lines, and only considered

units that were within a one day's walking distance from a road in order to be accessible. We then only selected landscape areas that according to the DEM included at least three potential sampling units that followed these criteria. A total of 21 landscape areas were considered over the whole peninsula. However, within each reindeer density district, the amount of sampling units was balanced in order to cover the three major bedrock types present. We ultimately found nine landscape areas that complied with all our delimitations.

Within each landscape area, the selection of sampling units was based on two different approaches of defining them. In the first approach (formal approach), we applied expert knowledge by defining *a priori* criteria in two steps. First we defined topographical criteria to locate habitats in GIS as described above. Secondly, we defined additional criteria to be evaluated in the field. Here, the sampling unit had to show characteristics indicating both target habitats (i.e. mesic and snowbed). This criterion corresponded to a visible shift in plant communities and had to be evaluated in the field because the differentiation of both target habitats existed on smaller spatial scales than could be represented by our DEM. In addition, the visually estimated vegetation cover had to be higher than 75%, and the habitats grain size had to be large enough to include a minimum of two transects for vegetation measurements (with at least one transect having a length of 10 m and every transect being 5 m apart; see more details below). If a potential sampling unit failed to meet any of these criteria, it was discarded and the next most accessible potential sampling unit was visited and inspected for possible field analyses. The sampling units of the formal approach correspond to the same habitats as in González et al. (2010) and Ravolainen et al. (2010).

In the second approach (subjective approach), we based the selection of sampling units on a subjective definition as follows. As we entered the potential landscape areas, we used expert knowledge in the field to subjectively assess topography to locate likely terrain for the habitats of

interest. When a typical plant community of a mesic or snowbed habitat was found, the habitat was considered a sampling unit and it was analyzed as long as habitat size complied to the additional field criteria used in the formal approach (i.e. large enough habitat area to include a minimum of two transects with at least one of them being 10 m long and each transect being horizontally spaced 5 m apart from each other).

Sometimes we sampled two sampling units per approach within one landscape area, in which case the closest set of sampling units, i.e. one from each of the two approaches, were termed “study area” being nested within landscape area (Fig. 1).

Measurement of plant community characteristics

Within each selected habitat, measurement of plant community characteristics was identical for both approaches, except for the placement of transects. In the formal approach, the starting point of each transect was given by the initial GPS coordinates and in the subjective approach starting points were chosen subjectively so that transects would cover the longest spatial extent of the targeted habitats (Fig. 1). For both approaches transects were marked by a ribbon, running downslope with a 5 m horizontal distance to each other. Depending on the spatial extent of the habitats, we sampled between 2 and 5 transects with lengths varying from 4 m to 32 m. Thereafter, we recorded plant species abundance using the point intercept method according to Bråthen & Hagberg (2004). A frame of 40 cm x 40 cm with 5 pins of 2 mm diameter attached, one to each of the four frame corners and one to the center (see Ravolainen et al., 2010), was placed at fixed intervals of 2 m along the ribbon. For each placement of the frame (i.e. for each plot), intercepts between pins and above ground vascular plant parts were recorded for each species separately. Species within the frame that were not hit by a pin were recorded with the value of 0.1. Table 1 presents a list of replication of all study units according to the spatial hierarchy of our design.

Response variables for data analyses

We converted point intercept data into biomass [g/plot] using weighted linear regression (Bråthen & Hagberg, 2004) and established calibration models (see Table S1 in Ravolainen et al. 2010), after which plant community measures were calculated for each plot in the data set. First we calculated three commonly used measures of within community (alpha-) diversity (Gini-Simpson index, Shannon entropy and Species Richness). Then we calculated biomass of the most dominant species (*Betula nana* L., *Empetrum hermaphroditum* Hagerup. and *Vaccinium myrtillus* L.) and biomass of plant functional groups (as in Bråthen et al., 2007). Certain plant functional groups such as hemi-parasites had very low abundance and were therefore merged into the group of forbs (Table 2). Species and plant functional groups differed between the two habitats of interest, reflecting that the mesic and the snowbed habitats were generally different in their species composition.

Statistical analysis

We analyzed the three measures of (within-) community diversity and the biomass of different species and plant functional groups as response variables separately for each habitat type. When fitting linear mixed effect models, the approach to defining habitats of interest (formal *versus* subjective), the reindeer density district (east *versus* west) and their interaction were used as fixed factors in the models. Bedrock type was included as a factor with three levels (sandstone; sandstone intermingled with schist; sandstone intermingled with schist and calcareous rock) and used as a co-variate (Table S1 of the supplemental information). The landscape areas and the study areas were set as random factors to account for spatial autocorrelation within areas. For some of the response variables we had to exclude study areas from the random effects structure because data existed for one study area per landscape area only. Models that had biomass of

dominant plant species or biomass of functional groups as response variable were $\log_e(x+v)$ transformed in order to assure model assumptions, with (v) representing the smallest biomass value of the sampled data in order to avoid negative values for plots with zero abundance. Diversity measures were not transformed. We used standard diagnostics to assess constancy and normality of residuals and controlled for outliers. All models were run using the lme function as part of the nlme package (Pinheiro et al., 2012) in R (version 2.12.1; The R Foundation for Statistical Computing). A list of all models, containing Akaike's Information Criterion and test statistics for the used fixed factors, can be found in the supplemental information (Tables S2, S3).

Results

Mesic habitat

The approach to defining sampling units affected almost all estimates of plant community diversity in the mesic habitat (Fig.2 a, b, c). The estimates of the diversity indices were in most cases significantly higher in the subjective compared with the formal approach. However, for one of the indices (Gini-Simpson), estimates were only higher in the western district (Fig.2 a).

Estimates of plant functional group biomass and biomass of dominant plant species were significantly different between the two approaches (Fig. 2 d). The biomass of forbs was estimated to be consistently higher when using the subjective approach in both districts. However, there were interaction effects between the approach type and the reindeer density district. For many response variables, differences between the two approaches were only significant in one of the two districts (prostrate *Salix*, grasses, evergreens, deciduous woody species, *Vaccinium myrtillus*, *Empetrum hermaphroditum*). Biomass estimates of other response variables (silica rich grasses and *Betula nana*) were lower in the eastern, but higher in the western district when the subjective approach was used.

Snowbed habitat

The approach to defining sampling units also had significant effects on the diversity estimates for the snowbed habitat (Fig.3 a, b, c). For both Shannon entropy and Species Richness, the subjective approach revealed higher estimates in the eastern but lower estimates in the western district (Fig.3 b, c).

Significant differences between the two approaches were also found for the biomass estimates of dominant plant species and of different plant functional groups (Fig.3 d). Similar to the mesic habitat, there were significant interaction effects between the approach to define sampling units and the reindeer density district. Biomass estimates of some plant functional groups were only affected by the approach in one of the two districts (forbs, grasses, silica rich grasses). For prostrate *Salix*, we found opposite effects of the approach, within the two districts. The biomass was **estimated** significantly lower in the eastern, but significantly higher in the western district when using the subjective approach.

Discussion

Differences in defining sampling units affect community estimates depending on ecological context

In our study, the sampling approach based on a subjective definition of sampling units revealed significant effects on many of our response variables in comparison to the approach based on formal rules. **Hence, the way sampling units were defined begets ecological conclusions to be drawn (Peterson et al., 2001).**

For instance, from our subjective approach our conclusion would be that mesic and snowbed habitats had very low but comparable biomass of silica rich grasses within the two



reindeer density district where data was collected. In contrast, our results based on a formal definition of sampling units show a considerably higher abundance of silica rich grasses in the eastern district where also reindeer density is higher. The role of silicate rich plants in plant herbivore interactions (Vicari & Bazely, 1993) indicate the acceptance of one conclusion or the other could lead to very different ecological outcomes and highlight the need for careful consideration in the definition of sampling units in ecological studies.

Previous studies have documented how individual preferences for certain sampling units could result in biased estimates, with for instance higher estimates of species richness compared to probabilistic sampling approaches (Chytrý, 2001; Botta-Dukát et al., 2007; Diekmann et al., 2007). However, the subjective selection in this study only rendered constantly higher estimates of species richness in the mesic habitats, while species richness in the snowbed habitats was only increased by the subjective approach in the eastern district. We can only speculate on the reasons for this lack of consistency. For the mesic habitat, the constantly higher estimates of species richness in the subjective approach might be due to the fact that we focused on habitats with many indicator species that can be easily distinguished visually, such as different forb species (see Fig. 2d). Such a preference could also explain the higher estimates of species richness and forbs of snowbeds in the eastern district, where high reindeer abundance might lead to generally low abundance of facilitating plant species such as forbs (Bråthen et al., 2007). The lower species richness estimates of the snowbed habitat in the western district might be due to a preference of the sampling units that were visually more strongly impacted by snow, causing a higher probability of selecting for late snowbeds as opposed to earlier snowbeds. Late emergence from snow causes marginal growing conditions for vascular plants and reduced species richness (Björk & Molau, 2007). However, the fact that these interpretations would only account for one specific district shows that the bias caused by the subjective definition of sampling units in species

richness depends on ecological context. We found similar context dependencies for other diversity indices and for many of the biomass response variables in our study (Fig. 2 and Fig. 3).

How to define sampling units to ensure comparability between studies?

Context dependency of the differences in estimates between the two approaches could also have relevance to the comparability of ecological studies. Idiosyncratic results from work on similar study systems are often found in ecological research (Chase et al., 2000; Hedlund et al., 2003; Badano & Cavieres, 2006). Our results indicate that idiosyncratic results within studies or among different studies may have their roots in the way sampling units have been defined. With context dependency being one of the greatest challenges of ecology today (Wardle et al., 2011), additional context dependency enforced by the way ecological sampling units are defined will make it even more difficult to tackle this challenge (see e.g. Franklin et al., 2002).

The definition of habitats in our formal approach involved abiotic characteristics known to represent the habitats in question (e.g. slope, curvature and altitude). Such terrain criteria were applied in a way that allowed us to accurately document each habitat characteristic. In contrast, we did not apply biotic criteria such as the usage of indicator plant species or indicator functional groups in an *a priori* way in this approach, for two reasons. First, plant composition was largely unknown across the potential sampling units of the two habitats, reflecting the absence of vegetation maps (at the grain size of our habitats) for the study area. Secondly, any preference for plant indicators was likely to interfere with the outcome of our research question (Ewald, 2003), i.e. what are the plant community characteristics of mesic and snowbed habitats? However, because our focus was on plants, simple biotic criteria of vegetation cover and a visual shift in type of plant community were not considered to interfere with our conclusions. Although the rules applied in the formal approach were quite simple, they were considered relevant to the

research questions set. Clearly, more specific research questions would demand more refined formal rules.

For applications in ecology, the reproducibility of studies and the comparison between studies are essential (Shrader-Frechette & McCoy, 1994). Therefore, for any true comparison between studies to be made, discrete sampling units such as habitats must be defined in the same way (Loehle, 2004). Our study shows that even slight deviations in the definition of sampling units could affect the comparability of results, even within the same study system. Still, it are only the results gained from the formal approach to defining sampling units that have concomitantly transparency to the definition used (i.e. by the set of formal rules applied), and that present the premise on which further ecological understanding can be developed. Hence, as sampling procedures that allow reproducibility and comparisons between studies are essential, so are the sampling procedures to allow accumulation of ecological knowledge. We therefore believe that the call for formal approaches in study designs (Legendre et al., 2002; Edwards et al., 2005; Edwards et al., 2006; Albert et al., 2010) should also be extended to formal approaches to the definition of sampling units.

The application of expert knowledge is a matter of discussion in several fields of ecology. There is a number of studies that address ways of eliciting expert knowledge for decision making in conservation or landscape ecology (Burgman et al., 2011; Martin et al., 2011; McBride & Burgman, 2012), including the use of expert opinion for modeling (Booker & McNamara, 2004; Kuhnert et al., 2010; Martin et al., 2011). In landscape ecology the use of expert knowledge has recently been challenged to adhere to the same scientific rigor as other data sampling (Morgan, 2014). We believe the application of expert knowledge deserves equal attention in terms of the definition of sampling units, and especially in the definition of habitats which should be done in a transparent way (Whittaker et al., 1973; Franklin et al., 2002).

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References

- Albert CH, Yoccoz NG, Edwards Jr TC, Graham CH, Zimmermann NE, Thuiller W. 2010. Sampling in ecology and evolution – bridging the gap between theory and practice. *Ecography* 33: 1028-1037.
- Anon, 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities.
- Badano EI, Cavieres LA 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography* 33: 304–313.
- Björk RG, Molau U. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research* 39: 34–43.
- Booker JM, McNamara LA. 2004. Solving black box computation problems using expert knowledge theory and methods. *Reliability Engineering and System Safety* 85: 331–340.
- Botta-Dukát Z, Kovács-Láng E, Rédei T, Kertész M, Garadnai J. 2007. Statistical and biological consequences of preferential sampling in phytosociology: Theoretical considerations and a case study. *Folia Geobotanica* 42: 141–152.
- Bråthen KA, Hagberg O. 2004. More efficient estimation of plant biomass. *Journal of Vegetation Science* 15: 653–660.
- Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10: 773–789.
- Burgman M, Carr A, Godden L, Gregory R, McBride M, Flander L, Maguire L. 2011. Redefining expertise and improving ecological judgment. *Conservation Letters* 4: 81–87.
- Carpenter SR. 2002. Ecological futures: Building an ecology of the long now. *Ecology* 83: 2069–2083.

- 346 Chase JM, Leibold MA, Downing AL, Shurin JB. 2000. The Effects of Productivity, herbivory,
347 and plant species turnover in grassland food webs. *Ecology* 81: 2485–2497.
- 348 Chytrý M. 2001. Phytosociological data give biased estimates of species richness. *Journal of*
349 *Vegetation Science* 12: 441–444.
- 350 Diekmann M, Kühne A, Isermann M. 2007. Random vs non-random sampling: Effects on
351 patterns of species abundance, species richness and vegetation-environment relationships.
352 *Folia Geobotanica* 42: 179–190.
- 353 Edwards Jr TC, Cutler DR, Zimmermann NK, Geiser L, Alegria J. 2005. Model-based
354 stratification for enhancing the detection of rare ecological events. *Ecology* 86: 1081–1090.
- 355 Edwards Jr TC, Cutler DR, Zimmermann NE, Geiser L, Moisen GG. 2006. Effects of sample
356 survey design on the accuracy of classification tree models in species distribution models.
357 *Ecological Modelling* 199: 132–141.
- 358 Ewald J. 2003. A critique for phytosociology. *Journal of Vegetation Science* 14: 291–296.
- 359 Franklin AB, Noon BR, George L. 2002. What is habitat fragmentation? *Studies in Avian Biology*
360 25: 20–29.
- 361 Fremstad E. 1997. Vegetasjonstyper i Norge. *NINA Temahefte* 12: 1-279.
- 362 Gilbert RO. 1987. *Statistical methods for environmental pollution monitoring*. New York: John
363 Wiley and Sons.
- 364 González VT, Bråthen KA, Ravolainen VT, Iversen M, Hagen SB. 2010. Large-scale grazing
365 history effects on arctic-alpine germinable seed banks. *Plant Ecology* 207: 321–331.
- 366 Hédli R. 2007. Is sampling subjectivity a distorting factor in surveys for vegetation diversity?
367 *Folia Geobotanica* 42: 1991–1998.
- 368 Hedlund, K, Regina IS, Van der Putten WH, Lepš J, Díaz T, Korthals GW, Lavorel S, Brown VK,
369 Gormsen D, Mortimer SR, Barrueco CR, Roy J, Smilauer P, Smilauerová M, Van Dijk C.
370 2003. Plant species diversity, plant biomass and responses of the soil community on

- 371 abandoned land across Europe: Idiosyncrasy or above-belowground time lags. *Oikos* 103: 45–
- 372 58.
- 373 Henden J-A, Ims RA, Yoccoz NG, Sørensen R, Killengreen ST. 2011. Population dynamics of
- 374 tundra voles in relation to configuration of willow thickets in southern arctic tundra. *Polar*
- 375 *Biology* 34: 533–540.
- 376 IUCN 2013. The IUCN Red List of Threatened Species. Version 2013.2. Available at
- 377 www.iucnredlist.org (accessed 21 November 2013).
- 378 Jeffers JNR. 1998. The statistical basis of sampling strategies for rivers: An example using river
- 379 habitat survey. *Aquatic Conservation: Marine And Freshwater Ecosystems* 8: 447–454.
- 380 Jennings MD, Faber-Langendoen D, Loucks OL, Peet RK, Roberts D. 2009. Standards for
- 381 associations and alliances of the U.S national vegetation classification. *Ecological*
- 382 *Monographs* 79: 173–199.
- 383 Jongman RHG, Bunce RGH, Metzger MJ, Múcher CA, Howard DC, Mateus VL. 2006.
- 384 Objectives and applications of a statistical environmental stratification of Europe. - *Landscape*
- 385 *Ecology* 21: 409–419
- 386 Kenkel NC, Juhász-Nagy P, Podani J. 1989. On sampling procedures in population and
- 387 community ecology. *Vegetatio* 83: 195–207.
- 388 Kuhnert PM, Martin TG, Griffiths SP. 2010. A guide to eliciting and using expert knowledge in
- 389 Bayesian ecological models. *Ecology Letters* 13: 900–914.
- 390 Legendre P, Dale MRT, Fortin M-J, Gurevitch J, Hohn M, Myers D. 2002. The consequences of
- 391 spatial structure for the design and analysis of ecological field surveys. *Ecography* 25: 601–
- 392 615.
- 393 Loehle C. 2004. Challenges of ecological complexity. *Ecological Complexity* 1: 3–6.
- 394 Martin TG, Burgman MA, Fidler F, Kuhnert PM, Low-Choy S, McBride M, Mengersen K. 2011.
- 395 Eliciting expert knowledge in conservation science. *Conservation Biology* 26: 1–10.

- 396 McBride MF, Burgman MA. 2012. What is expert knowledge, how is such knowledge gathered,
397 and how do we use it to address questions in landscape ecology? In: Perera AH, Drew CA,
398 Johnson CJ eds. *Expert knowledge and its application in landscape ecology*. New York:
399 Springer Science+Business Media: 11–38.
- 400 Morgan MG. 2014. Use (and abuse) of expert elicitation in support of decision making for public
401 policy. *Proceedings of the National Academy of Sciences of the United States of America* 111:
402 7176–7184.
- 403 Oksanen L, Virtanen R. 1995. Topographic, altitudinal and regional patterns in continental and
404 sub-oceanic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica* 153: 1–80.
- 405 Olsen AR, Sedransk J, Edwards D, Gotway CA, Liggett W, Rathbun S, Reckhow K, Young L.
406 1999. Statistical issues for monitoring ecological and natural resources in the United States.
407 *Environmental Monitoring and Assessment* 54: 1–45.
- 408 Peterson CH, McDonald LL, Green RH, Erickson WP. 2001. Sampling design begets
409 conclusions: the statistical basis for detection of injury to and recovery of shore- line
410 communities after the “ Exxon Valdez ” oil spill. *Marine Ecology Progress Series* 210: 255–
411 283.
- 412 Peterson CH, McDonald LL, Green RH, Erickson WP. 2002. The joint consequences of multiple
413 components of statistical sampling designs. *Marine Ecology Progress Series* 231: 309–314.
- 414 Pinheiro J, Bates D, DebRoy S, Sarkar D. 2012. nlme: Linear and nonlinear mixed effects
415 models. R package version 3.1-104.
- 416 Ravolainen VT, Yoccoz NG, Bråthen KA, Ims RA, Iversen M, González VT. 2010. Additive
417 partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure
418 of tundra plant communities. *Ecosystems* 13: 157–170.

- 419 Roleček, J, Chytrý M, Hájek M, Lvončík S, Tichý L. 2007. Sampling design in large-scale
420 vegetation studies: Do not sacrifice ecological thinking to statistical purism! *Folia*
421 *Geobotanica* 42: 199–208.
- 422 Schreuder HT, Gregoire TG, Weyer JP. 2001. For what applications can probability and non-
423 probability sampling be used? *Environmental Monitoring and Assessment* 66: 281–291.
- 424 Shrader-Frechette K, McCoy ED. 1994. Applied ecology and the logic of case studies.
425 *Philosophy of Science* 61: 228–249.
- 426 Vicari M, Bazely DR. 1993. Do grasses fight back? The case for antiherbivore defences. *Trends*
427 *in Ecology and Evolution* 8: 137–141.
- 428 Walker DA, Raynolds MK, Daniëls FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE,
429 Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA, CAVM Team.
430 2005. The circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16: 267–282.
- 431 Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH. 2011. Terrestrial ecosystem
432 responses to species gains and losses. *Science* 332: 1273–1277.
- 433 Whittaker RH, Levin SA, Root RB. 1973. Niche, habitat, and ecotope. *The American Naturalist*
434 107: 321–338.
- 435 Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time.
436 *Trends in Ecology and Evolution* 16: 446–453.

437 Table 1. Sample size presented for each of the hierarchical levels of the sampling design for each
 438 of the two approaches and their summarized sample size. The formal and the subjective approach
 439 share samples at both levels above the level of sampling units.

<u>nested hierarchy</u>		<u>replication of units</u>		
		formal	subjective	total for both approaches
mesic habitat	landscape area	9	9	9
	study area	11	11	11
	habitats/sampling units	11	11	22
	transects	30	25	55
	plots	199	152	351
snowbed habitat	landscape area	6	6	6
	study area	7	7	7
	habitats/sampling units	7	7	14
	transects	18	16	34
	plots	85	103	188

440 Table 2. Major plant functional groups and their associated species encountered in the sampling
441 units of mesic and snowbed habitats along with a list of the most dominant plant species

<i>Calluna alpina</i> L.	<i>Rhodiola rosea</i> L.	<i>Calamagrostis neglecta</i> Timm	Deciduous woody plants
<i>Chamaenerion alpinum</i> (L.) Gaertn.	<i>Rubus chamaemorus</i> L.	<i>Calamagrostis phragmitoides</i> Adans.	<i>Arctostaphylos alpinus</i> (GCI)
<i>Chamaenerion dioicum</i> (L.) Gaertn.	<i>Rumex acetosa</i> L.	<i>Festuca ovina</i> L.	<i>Loiseleuria procumbens</i> (L.) Loisel.
<i>Chamaenerion alpinum</i> L.	<i>Sagina saginoides</i> (L.) H.Karst.	<i>Festuca rubra</i> L.	
<i>Chamaenerion viviparum</i> (L.) Delarbr.	<i>Saussurea alpina</i> DC.	<i>Phleum alpinum</i> L.	Evergreen woody plants
<i>Chamaenerion palustre</i> L.	<i>Saxifraga caespitosa</i> Lag. & Rodr.	<i>Poa alpina</i> L.	<i>Vaccinium vitis-idaea</i> L.
	<i>Sibbaldia procumbens</i> L.	<i>Poa pratensis</i> ssp. <i>alpigena</i> (Fr.) Hiit.	<i>Andromeda polifolia</i> L.
<i>Chamaenerion periclymenum suecicum</i> L.		<i>Vahlodea atropurpurea</i> (Wahlenb.) Hartm.	<i>Dryas octopetala</i> L.
<i>Chamaenerion rotundifolia</i> L.	<i>Silene acaulis</i> L.		<i>Harrimanella hypnoides</i> (L.) Coville
<i>Chamaenerion glabella</i> Pursh	<i>Solidago virgaurea</i> L.	Silica rich grasses	<i>Juniperus communis</i> L.
<i>Chamaenerion anagallidifolium</i> LAM.	<i>Stellaria nemorum</i> L.	<i>Deschampsia cespitosa</i> (L.) P.Beauv.	<i>Phyllocladus caerulea</i> (L.) Bab.
<i>Chamaenerion hornemannii</i> Reichenb.	<i>Taraxacum collinum</i> Zinn	<i>Nardus stricta</i> L.	
<i>Chamaenerion frigida</i> Pugsley	<i>Thalictrum alpinum</i>		Dominant plant species
<i>Chamaenerion wettsteinii</i> G. Gussarova	<i>Trientalis europaea</i> L.	Sedges/Rushes	<i>Betula nana</i> L.
<i>Chamaenerion sylvaticum</i> L.	<i>Trollius europaeus</i> L.	<i>Carex aquatilis</i> Wahlenb.	<i>Vaccinium myrtillus</i> L.
<i>Chamaenerion rivale</i> L.	<i>Veronica alpina</i> ssp. <i>alpina</i> L.	<i>Carex bigelowii</i> Torr. ex Schwein.	<i>Vaccinium uliginosum</i> L.
<i>Chamaenerion cordatum</i> (L.) R.Br.	<i>Viola biflora</i> L.	<i>Carex brunnescens</i> (Pers.) Poir.	<i>Empetrum hermaphroditum</i> Hagerup
<i>Chamaenerion sylvaticum</i> L.	<i>Viola palustris</i> L.	<i>Carex canescens</i> L.	
<i>Chamaenerion theca norvegica</i>		<i>Carex lachenalii</i> Schkuhr	
<i>Chamaenerion merum</i> Sch.Bip. & F.W.Schultz	Prostrate Salix species	<i>Carex vaginata</i> Tausch	
<i>Chamaenerion theca supina</i> (L.) DC.	<i>Salix reticulata</i> L.	<i>Eriophorum angustifolium</i> Honck.	
<i>Chamaenerion digyna</i> Hill	<i>Salix herbacea</i> L.	<i>Eriophorum vaginatum</i> L.	
<i>Chamaenerion sylvatica palustris</i> L.	<i>Salix polaris</i> Wahlenb.	<i>Luzula multiflora</i> (Ehrh.) Lej.	
<i>Chamaenerion lapponica</i> L.		<i>Luzula spicata</i> (L.) DC.	
<i>Chamaenerion cula vulgaris</i> L.	Grasses	<i>Luzula wahlenbergii</i> Rupr.	
<i>Chamaenerion crantzii</i> (Crantz) Fritsch	<i>Agrostis capillaris</i> L.		
<i>Chamaenerion erecta</i> H.Karst.	<i>Anthoxanthum nipponicum</i> Honda		
<i>Chamaenerion acris</i> L.	<i>Deschampsia flexuosa</i> P.Beauv.		

Figure 1. The figure shows the geographical location of the sampling region (Varanger Peninsula, northern Norway) and nestedness of the sampling design. The shades of gray delimit the districts of contrasting reindeer density. Open squares show the raster of 2 x 2 km landscape areas where major roads, power lines, glaciers and large water bodies have been omitted. Black squares correspond to landscape areas that adhered to all other delimitations in our design (see Materials and Methods section for details). One landscape area contained up to two study areas (dashed line) which inherited a pair of formally (GPS) and subjectively (eye) defined sampling units. The recording of vegetation characteristics within each habitat was conducted along transects (dashed lines within habitats).

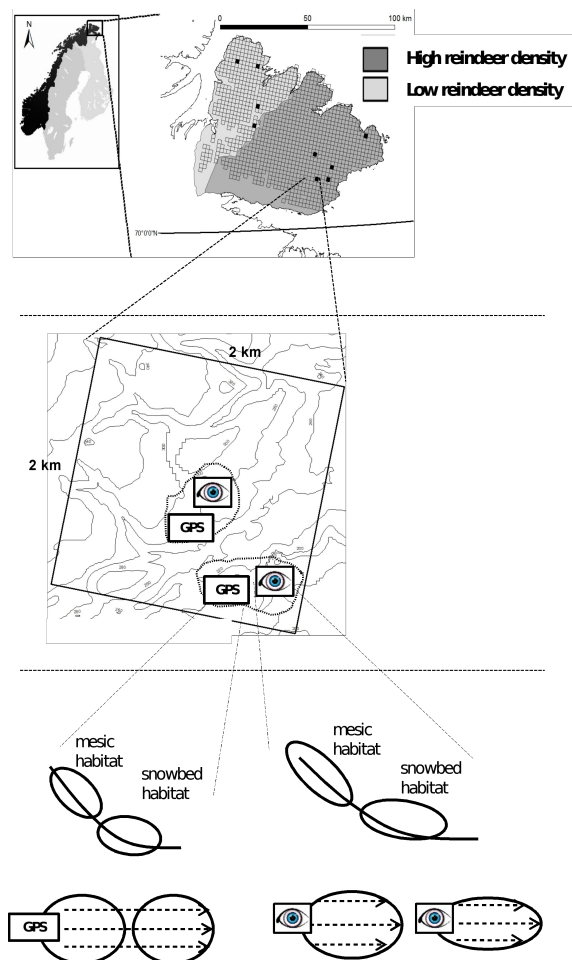


Figure 2. Effect size (mean $\pm$ 95% confidence interval) of the response difference between the subjective over the formal approach of defining sampling units within the mesic habitat for estimates of diversity (a, b, c) and estimates of biomass of dominant plant species and functional groups (d). Effect sizes above or below the dotted line can be interpreted as the subjective approach having higher or lower estimates than the formal approach. Effect sizes of biomass estimates are back transformed values from a logarithmic scale, using the exponential on effect sizes from our model, and may be interpreted as ratio of the subjective/formal approach. The numbers at the base of each figure represent estimates of the respective diversity index (a, b, c) and the geometric mean of the biomass estimates (d) from the formal approach for each respective response variable. Geometric means can be interpreted as approximate biomass estimates for the respective district.

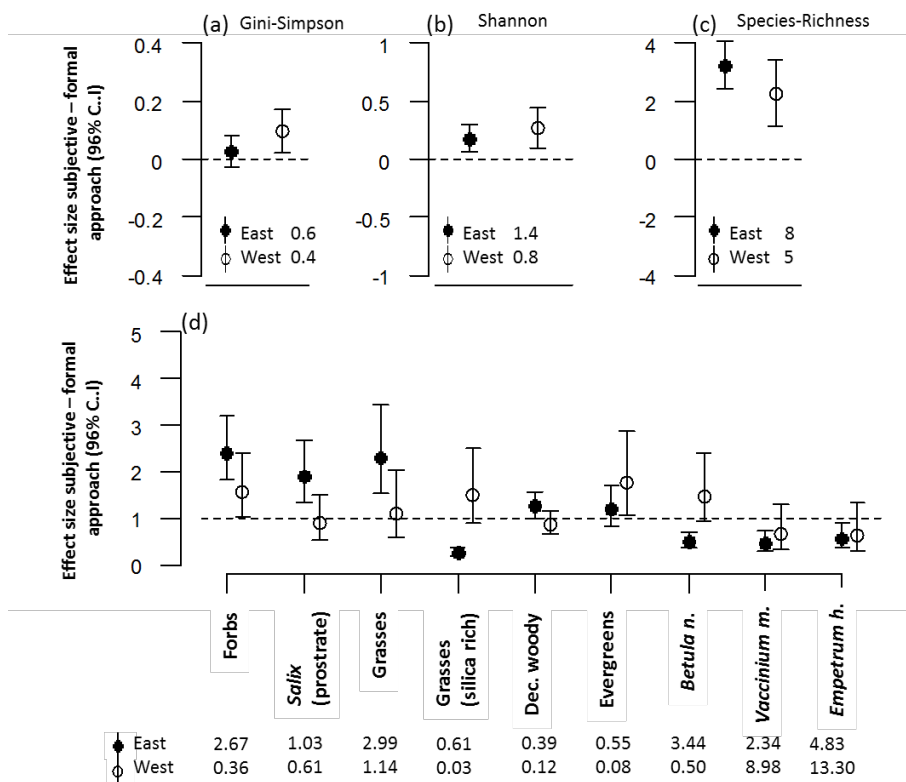


Figure 3. Effect size (mean $\pm$ 95% confidence interval) of the response difference between the subjective over the formal approach of defining sampling units within the snowbed habitat for estimates of diversity (a, b, c) and estimates of biomass of dominant plant species and functional groups (d). Effect sizes above or below the dotted line can be interpreted as the subjective approach having higher or lower estimates than the formal approach. Effect sizes of biomass estimates are back transformed values from a logarithmic scale, using the exponential on effect sizes from our model, and may be interpreted as ratio of the subjective/formal approach. The numbers at the base of each figure represent estimates of the respective diversity index (a, b, c) and the geometric mean of the biomass estimates (d) from the formal approach for each respective response variable. Geometric means can be interpreted as approximate biomass estimates for the respective district, hence the slightly negative value for *Empetrum hermaphroditum* which had had very low biomass recordings in the eastern district.

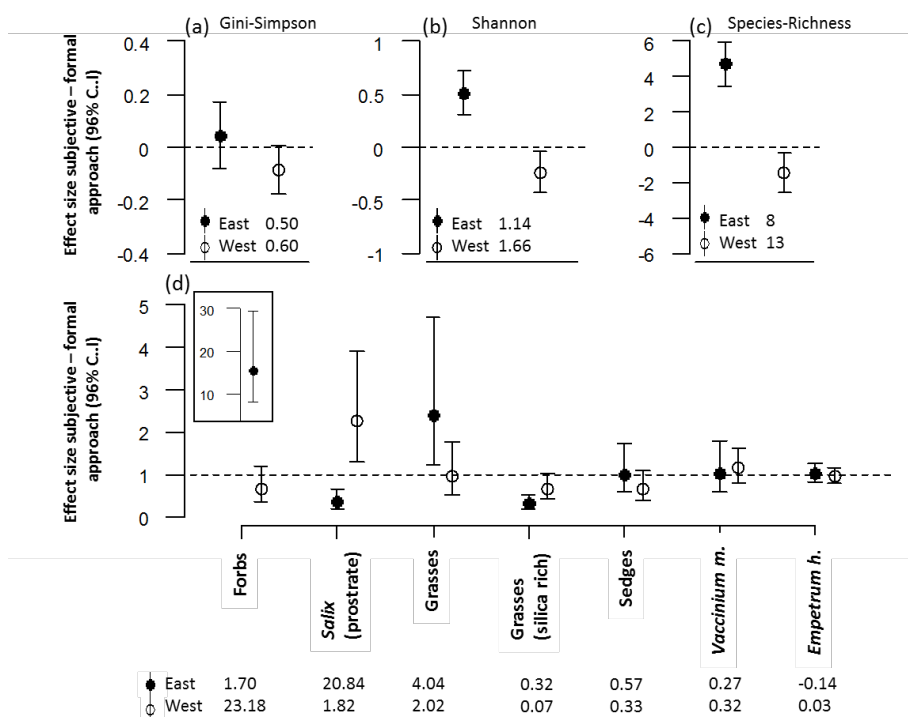


Table 1(on next page)

replication of units according to hierarchical levels of sampling design

Sample size presented for each of the hierarchical levels of the sampling design for each of the two approaches and their summarized sample size. The formal and the subjective approach share samples at both levels above the level of sampling units.

Table 1. Sample size presented for each of the hierarchical levels of the sampling design for each of the two approaches and their summarized sample size. The formal and the subjective approach share samples at both levels above the level of sampling units.

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Table 2(on next page)

Division of plant species into functional groups

Major plant functional groups and their associated species encountered in the sampling units of mesic and snowbed habitats along with a list of the most dominant plant species

Table 2. Major plant functional groups and their associated species encountered in the sampling units of mesic and snowbed habitats along with a list of the most dominant plant species

Forbs <i>Alchemilla alpina</i> L. <i>Antennaria alpina</i> (L.) Gaertn. <i>Antennaria dioica</i> (L.) Gaertn. <i>Bartsia alpina</i> L. <i>Bistorta vivipara</i> (L.) Delarbre <i>Caltha palustris</i> L. <i>Chamaepericlymenum suecicum</i> L. <i>Campanula rotundifolia</i> L. <i>Draba glabella</i> Pursh <i>Epilobium anagallidifolium</i> LAM. <i>Epilobium hornemannii</i> Reichenb. <i>Euphrasia frigida</i> Pugsley <i>Euphrasia wettsteinii</i> G. Gussarova <i>Geranium sylvaticum</i> L. <i>Geum rivale</i> L. <i>Listera cordata</i> (L.) R.Br. <i>Melampyrum sylvaticum</i> L. <i>Omalotheca norvegica</i> (Gunnerus) Sch.Bip. & F.W.Schultz <i>Omalotheca supina</i> (L.) DC. <i>Oxyria digyna</i> Hill <i>Parnassia palustris</i> L. <i>Pedicularis lapponica</i> L. <i>Pinguicula vulgaris</i> L. <i>Potentilla crantzii</i> (Crantz) Fritsch <i>Potentilla erecta</i> H.Karst. <i>Ranunculus acris</i> L.	<i>Rhodiola rosea</i> L. <i>Rubus chamaemorus</i> L. <i>Rumex acetosa</i> L. <i>Sagina saginoides</i> (L.) H.Karst. <i>Saussurea alpina</i> DC. <i>Saxifraga Caespitosa</i> Lag. & Rodr. <i>Sibbaldia procumbens</i> L. <i>Silene acaulis</i> L. <i>Solidago virgaurea</i> L. <i>Stellaria nemorum</i> L. <i>Taraxacum coll</i> Zinn <i>Thalictrum alpinum</i> <i>Trientalis europaea</i> L. <i>Trollius europaeus</i> L. <i>Veronica alpina ssp. Alpina</i> L. <i>Viola biflora</i> L. <i>Viola palustris</i> L. Prostrate Salix species <i>Salix reticulata</i> L. <i>Salix herbacea</i> L. <i>Salix polaris</i> Wahlenb. Grasses <i>Agrostis capillaris</i> L. <i>Anthoxanthum nipponicum</i> Honda <i>Deschampsia flexuosa</i> P.Beauv.	<i>Calamagrostis neglecta</i> Timm <i>Calamagrostis phragmitoides</i> Adans. <i>Festuca ovina</i> L. <i>Festuca rubra</i> L. <i>Phleum alpinum</i> L. <i>Poa alpina</i> L. <i>Poa pratensis ssp. Alpigena</i> (Fr.) Hiit. <i>Vahlodea atropurpurea</i> (Wahlenb.) Hartm. Silica rich grasses <i>Deschampsia cespitosa</i> (L.) P.Beauv. <i>Nardus stricta</i> L. Sedges/Rushes <i>Carex aquatilis</i> Wahlenb. <i>Carex bigelowii</i> Torr. ex Schwein. <i>Carex brunnescens</i> (Pers.) Poir. <i>Carex canescens</i> L. <i>Carex lachenalii</i> Schkuhr <i>Carex vaginata</i> Tausch <i>Eriophorum angustifolium</i> Honck. <i>Eriophorum vaginatum</i> L. <i>Luzula multiflora</i> (Ehrh.) Lej. <i>Luzula spicata</i> (L.) DC. <i>Luzula wahlenbergii</i> Rupr.	Deciduous woody plants <i>Arctous alpinus</i> (GCI) <i>Loiseleuria procumbens</i> (L.) Loisel. Evergreen woody plants <i>Vaccinium vitis-idaea</i> L. <i>Andromeda polifolia</i> L. <i>Dryas octopetala</i> L. <i>Harrimanella hypnoides</i> (L.) Coville <i>Juniperus communis</i> L. <i>Phyllodoce caerulea</i> (L.) Bab. Dominant plant species <i>Betula nana</i> L. <i>Vaccinium myrtillus</i> L. <i>Vaccinium uliginosum</i> L. <i>Empetrum hermaphroditum</i> Hagerup
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