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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Introduction

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

In situations where sampling units are not clearly defined, the availability of relevant sampling units is not known before entering the field, i.e. there is no well-defined sampling frame and in its vacancy, expert knowledge is applied in order to guide sampling to ecological units that are decided to be suitable in the field. This situation is particularly common in ecological studies where the spatial resolution of geographical and environmental data is at a scale too coarse to reflect the spatial extent or grain of the sampling units of interest (Roleček et al., 2007). Only a 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; Hédl, 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 km^2, 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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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.

	nested hierarchy	**replication of units**		
		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

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

milla alpina L.
naria alpina (L.) Gaertn.
naria dioica (L.) Gaertn.
a alpina L.
a vivipara (L.) Delarbre
palustris L.
aepericlymemum suecicum L.
anula rotundifolia L.
glabella Pursh
ium anagallidifolium LAM.
ium hornemannii Reichenb.
asia frigida Pugsley
asia wettsteinii G. Gussarova
ium sylvaticum L.
rivale L.
cordata (L.) R.Br.
npyrum sylvaticum L.
otheca norvegica
nerus) Sch.Bip. & F.W.Schultz
otheca supina (L.) DC.
digyna Hill
ssia palustris L.
ılaris lapponica L.
cula vulgaris L.
illa crantzii (Crantz) Fritsch
illa erecta H.Karst.
nculus acris L.

Rhodiola rosea L.
Rubus chamaemorus L.
Rumex acetosa L.
Sagina saginoides (L.) H.Karst.
Saussurea alpina DC.
Saxifraga Caespitosa Lag. & Rodr.
Sibbaldia procumbens L.
Silene acaulis L.
Solidago virgaurea L.
Stellaria nemorum L.
Taraxacum coll Zinn
Thalictrum alpinum
Trientalis europaea L.
Trollius europaeus L.
Veronica alpina ssp. Alpina L.
Viola biflora L.
Viola palustris L.

Prostrate *Salix* species
Salix reticulata L.
Salix herbacea L.
Salix polaris Wahlenb.

Grasses
Agrostis capillaris L.
Anthoxanthum nipponicum Honda
Deschampsia flexuosa P.Beauv.
Calamagrostis neglecta Timm
Calamagrostis phragmitoides Adans.
Festuca ovina L.
Festuca rubra L.
Phleum alpinum L.
Poa alpina L.
Poa pratensis ssp. Alpigena (Fr.) Hiit.
Vahlodea atropurpurea (Wahlenb.) Hartm.

Silica rich grasses
Deschampsia cespitosa (L.) P.Beauv.
Nardus stricta L.

Sedges/Rushes
Carex aquatilis Wahlenb.
Carex bigelowii Torr. ex Schwein.
Carex brunnescens (Pers.) Poir.
Carex canescens L.
Carex lachenalii Schkuhr
Carex vaginata Tausch
Eriophorum angustifolium Honck.
Eriophorum vaginatum L.
Luzula multiflora (Ehrh.) Lej.
Luzula spicata (L.) DC.
Luzula wahlenbergii Rupr.

Deciduous woody plants
Arctous alpinus (GCI)
Loiseleuria procumbens (L.) Loisel.

Evergreen woody plants
Vaccinium vitis-idaea L.
Andromeda polifolia L.
Dryas octopetala L.
Harrimanella hypnoides (L.) Coville
Juniperus communis L.
Phyllodoce caerulea (L.) Bab.

Dominant plant species
Betula nana L.
Vaccinium myrtillus L.
Vaccinium uliginosum L.
Empetrum hermaphroditum Hagerup

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).

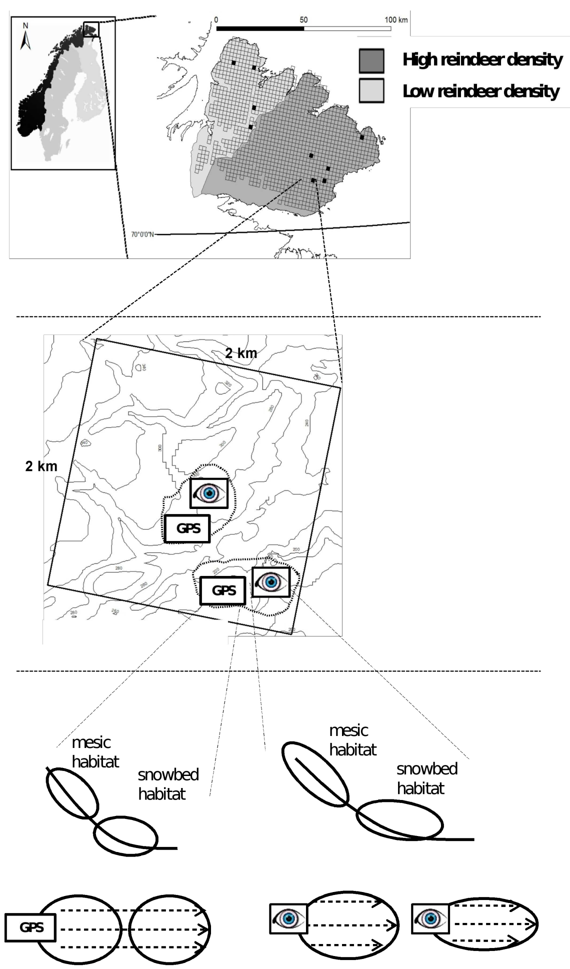

Figure 2. Effect size (mean ± 95% confidence interval) of the response difference between the subjective over the formal approach of defining sampling units within the mesic habitat for estimates of diversity (a, b, c) and estimates of biomass of dominant plant species and functional groups (d). Effect 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.

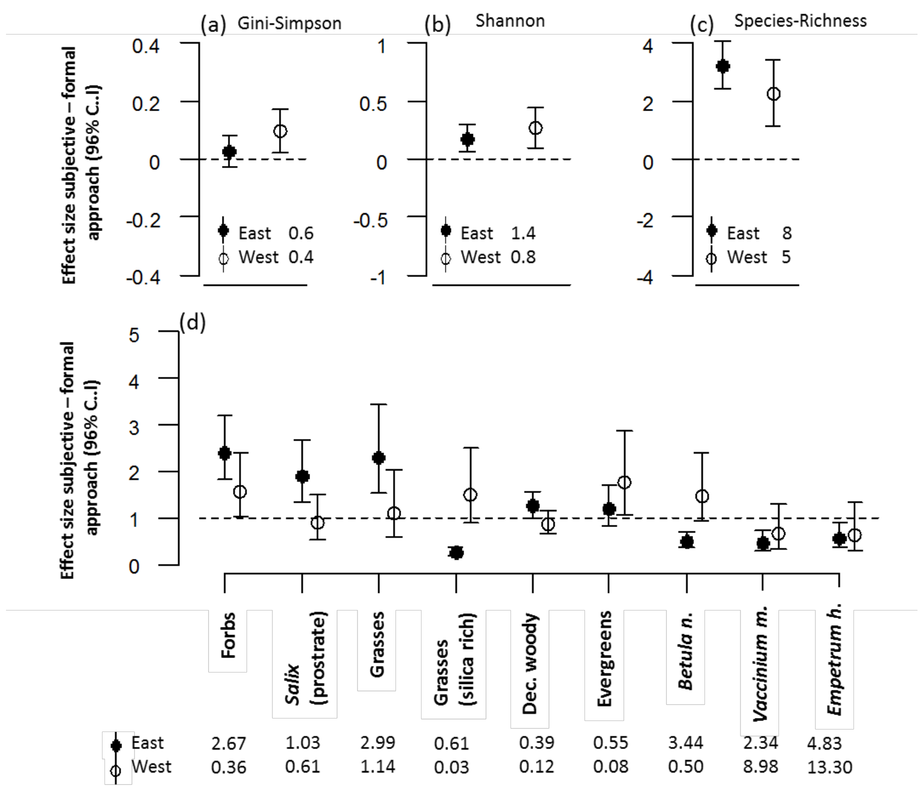

Figure 3. Effect size (mean ± 95% confidence interval) of the response difference between the subjective over the formal approach of defining sampling units within the snowbed habitat for estimates of diversity (a, b, c) and estimates of biomass of dominant plant species and functional groups (d). Effect 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.

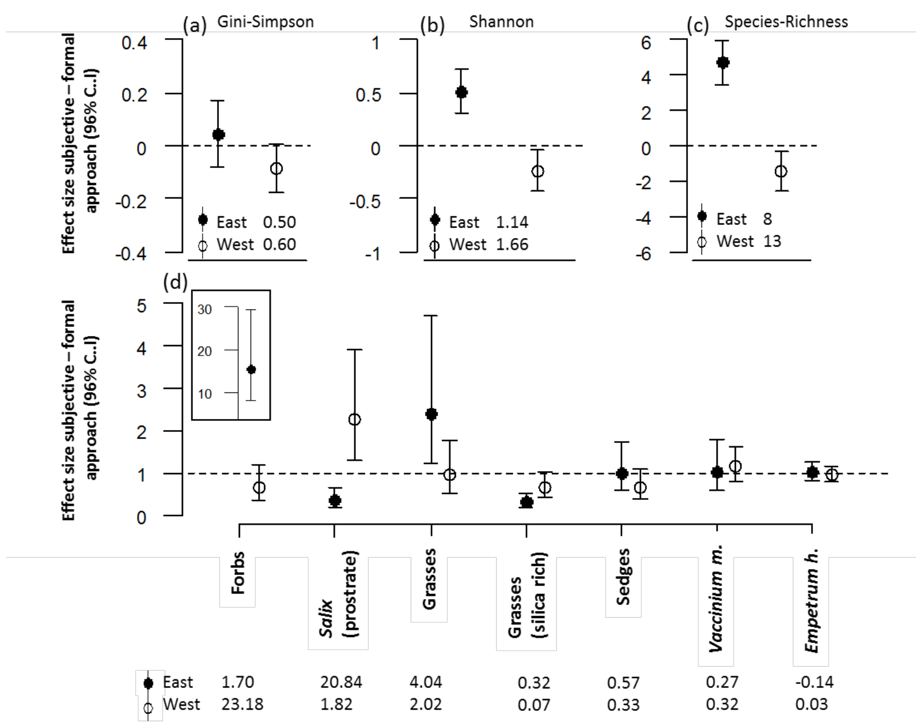

Table 1 (on next page)

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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	plots	85	103	188

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

Alchemilla alpina L.
Antennaria alpina (L.) Gaertn.
Antennaria dioica (L.) Gaertn.
Bartsia alpina L.
Bistorta vivipara (L.) Delarbre
Caltha palustris L.
Chamaepericlymemum suecicum L.
Campanula rotundifolia L.
Draba glabella Pursh
Epilobium anagallidifolium LAM.
Epilobium hornemannii Reichenb.
Euphrasia frigida Pugsley
Euphrasia wettsteinii G. Gussarova
Geranium sylvaticum L.
Geum rivale L.
Listera cordata (L.) R.Br.
Melampyrum sylvaticum L.
Omalotheca norvegica (Gunnerus) Sch.Bip. & F.W.Schultz
Omalotheca supina (L.) DC.
Oxyria digyna Hill
Parnassia palustris L.
Pedicularis lapponica L.
Pinguicula vulgaris L.
Potentilla crantzii (Crantz) Fritsch
Potentilla erecta H.Karst.
Ranunculus acris L.
Rhodiola rosea L.
Rubus chamaemorus L.
Rumex acetosa L.
Sagina saginoides (L.) H.Karst.
Saussurea alpina DC.
Saxifraga Caespitosa Lag. & Rodr.
Sibbaldia procumbens L.
Silene acaulis L.
Solidago virgaurea L.
Stellaria nemorum L.
Taraxacum coll Zinn
Thalictrum alpinum
Trientalis europaea L.
Trollius europaeus L.
Veronica alpina ssp. Alpina L.
Viola biflora L.
Viola palustris L.

Prostrate *Salix* species

Salix reticulata L.
Salix herbacea L.
Salix polaris Wahlenb.

Grasses

Agrostis capillaris L.
Anthoxanthum nipponicum Honda
Deschampsia flexuosa P.Beauv.
Calamagrostis neglecta Timm
Calamagrostis phragmitoides Adans.
Festuca ovina L.
Festuca rubra L.
Phleum alpinum L.
Poa alpina L.
Poa pratensis ssp. Alpigena (Fr.) Hiit.
Vahlodea atropurpurea (Wahlenb.) Hartm.

Silica rich grasses

Deschampsia cespitosa (L.) P.Beauv.
Nardus stricta L.

Sedges/Rushes

Carex aquatilis Wahlenb.
Carex bigelowii Torr. ex Schwein.
Carex brunnescens (Pers.) Poir.
Carex canescens L.
Carex lachenalii Schkuhr
Carex vaginata Tausch
Eriophorum angustifolium Honck.
Eriophorum vaginatum L.
Luzula multiflora (Ehrh.) Lej.
Luzula spicata (L.) DC.
Luzula wahlenbergii Rupr.

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Andromeda polifolia L.
Dryas octopetala L.
Harrimanella hypnoides (L.) Coville
Juniperus communis L.
Phyllodoce caerulea (L.) Bab.

Dominant plant species

Betula nana L.
Vaccinium myrtillus L.
Vaccinium uliginosum L.
Empetrum hermaphroditum Hagerup

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