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Highly Overlapping Winter Diet in Two Sympatric Lemming Species Revealed by DNA Metabarcoding

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Abstract

Sympatric species are expected to minimize competition by partitioning resources, especially when these are limited. Herbivores inhabiting the High Arctic in winter are a prime example of a situation where food availability is anticipated to be low, and thus reduced diet overlap is expected. We present here the first assessment of diet overlap of high arctic lemmings during winter based on DNA metabarcoding of feces. In contrast to previous analyses based on microhistology, we found that the diets of both collared (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) on Bylot Island were dominated by *Salix* while mosses, which were significantly consumed only by the brown lemming, were a relatively minor food item. The most abundant plant taxon, *Cassiope tetragona*, which alone composes more than 50% of the available plant biomass, was not detected in feces and can thus be considered to be non-food. Most plant taxa that were identified as food items were consumed in proportion to their availability and none were clearly selected for. The resulting high diet overlap, together with a lack of habitat segregation, indicates a high potential for resource competition between the two lemming species. However, *Salix* is abundant in the winter habitats of lemmings on Bylot Island and the non-*Salix* portion of the diets differed between the two species. Also, lemming grazing impact on vegetation during winter in the study area is negligible. Hence, it seems likely that the high potential for resource competition predicted between these two species did not translate into actual competition. This illustrates that even in environments with low primary productivity food resources do not necessarily generate strong competition among herbivores.

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Competing Interests: Ludovic Gielly and Pierre Taberlet are co-inventors of a patent concerning g-h primers and the subsequent use of the P6 loop of the chloroplast trnL (UAA) intron for plant identification using degraded template DNA. The patent has the following numbers: CA 2581347 (Canada Patent), 2006/040448 (PCT Patent), EP1797201 (EPO Patent), 20090081646 and 20110143354 (both United States Patent Application). These patents, titled "Universal primers and their use for detecting and identifying plant materials in complex mixtures", only restrict commercial applications and have no impact on the use of this locus by academic researchers. Eva Bellemain is employed by SPYGEN. This does not alter the authors' adherence to the PLOS ONE policies on sharing data and materials

Introduction

Closely related species living in sympatry are expected to reduce overlap in resource or habitat use to minimize competition [1–4]. Among small mammals, several species typically coexist, and thus the potential for competition is high. This should be especially true when resources are limited such as in low-productivity environments. In desert rodents, strong competitive interactions have indeed been found [5, 6]. However, for tundra rodents, a group living in another low-productivity environment, evidence for competitive interactions has been more equivocal [2, 7–10].

Lemmings and voles are dominant herbivores in the circumpolar tundra [11–13]. These small mammals are year-round residents and thus must survive on local primary production throughout the year. Lemmings are well-known for their regular, large-amplitude population cycles [12, 14, 15]. Every three to five years, populations reach very high densities, which can sometimes severely impact their food resources [16–18]. The impact of lemming grazing may be especially pronounced under the snow during the long Arctic winter because individuals tend to concentrate in restricted areas, such as those with deep snow (i.e. snow beds, [19–21]), and because no new plant growth occurs during this period. However, resource use by lemmings during winter remains poorly known due to the formidable challenges involved in studying them beneath the snow under the harsh Arctic conditions. Yet, events occurring during the winter, such as reproduction, may play a key role in lemming population dynamics [22–26].

It is common that two species of lemmings live in sympatry in the Arctic. Typically, when this occurs, one species belongs to the genus *Lemmus* and the other to the genus *Dicrostonyx*. These two genera tend to have different ecologies, including different habitat and food preferences. *Lemmus* generally prefers wetter habitats whereas *Dicrostonyx* prefers drier habitats [27–29]. However, habitat segregation may be less clear in winter. In Arctic Canada, both genera tend to concentrate in deep snow patches that, on the treeless tundra, are often limited to areas where topography is conducive to high snow accumulation such as the leeward side of slopes [20, 21]. Generally, *Lemmus* feed primarily on monocots and, to a lesser extent, mosses, whereas *Dicrostonyx* feed mostly on dicots [8, 19, 30–32]. Although broad dietary patterns have been generally consistent among study sites and show relatively little diet overlap between these two genera, some variability has been found [8, 32]. Differences in diet among localities have been mainly attributed to variations in forage availability, suggesting some flexibility in resource use of lemmings ([8, 32], see also [33]). However, whether dietary overlap between coexisting species increases during winter in areas where both species concentrate in snow beds such as in Arctic Canada remains unknown.

Previous studies that examined diets in lemmings were based on microhistological identification of plant fragments in stomach contents or fecal pellets (hereafter called traditional methods). Recently, a new method, DNA metabarcoding, has become available to study animals' diets (reviewed in [34]). This method is based on amplifying and high-throughput sequencing a standardized DNA region from feces or stomach contents, and subsequently identifying and counting the taxa composing the diet by comparing the obtained sequences to a taxonomic reference library [34–36]. It has lately been used successfully to study diets of various herbivores such as brown bear (*Ursus arctos*) [37], golden marmot (*Marmota caudata*) [37], chamois (*Rupicapra rupicapra*) [38], European bisons (*Bison bonasus*) [39] and small rodents [40, 41]. Compared to traditional methods, DNA metabarcoding generally provides finer taxonomic resolution, has the potential to identify more taxa, and can allow the analysis of a large number of samples without observer biases [35, 40].

We here present the first analysis of collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus)* lemmings' winter diets based on DNA metabarcoding of fecal pellet contents. Considering that these two species use similar habitats during winter in the Canadian High Arctic [20], we hypothesized that they should minimize interspecific competition by showing little interspecific diet overlap. Our hypothesis appeared strong because the two species are thought to have different dietary preferences [31]. We also examined how plant availability affected diet and quantified food selection and diet diversity of each species. We finally discuss the consequences of our findings for species interactions in Arctic food webs.

Methods

Study area

The study site is located in the Qarlikturvik glacial valley (73°08'N, 80°00'W) of Bylot Island, Sirmilik National Park, Nunavut Territory, Canada. The study area (40 km^2) consists of tundra polygons, thaw lakes and ponds forming wetlands at the bottom of the valley and is surrounded by mesic tundra on higher ground and nearby slopes and hills. Mesic tundra accounts for most of the landscape whereas wetlands cover about 23% of the study area and dry, xeric tundra with a sparse vegetation cover occupies <5% of the area and is limited to the tops of hills and ridges [42]. Wetlands have extensive grass/sedge meadows dominated by mosses and graminoids (*Dupontia fisheri*, *Eriophorum scheuchzeri* and *Carex aquatilis*; [43]). The mesic tundra is dominated by prostrate shrubs (*Salix arctica, S. herbacea*, *Cassiope tetragona, Dryas integrifolia*; erect shrubs are very scarce), with a sparse cover of forbs (*Saxifraga* spp., *Potentilla* spp., *Ranunculus* spp., *Pedicularis* spp.), graminoids (*Arctagrostis latifolia*, *Alopecurus alpinus*, *Poa* spp., *Luzula* spp.), mosses and lichens. Small, intermittent streams running through upland areas often create gullies but their floristic composition is generally similar to the surrounding mesic tundra [44]. Plant names follow the nomenclature and taxonomy of the Annotated Checklist of the Panarctic Flora [45] for vascular plants and bryophyte floras of Arctic Canada [46–48] for bryophytes (mosses and liverworths). Nomenclature of the bryophyte reference library follows tropicos.org [49].

The most important herbivores present on the island are the two lemming species, which are present throughout the year, and the greater snow goose (*Chen caerulescens atlantica*), which is present only in summer. No other herbivorous small mammal is present and large mammalian herbivores are absent. Arctic hares (*Lepus arcticus*) and Rock ptarmigans (*Lagopus mutus*) are present in very small numbers. During winter, the two lemming species share the same habitats and concentrate in mesic tundra, especially in the small gullies along streams where snow accumulates [20, 21]. Based on characteristics of vegetation and topography, we recognize three habitats for wintering lemmings: mesic tundra, stream gullies and wetlands.

Collection of lemming pellets

We sampled lemming winter nests across the study area shortly after snowmelt in 2011, following a winter of high lemming density [44]. In each of the three habitats, 20 transects, each 500 m long, were distributed randomly. All winter nests (n = 347) found along transects were collected and their habitat and position recorded. More details of the winter nest sampling are given in [50]. Additional winter nests were collected from a systematic search of three grids (7 to 11 ha each) used for summer live-trapping of lemmings (n = 327 nests) and from winter nest boxes (n = 10 nests) described by [51]. In this study, we used a subset of 74 of those winter nests; 55 from transects, 9 from trapping grids and 10 from nest boxes.

Lemming species using winter nests were identified based on the size, shape and color of feces found in nests [20, 52]. This visual identification was based on a sample of 15 pellets from each winter nest and was confirmed by DNA analysis (see below). Some nests (12 out of 74) had been used by both species, and from two of these nests we sampled pellets of both species. The final sample size was thus 76 samples (n = 22 collared lemmings and 54 brown lemmings). Pellets were dried in a filter bag placed in silica gel.

Lemming species identification using genetic methods

We took a random sample of three to five pellets from each 15-pellet sample used for visual species identification. To verify the accuracy of the genetic identification, we analyzed 6 muscle samples of each lemming species using the same methods. These samples were provided by concurrent studies on stable isotopes [3, 53]. We extracted DNA of these samples, i.e. both pellets and muscle, using methods described in [40] and in Supporting information (S1 Text). The same DNA extracts were then used both for lemming species identification and for diet analysis.

For both lemming species, we first downloaded from GenBank all the available mitochondrial Cytochrome Oxydase I (COI) sequences of the standard barcode for animals [54]. After aligning the retrieved sequences, we calculated a consensus sequence for each species. We then identified two locations where the lemming species differ by two consecutive nucleotides, with 61 nucleotides in between these locations. We designed a pair of primers specific for each species, by locating the 3′-end of each forward and reverse primers on these two different consecutive nucleotides (S1 Table). Each primer for brown lemmings was tagged with an additional 10 base pairs poly-A on the 5′-end to differentiate the two lemming genera by amplicon size (104 bp for collared and 125 bp for brown).

The DNA extracts were amplified in a 40 μl volume reaction containing 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.25 μM of each primer and 0.8 U AmpliTaq Gold DNA Polymerase (Life). After 10 min at 95°C, PCR reactions were performed for 35 cycles of 30 sec in 95°C, 30 sec in 58°C and 30 sec in 72°C. Amplicons were checked and amplicon sizes estimated on the QIAxcel System (QIAGEN). See S1 Fig. for an example of a capillary electrophoresis output from the program.

Lemming diet analysis using DNA metabarcoding

We analysed the vascular plant and bryophyte content of the DNA extracts of lemming pellets using DNA metabarcoding. The method is based on first amplifying a targeted plastid DNA region (*trn*L (UAA) intron) using universal primer for plants, and thereafter high-throughput DNA sequencing [40, 55]. We used two complementary primer pairs, *g-h* and *c-h* [55, 56]. The *g-h* primer pair gives precise taxonomic results for small rodent diets [40] but is biased towards seed plants. To assess also the abundance of bryophytes in lemming diets, we used primer pair *c-h*, which is universal for all plant taxa. Details of the DNA analysis are given in [40] and in Supporting information (S1 Text).

Sequence reads were analyzed using the OBITools software package (http://metabarcoding.org/obitools/doc/index.html). As reference for the primer pair *g-h*, we used a combined reference library of 815 arctic [57] and 835 north boreal [58] vascular plant species. Sequences with poor match with these reference libraries were compared with data retrieved from the EMBL Nucleotide Sequence Database (version 111, available at http://www.ebi.ac.uk/embl/). For the *c-h* primer pair, we used the same taxonomic reference library of arctic and boreal vascular plant species, supplemented with a new library of 455 arctic and boreal bryophyte species (see details below and a detailed list of taxa in S2 Table). For both primer pairs, the retrieved taxon lists were compared with the local flora of Bylot Island (Benoit Tremblay, *in prep*). Among all sequences identified at the family or genus level, 0.2% belonged to taxa absent from the site (e.g. *Pinus*, *Picea*, *Betula*). These were considered identification errors or contamination and removed from the dataset. At the species level, some identified species were absent from the general area but in most cases, a closely related species was known to be present but not included in our reference libraries. In those cases, we assigned the sequences to the species known to be present at the site. Details of sequence cleaning and annotation are described in [33] and in Supporting information (S1 Text).

Reference library of arctic and boreal bryophytes

Sampling for construction of the bryophyte taxonomic reference library was carried out in two museum collections (the Bryophyte herbaria at the Norwegian University of Science and Technology (TRH) and V. L. Komarov Botanical Institute (LE)), and the selected specimens were checked by taxonomic experts. For most species, we sampled two specimens originating from different parts of the species distribution area to cover possible intraspecific sequence variation. All DNA extracts are preserved in the DNA Bank of the Natural History Museum, University of Oslo, Norway.

Approximately 5 mm^2 of dried leaf tissue was ground in 2.0 mL tubes with tungsten carbide beads for 2 min at 15 Hz in a mixer mill (MM301, Retsch). A Gene Mole extraction robot was used to extract the DNA using the MoleStripTM Plant DNA kit. Amplification and sequencing of the P6 loop of the *trn*L intron was performed using the *c* and *d* primers [55]. PCRs (10 μL) contained 3μL 1:10 diluted DNA, 0.4 μM of each primer ([55]), 1 mM dNTPs, 0.1% bovine serum albumin, 2.5 mM $MgCl_2$, 1x PCR buffer and 0.4 UAmpliTaq DNA polymerase (Applied Biosystems). After 10 min at 95°C, PCR reactions were performed using 30 cycles of 30 sec in 95°C, 30 sec in 50°C and 2 min in 72°C, followed by a final extension of 5 min at 72°C. PCR products were sequenced in both directions on an ABI 3730 sequencer. Quality checking and cleaning of the library was performed by comparing all sequences to published sequences with NCBI/BLAST, and by carrying out phylogenetic analyses including sequences from closely related taxa to verify taxonomic identity. In some cases, new specimens were selected and sequenced after the first round of library cleaning. Formatting of the reference library, including annotations of the sequences, was carried out using the OBITools. The final library was formatted by *in silico* PCR on the obtained sequences (using the program ecoPCR; [59]), with the *trn*L *c* and *trn*L *h* primers (five mismatches allowed between primer and the target sequence). The library is deposited in the Dryad Digital Repository (http://datadryad.org/), doi: 10.5061/dryad.4rr39.

Plant availability

To assess plant availability, we used the data of [44] (data given in S3 Table). In their study, plant biomass was sampled at the end of the 2010 growing season (early August) in snowbeds (n = 16) where signs of lemming use had been found in previous years. Plant biomass data thus represent what was available for the lemmings at the onset of winter. Snowbeds were sampled in two different habitats; stream gullies (n = 8) and mesic tundra (n = 8). The snowbeds were separated from each other by at least 50 m. Within each snowbed, one quadrate (20 × 50 cm) was located randomly and plant availability was estimated. Vascular plant biomass was measured by clipping all aboveground vascular plant material at the ground level. Dead material was removed and the remaining live material was sorted by family, genus or species, dried to constant mass at 45°C, and weighted. Moss proportion cover (to the nearest 5%) was visually estimated for each genus or species; all aboveground live (i.e. green) material was clipped, dried to constant mass at 45°C and weighed. Total biomass was divided by the surface area of the sampled quadrates and multiplied by the proportion estimates for each taxon.

Ethics statement

All necessary permits were obtained for the described field work on Bylot Island which is within the Sirmilik National Park (Parks Canada permit #SIR-2011–8213). No protected species were sampled.

Data analyses

The resulting datasets of lemming diets consisted of a count of sequences per plant taxon per pellet sample. We combined the information obtained from the two primer pairs as follows. We first calculated the proportion of each plant family for every sample (sample representing pellets of a given species from a given winter nest) based on the number of DNA sequences identified, for each primer pair separately. For the *g*-*h* primer pair, we discarded the few bryophyte sequences identified and retained only the vascular plants (including ferns) for those calculations. We then weighted (i.e. multiplied) the proportion of each vascular plant family of each sample in the *g*-*h* dataset by the corresponding, overall proportion of vascular plants determined with the *c*-*h* primer pair. Finally, we combined those weighted proportions of vascular plant families with the proportions of moss families determined with the *c*-*h* primer pair. For one collared lemming sample, amplification by the *g*-*h* primer pair failed and we thus used data from the *c*-h primer for proportion of vascular plant families. Even though DNA metabarcoding data for plants probably reflects small rodent diets well [40], some biases may still occur [34, 40] and we therefore also report the number of samples in which a given taxon was found (S4 Table).

We tested for differences in proportion of various food items (i.e. monocots, dicots and plant families accounting for >2% of the diet) between habitats (three levels) and lemming species (two levels) using ANOVAs. Data were rank-transformed before analysis because variances were heterogeneous and residuals were not normally distributed. Interactions between habitat and species were examined with the aligned rank transformation [60] but were never significant ($P > 0.05$) and are thus not reported.

We assessed diet overlap between the lemming species using Schoener's diet overlap index [61]. The index varies between zero and one, zero indicating no diet overlap and one indicating complete overlap. We calculated index values at plant family level in two different ways; 1) including all plant families and 2) excluding Salicaceae as they dominated the diets (see results). To assess diet diversity, we calculated an index of trophic niche width using the Shannon entropy (denoted hereafter as TNW) (equation given in [62]).

We further assessed whether intraspecific diet overlap (i.e. among individuals of the same species) differed between lemming species, using the individual specialization index (IS), which is an extension of the Schoener's overlap index [63], assuming that pellets found in different nests originated from different individuals. To ensure that the index values of the two species were comparable in spite of different sample size, we resampled 100 times a random sample of brown lemming individuals corresponding to the sample size of collared lemmings ($n = 22$). We then compared the simulated IS for brown lemmings (i.e. average of the resampled IS) to their observed IS (i.e. acquired by including all individuals). As these values were identical, we did not use the resampled data in further analyses. Finally, we tested whether the lemming species differed in terms of IS using ANOVA. Diet overlap and diversity analyses were done in the software R 3.0.3. [64], and package RInSp [65] was used for the within species analysis.

We evaluated food selection by combining data on diet composition and plant availability. We used the selection ratio of Manly [66], which is the ratio of mean proportion of food item *i* in the diet over mean availability of that item. We calculated variance using the formulas of Manly for a situation where both use and availability were sampled. Because plant availability was only estimated in stream gullies and mesic tundra habitats, we excluded lemming pellet samples collected in wetlands from food selection analysis. Pellet samples from the two remaining habitats were pooled because diet did not differ between these two habitats (see results) and availability is similar [44]. Sample sizes for this analysis were 47 for brown lemmings and 20 for collared lemmings. Vascular plants and mosses were sampled using different techniques, and thus availability is not comparable between these two groups. Selection was therefore analyzed separately for vascular plants and mosses; hence, availability and use sum up to 1 within each of these taxonomic groups. We excluded Ericaceae, an abundant vascular plant family not consumed by lemmings (see results), from the calculations of plant availability because its inclusion would have biased selection for all other vascular plant families towards positive.

Results

Bryophyte reference library

For the bryophyte taxonomic reference library, sequences covering the complete P6 loop in the chloroplast *trn*L (UAA) intron were obtained from 498 specimens representing two divisions: Bryophyta (mosses) and Marchantiophyta (liverworts). The library includes 18 orders of mosses, 45 families, 137 genera, and 340 species. Liverworts were represented by 86 species from 45 genera, 28 families and three orders (see S2 Table, for a complete taxon list).

Lemming species identification

We were able to test genetically the lemming species identified in the field based on pellet size, shape and color for 74 of our 76 pellet samples (54 brown and 20 collared lemmings). The genetic identification was based on the difference between amplicon size. The amplicone sizes estimated by the QIAxcel System were on average 128 bp for collared lemming and 146 bp for brown lemming. While these were longer than presumed (see methods), the relative difference remained. (S1 Fig.). The genetic analysis confirmed field species identification in 98.6% of the cases. Only one pellet sample identified as brown lemming in the field turned out to be a collared lemming according to the genetic analysis. All muscle samples (n = 12) were identified to the correct species.

Taxonomic precision of lemming diet data

A total of 45,633 sequences were obtained with the *g*-*h* primer pair (608 sequences/sample on average) and 22,707 with the *c*-*h* primer pair (299 sequences/sample on average). Overall, 99.5% of the sequences were identified at the family level, 32.6% at the genus level and 7.5% at the species level. The low resolution at genus and species levels was largely caused by Salicaceae, a common family in our samples (see results) for which the *g*-*h* primer pair has in general low resolution [57]. Excluding this family for the *g*-*h* primer pair, 72.7% and 16.7% of the sequences were identified at the genus and species levels, respectively.

Lemming diet

For collared/brown lemmings, we collected 8/15 pellet samples in mesic tundra, 12/22 in stream gullies and 2/7 in wetlands and 0/10 in unknown habitat. The proportion of monocotyledons/dicotyledons (and mosses for brown lemmings) did not differ between mesic tundra and stream gullies for either of the species (collared, $p > 0.329$; brown, $p > 0.291$; wetland excluded due to small sample size) or for any individual plant family that we examined (collared, $p > 0.08$; brown, $p > 0.06$ for all tests); therefore, habitats were pooled for subsequent analyses.

The winter diet of collared lemmings was composed of 86% dicotyledons, 14% monocotyledons and <1% mosses (n = 22). In comparison, the diet of brown lemmings was composed of 65% dicotyledons, 9% monocotyledons and 26% mosses (n = 54). Even though the diet of brown lemmings had less dicotyledons than the one of collared lemmings ($F_{1,74} = 21.4$, $p < 0.001$), there was a high overlap in diet composition (overlap index = 0.75) between the two species with respect to these two broad groups of vascular plants.

At the family level, diets of both lemmings were clearly dominated by Salicaceae (Fig. 1). Among vascular plants, Poaceae was also found to be relatively abundant in both species diets. Even though collared lemmings consumed more Salicaceae ($F_{1,74} = 28.8$, $p < 0.001$) and Poaceae ($F_{1,74} = 8.9$, $p = 0.004$) than brown lemmings (n = 54) overall, we noted again a high overlap in vascular plant families (overlap index = 0.67) between the two species. Salicaceae is represented at the site only by the genus *Salix*, which was thus identified as the dominant food item of both lemming species. See Table 1 for the full list of genera and species identified and S4 Table for the number of samples in which a given taxon was found.

The high diet overlap between lemming species was mainly caused by the dominance of Salicaceae as the remaining proportions of taxa in diets differed between species (overlap index = 0.32). In addition to Salicaceae and Poaceae, the diet of collared lemming included 10 other vascular plant families and 3 moss families but these comprised only 4% of the diet (Fig. 1). In the diet of brown lemmings we found more families; in addition to Salicaceae and Poaceae, 12 vascular plant families and 10 moss families composed on average 37% of the diet (Fig. 1). Of these, the moss families Polytrichaceae and Aulocomniaceae and the vascular plant families Polygonaceae and Saxifragaceae were most prominent (Fig. 1). Thus, diet diversity of brown lemmings was higher in terms of numbers of families, but also when measured with the diet diversity index TNW; index value for collared lemmings was 0.60, while it was 1.60 for brown lemmings. On the other hand, the two lemming species did not differ significantly in terms of intraspecific diet specialization. Although the IS index was 0.64 for brown lemming and 0.85 for the collared lemming, this difference was not significant ($F_{1,74} = 0.31$, $p = 0.58$).

Food selection

The most abundant vascular plant family, Ericaceae, accounted for 58% of the plant biomass in the winter habitats of lemmings on Bylot Island [44]. However, it was not consumed by either lemming species and the sole species of this family present, *Cassiope tetragona*, was avoided; it was thus considered non-food for lemmings. Within the plant taxa that were eaten, no taxa were strongly selected or avoided. For collared lemming, Salicaceae was consumed in proportion to its availability, Poaceae tended to be selected for whereas Juncaceae, Rosaceae, and possibly Fabaceae were avoided (Table 2). For brown lemmings, Salicaceae was also consumed in proportion to availability and Juncaceae was avoided. Polygonaceae and Saxifragaceae had high selection ratios due to their very low availability but these were not significant due to the high variance. Among mosses, Aulacomniaceae and Dicranaceae had high selection ratios but these were not significantly different from 1, also due to their high variance (Table 1). Polytrichaceae, the most common moss family, tended to be selected whereas other abundant moss families like Amblystegiaceae, Hylocomiaceae and Scapaniaceae were not consumed.

Discussion

Our study is the first to examine the winter diet of lemmings using DNA metabarcoding techniques, as all previous studies have relied on microhistological analysis. Due to this novel method, we were able to elucidate lemming winter diets at an unprecedented level of details. Our analysis of two sympatric lemming species revealed similarities with previous studies but also

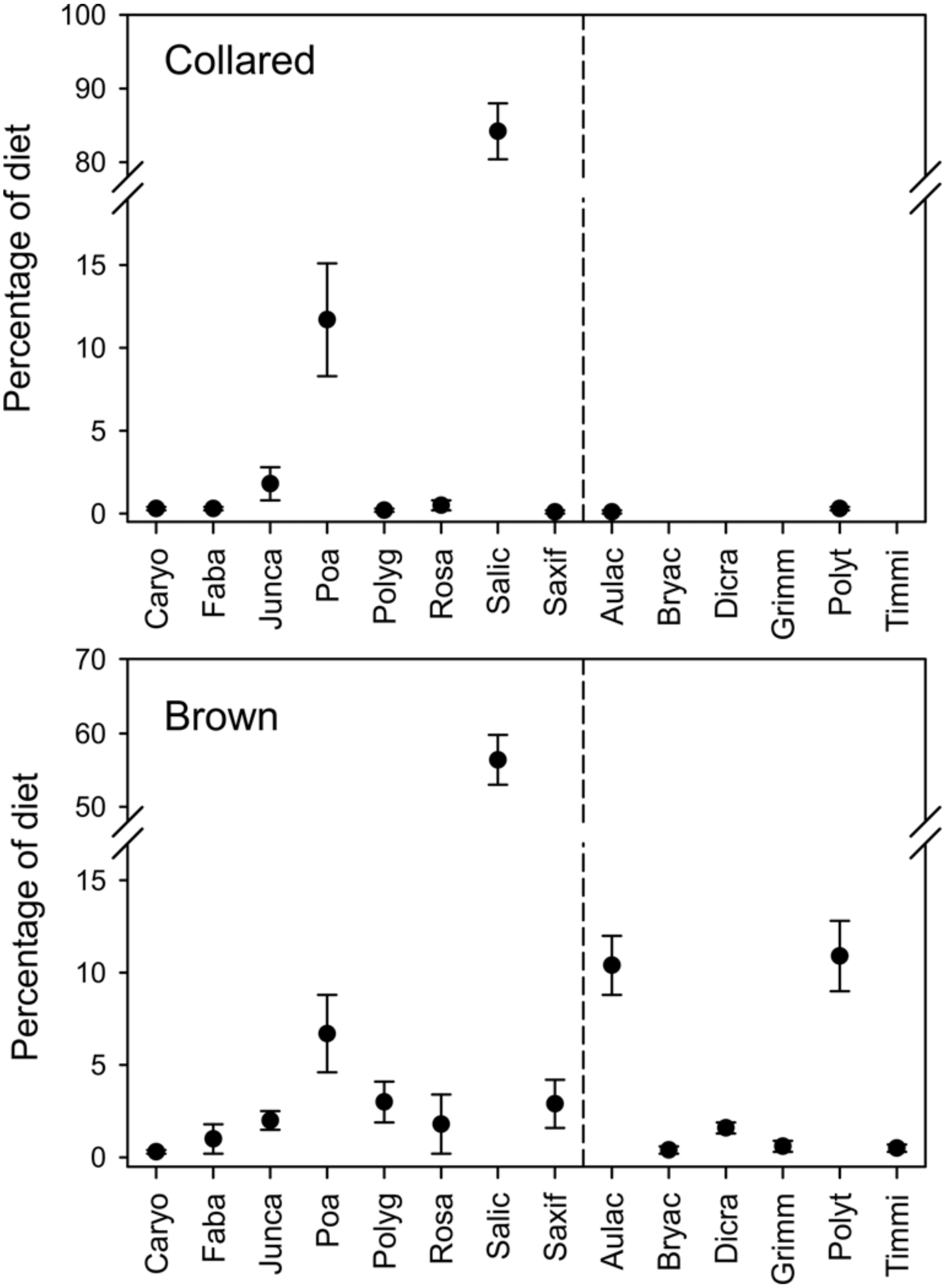

Figure 1. Composition of winter diets of collared and brown lemmings. Diets (mean ± SE) of collared (n = 22) and brown lemming (n = 54) during the winter 2010–11 on Bylot Island, Nunavut, Canada, based on DNA metabarcoding sequences extracted from pellets. Vascular plant and moss families are separated by a dashed line. Other or unidentified items accounted for 0.5% and 1.2% of the collared and brown lemming diet, respectively (not shown on graph). Taxa without dot on the graph were not found. Families are Caryophyllaceae (Caryo), Fabaceae (Faba), Juncaceae (Junca), Poaceae (Poa), Polygonaceae (Polyg), Rosaceae (Rosa), Salicaceae (Salic), Saxifragaceae (Saxif), Aulacomniaceae (Aulac), Bryaceae (Bryac), Dicranaceae (Dicra), Grimmiaceae (Grimm), Polytrichaceae (Polyt) and Timmiaceae (Timm).

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Table 1. Food items identified in lemming winter diets.

Family	MOTUs identified
Vascular plants	
Asteraceae	Asteroideae, Gnaphalieae, Carduinae
Brassicaceae	*Cardamine* sp., *Cardamine pratensis*, *Draba* sp.
Caryophyllaceae	*Cerastium* sp., *Cerastium arcticum*, *Stellaria* sp., *Stellaria longipes*
Cyperaceae	*Carex* sp., *Carex aquatilis*, *Eriophorum* sp, *Eriophorum angustifolium*
Fabaceae	*Astragalus* sp., *Oxytropis* sp.
Juncaceae	*Luzula* sp., *Luzula nivalis/L. confusa*
Orobanchaceae	*Pedicularis* sp., *Pedicularis sudetica*
Papaveraceae	*Papaver* sp.
Poaceae	Pooideae, Poeae, Triticeae, Agrostidinae, Poinae, *Festuca* sp., *Poa* sp., *Deschampsia brevifolia/D. sukatchewii*, *Pleuropogon sabinei*
Polygonaceae	*Bistorta vivipara*, *Oxyria digyna*
Ranunculaceae	*Ranunculus* sp., *Ranunculus pygmaeus*
Rosaceae	*Dryas* sp., *Potentilla* sp.
Salicaceae	*Salix* sp.
Saxifragaceae	*Saxifraga* sp., *Saxifraga hirculus*, *Saxifraga oppositifolia*
Pteridophytes	
Equisetaceae	*Equisetum* sp.
Mosses	
Aulacomniaceae	*Aulacomnium* sp., *Aulacomnium turgidum*
Bartramiaceae	(identified to family level only)
Bryaceae	*Bryum* sp., *Pohlia wahlenbergii*[1], *Bryum pallens*
Dicranaceae	*Dicranum* sp., *Dicranum brevifolium*
Ditrichaceae	*Ditrichum* sp., *Distichium* sp., *Distichium capillaceum*
Grimmiaceae	*Racomitrium* sp., *Racomitrium lanuginosum*, *Racomitrium canescens*
Polytrichaceae	*Polytrichum* sp., *Polytrichum hyperboreum*
Pottiaceae	*Tortula* sp.
Rhabdoweisiaceae	(identified to family level only)
Timmiaceae	(identified to family level only)

List of MOTUs (molecular operational taxonomic units) at the subfamily, tribe, genus or species level, identified in lemming winter diets on Bylot Island.

[1] Species included in Bryaceae in the data analysis, but in Mniaceae in the Bryophyte reference library.

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some startling differences. Interestingly, our results do not fit our prediction that these sympatric species should have clearly different winter diets, as the diet of both species showed a high degree of overlap. Diets of both lemming species were by far dominated by *Salix* and moss consumption was relatively low.

Lemming winter diets

On Bylot Island, mosses were barely consumed by collared lemmings and their winter diet was dominated by dicotyledons, in line with previous studies [8, 30, 32]. However, within dicotyledons, variable patterns of consumption have been found among studies. A dominance of *Salix* was found both in Northern Alaska and Northern Greenland [19, 30] but of *Dryas* at Pearce Point and Igloolik in Northern Canada [8, 32]. These dietary differences seem to largely reflect differences in availability among sites as willow was abundant and *Dryas* scarce in Alaska but

Table 2. Availability, use and selection of major food items (>1% of the diet) consumed by lemmings in winter.

Food item	Availability	Use	Selection ratio (w_i)	SE of Selection ratio	
(a) Collared lemming					
Vascular plant families[1]					
Fabaceae	0.013	0.003	0.2	0.5	(–)
Juncaceae	0.113	0.018	0.2	0.1	–
Poaceae	0.054	0.124	2.2	2.4	0
Rosaceae	0.043	0.005	0.1	0.2	–
Salicaceae	0.713	0.839	1.2	0.2	0
(b) Brown lemming					
Vascular plant families[1]					
Fabaceae	0.013	0.010	0.8	1.9	0
Juncaceae	0.113	0.029	0.3	0.2	–
Poaceae	0.056	0.091	1.6	1.7	0
Polygonaceae	0.008	0.049	6.5	19	0
Rosaceae	0.043	0.048	1.1	1.7	0
Salicaceae	0.713	0.727	1.0	0.2	0
Saxifragaceae	0.004	0.036	8.4	33	0
Moss families[2, 3]					
Aulacomniaceae	0.027	0.334	16.1	28	0
Dicranaceae	0.015	0.062	4.1	8.3	0
Polytrichaceae	0.267	0.501	1.9	0.8	0

Availability is based on biomass of vascular plants and mosses sampled in stream gullies and mesic tundra in August 2010, at peak growth (n = 16 plots). Both availability and use are presented as proportions. Selection was analyzed separately for vascular plants and mosses and availability and use sum to 1 within each of these taxonomic groups (0 = no selection, + = positive selection, – = negative selection; based on 95% confidence interval; signs in parenthesis indicates selection ratio based on 90% confidence interval).

[1] Ericaceae, which accounted for 58% of all vascular plant biomass, was excluded because it was not consumed by either lemming species.

[2] Selection could not be calculated for Bryaceae, Grimmiaceae and Timmiaceae because these plants were not found that year in our availability sampling plots.

[3] Other important moss families present at the site and not consumed by lemmings include Scapaniaceae (availability = 0.228), Amblystegiaceae (0.195), Hylocomiaceae (0.193), Ptilidiaceae (0.043) and Ditrichaceae (0.019).

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the reverse was true at Pearce Point and Igloolik [8]. Generally, *Salix* was consumed by collared lemmings in higher proportion than its availability or preferred in feeding trials [8, 31]. On Bylot Island, *Salix* was very abundant in snowbeds and consumed in proportion to its availability whereas Rosaceae (*Dryas* and *Potentilla*) were not very common and were actually avoided by collared lemmings. The abundant use of *Salix* on Bylot Island thus fits well with the previous observations on the use of *Salix vs Dryas* being determined by their availability.

Mosses were consumed by brown lemmings, but accounted for a lower proportion of their winter diet on Bylot Island (26%) than at Barrow, Alaska (40%; [30]) and Igloolik, Nunavut (>80%, [32]). In sharp contrast with previous studies, we found that dicotelydons (primarily *Salix*), instead of monocotyledons, dominated the winter diet of brown lemmings. Grasses and sedges were the dominant vascular plant food items eaten by brown lemmings in both summer and winter at all other sites [30, 32, 67] with *Salix* being a negligible component of their diet. Furthermore, feeding trials with captive animals have shown that brown lemmings find *Salix* rather unpalatable [31, 67]. On Bylot Island, grasses and sedges are abundant in the wet summer habitat of the brown lemmings, but scarce in their preferred winter habitat, i.e. snow beds in stream gullies [20]. In contrast, *Salix* is very abundant in the stream gullies and the surrounding mesic tundra and its availability pattern may explain this unexpected result. A gradual switch to willows in fall may allow the digestive tract of brown lemmings to adapt to the relatively high content of secondary compounds present in *Salix* [67]. This hypothesis is supported by the findings of Rodgers and Lewis [31] who noted that naïve animals born and raised in captivity consumed more shrubs (and especially *Salix*) than animals captured in the wild. Moreover, DNA metabarcoding analysis of the stomach contents of five individuals collected from Bylot Island indicates that Salicaceae and Rosaceae are important food items during the summer as well (Soininen and Gauthier, unpublished data). Finally, because microhistological methods have a tendency to overestimate monocotyledon proportions in diets [68, 69], their proportion may have been overestimated in previous studies. However, our findings reveal that brown lemming diets may be more flexible and spatially variable than previously believed.

In summary, we found indication that diet of both lemming species on Bylot Island is heavily affected by food availability, which adds to increasing evidence showing that availability is an important determinant of small rodent diets [3, 8, 41]. Furthermore, the large differences between locations revealed by our study may imply that both competitive interactions between lemmings species and lemming-vegetation interactions may vary greatly across the arctic tundra.

Species interactions and food web dynamics

The observed interspecific overlap index is clearly very high and the same level as within herbivore species in other studies [70]. While herbivores may segregate diets also by means of habitat selection [71] and selection for different plant parts [19], this is unlikely to be the case for collared and brown lemmings. First, the species have similar winter habitat preferences [20]. Second, small rodents share many characteristics of digestive morphophysiology and are thus unlikely to have preferences for different plant parts. Brown and collared lemmings hence present a high potential for exploitation competition during winter. Whether this potential translates into actual competition would depend on food limitation. *Salix* is abundant (forming up to 80% of non-Ericaceae biomass) on Bylot Island, and lemming winter grazing has a negligible impact on snowbed vegetation, even during a year of peak lemming abundance [44]. This suggests that the high potential for exploitation competition is not currently expressed due to a lack of food limitation. This is further suggested by the low interspecific diet overlap of the non-*Salix* portion of the diet. Our results thus highlight that even in the High Arctic, food resources may be abundant enough for herbivores to cope with high diet overlap.

A recent analysis of the Bylot Island food web [72], shows that lemmings consume a very small proportion of the annual primary production. Our results suggest that Salicaceae could be exposed locally to heavy winter browsing by lemmings, especially during peaks in population density. On the other hand, little evidence has been found that lemming grazing during winter has a strong impact on *Salix* biomass in snowbed vegetation on Bylot Island [44]. However, only total biomass was sampled by cutting plant material in the latter grazing impact experiment. Therefore, other potentially important effects of lemmings on *Salix* demography, such as mortality of new recruits [73, 74], was not quantified. Thus, the impact of overwintering lemmings on *Salix* demography could still be substantial in spite of a low effect on total biomass.

Recently, increasing growth of erect shrubs, and especially *Salix*, has been observed in response to climate warming in many locations throughout the circumpolar Arctic (reviewed in [75]). On the other hand, herbivory appears to be a factor limiting shrub encroachment in many areas [75, 76]. Small herbivores, such as voles and lemmings, can have a substantial impact on *Salix* shrubs as saplings can suffer up to 90% mortality in Finnmark, Northern Norway, in peak years of small rodent abundance [74] (V. T. Ravolainen unpublished data). Even though prostrate *Salix* species (*S. arctica* and *S.herbaceae*) dominate in the snowbeds used by lemmings at our study site, erect shrubs (*S. richardsonii*) are occasionally present. As snowbeds are generally favorable to the growth of erect shrubs [74, 77], the consumption of *Salix* by both lemming species present on Bylot Island is a factor that could potentially limit encroachment of erect shrubs in this habitat despite a warming climate [78].

Methodological progress

Shape, size and color of fecal pellets collected in the field have been used as criteria to identify lemming species in previous studies when both brown and collared are present [20, 32, 52]. For the first time, we validated this technique using genetic techniques and showed that it was highly reliable (>98% correct identification). Thus, misidentification of lemming fecal pellets was not an issue in our study.

DNA metabarcoding of feces has been successfully used to describe diets of several large herbivores, including gazelles, chamois and brown bear [37, 38, 79]. Still, inference of the quantity of each ingested taxon from the number of DNA sequences retrieved should be done with some caution. Several potential biases, such as taxon-specific numbers of chloroplasts in the consumed tissue and differential digestion may influence the observed patterns [34]. However, for stomach contents, results of food item proportions in small rodent diets gained by DNA metabarcoding correspond rather well to those gained by microhistological methods [40]. Furthermore, Willerslev et al. [58] have recently demonstrated that DNA metabarcoding results of sheep rumen content corresponded well to known proportions in their diets. As previous studies on small rodents have used mainly stomach contents [33, 40, 41], no evaluations between food intake and DNA metabarcoding results of feces are published yet. Still, preliminary results of a study comparing small rodent stomach content and feces from the rectum of the same individual (n = 40) showed a good correspondence [80], indicating that differential digestion is among taxa unlikely to be a major issue in small rodents. In addition, the surprising abundance of Salicaceae in our results is unlikely to be an artifact. The DNA fragment amplified by the primer pair *g-h* for *Salix* is of no shorter length than for example the Poaceae genera we identified (Salix being 56bp and the grass genera 52–53bp). It is therefore unlikely that *Salix* DNA would have been better preserved during digestion than other taxa. We are thus confident that our results reflect actual diet proportions rather well.

The newly constructed bryophyte reference library comprising common arctic and north boreal species allowed us to achieve a high and reliable taxonomic resolution of the moss component of lemming diets. Mosses are a key plant group in the arctic ecosystems, both in terms of biomass and function [81, 82] and as a food item for many herbivores [33, 83, 84]. DNA-based identification of mosses species in the diets of arctic herbivores is currently developing [33, 41, 85], as microhistologic identification of moss species in diet samples is virtually impossible. Reliable reference data of bryophyte DNA is therefore essential especially for the Arctic. Existing public reference DNA databases such as GenBank provide more limited information on bryophyte taxa as compared to the vascular plant groups. Moreover, specimen identification errors, taxonomic complexities and discrepancies between different nomenclatures may lead to erroneous identification of the DNA sequence data. Local reference libraries, as used for both vascular plants [57, 58] and bryophytes in this study, are constructed based on material that is collected and verified by taxonomic experts, and archived and stored in museum collections for future reference. Hence, high quality of taxonomic assignment is ensured.

Conclusion

The taxonomic resolution achieved by the DNA metabarcoding method made it possible to assess lemming winter diet composition at an unpreceded level of detail. We can thus conclude that the two lemming species on Bylot Island show high diet overlap during winter and consequently have a high potential for competition for food. However, this potential apparently does not translate into actual competition because their main food item, *Salix*, is abundant, lemming grazing has little impact on the vegetation, and the non-*Salix* portion of diets overlaps little between the species. It seems therefore unlikely that the species would suffer from strong food competition in the focal system. Our results highlight that even during the long high arctic winter, plant food resources—in relation to their use—may be abundant enough for herbivores to allow for high diet overlap. Moreover, our study underlines that in order to understand interspecific resource competition, it is important to assess how patterns of use and availability are related.

Supporting Information

S1 Text. Additional methodological details of the DNA metabarcoding analysis.
(DOCX)

S1 Table. Primer pairs used for detecting lemming species. Primer pairs and corresponding COI-fragment used for detection of lemming genera *Lemmus* and *Dicrostonyx*.
(DOCX)

S2 Table. Bryophyte reference library. Taxonomic content of the Arctic-boreal bryophyte reference library Version 1.0 with sequences of the short P6 loop of the *trn*L plastid region (available from the Dryad Digital Repository, http://datadryad.org/). Column "lib_refN" refers to the reference number in the library
(DOCX)

S3 Table. Plant family availability data. Plant biomass (g/m^2) in August 2010 sampled on Bylot Island. In column "Plot ID" M refers to mesic habitat and R to river gully habitat. Plant family names are abbreviated (-ceae removed), in columns "Other" and "Total" v refers to vascular plants and b to bryophytes.
(DOCX)

S4 Table. Plant families found in lemming diets. Frequency of occurrence of plant families in the winter diets of collared and brown lemmings during the winter 2010–11 on Bylot Island based on DNA metabarcoding of pellets. For vascular plants, data are based on primer pair *g-h*, for mosses on primer pair *c-h*.
(DOCX)

S1 Fig. An example of a capillary electrophoresis output from QIAxcel System. Colums represent 12 different samples. Horizontal bands represent DNA fragments, numbers along the edge of columns show scale in bp length. Two band sizes can be seen along 150bp line, indicating samples of *Lemmus* (146bp, samples 1–4 and 11–12) and *Dicrostonyx* (128bp, samples 5–10).
(TIF)

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Author Contributions

Conceived and designed the experiments: EMS G. Gauthier FB DB NGY LG PT. Performed the experiments: EMS FB LG PT. Analyzed the data: EMS G. Gauthier NGY. Wrote the paper: EMS G. Gauthier FB DB NGY LG PT G. Gussarova EB. Created the reference library for bryophytes: G. Gussarova EB CB KH HKS LE ASN.

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Soininen et al: High overlapping diet in two sympatric lemming species during winter revealed by DNA metabarcoding - Supplementary material

Appendix 1: Additional methodological details of the DNA metabarcoding analysis

Appendix 2: Bryophyte reference library

Appendix 3: Supplementary figures and tables

Appendix 1: Additional methodological details of the DNA metabarcoding analysis

DNA analysis

Prior to DNA extraction of pellets, 1 ml of Tissue Lysis Buffer (consisting of 0.1 M Tris-HCl, 0.1 M EDTA, 0.01 M NaCl and 1% of N-lauryl sacrosine, pH adjusted between 7.5-8) was added to each sample and samples were kept overnight in a fridge to enable them getting soaked. Pellets were subsequently grinded using a toothpick and orbitally shaked for 2 h at 56 °C. After this, 100 µl were sampled out from each sample and underwent DNA extraction.

Total DNA of pellets and muscle samples was extracted with the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany), following the manufacturer's instructions. The DNA extracts were recovered in a total volume of 300 µl. Mock extractions without samples were systematically performed to monitor possible contaminations.

DNA of the P6 loop of the cholorplast *trn*L (UAA) intron was amplified using primer pairs *g-h* and *c-h* [1,2], i.e. each sample was amplified once with each primer combination. Each sample was tagged at the 5' end with an individual tag (7 to 9 bp long) with at least three differences between tags. The amplifications were carried out in a final volume of 25 µl, using 2.5 µl of DNA extract as a template. The amplification mixture contained 1 U of AmpliTaq® Gold DNA Polymerase (Applied Biosystems, Foster City, CA), 10 mM Tris-HCl, 50 mM KCl, 2 mM of $MgCl_2$, 0.2 mM of dNTP, 0.3 µM of each primer and 0.005 mg of bovine serum albumin (BSA, Roche Diagnostic, Basel, Switzerland). For amplification of the primer pair *g-h*, the mixture underwent 10 min at 95 °C, followed by 45 cycles of 30s at 95°C and 30s at 55°C. No elongation step was included. For the primer pair *c-h* amplification, the mixture underwent 10 min at 95 °C, followed by 45 cycles of 30s at 95°C, 30s at 50°C and 1 min at 72°C.

PCR products were purified using the MinElute PCR purification kit (Qiagen GmbH, Hilden, Germany). DNA quantification was carried out using the BioAnalyzer (Agilent Technologies, Inc., Santa Clara, CA). Taking these concentrations into account PCR products were pooled leading to equal amounts per sample. Then, a mix was made taking into account these DNA concentrations in order to obtain the same number of moles per PCR product corresponding to the different pellet samples. Pyrosequencing was done on a 454 GS Junior System using Titanium chemistry.

Sequence cleaning

The samples included in this study were analysed as a part of a larger dataset, composed of 192 samples of small rodent diets (partly published in [3] and [4]). In the following, we refer to this dataset as the "full dataset". The sequence data was analyzed using software package OBITools (available at http://metabarcoding.org/obitools). First, tag and primer sequences were identified to sort sequences to individual samples (*ngsfilter*). Up to two erroneous base pairs were allowed per primer, but sequences with an error in the tag sequence were removed. Also, sequences with fewer than four reads in the full dataset were discarded. Sequences with unrealistic short length were discarded, using a threshold of 50 bp for the *c-h* primer pair and a threshold of 8 bp for the primer pair *g-h*. Potential PCR errors were discarded using *obiclean* software (included in OBITools). The software identifies progressive changes of one bp and defines clusters which include maximum threshold proportion of changed sequences. We used 10% as the clustering threshold. Thereafter, the program retains the most abundant sequence of the cluster.

Sequence annotation

As taxonomic reference libraries for the primer pair *g-h*, we first used a combined library of 815 arctic vascular plant species [5] and 835 north boreal vascular plant species [6]. We included in the final dataset all sequences with a ≥ 98% match with this reference library. Of the remaining sequences, we included those with a ≥ 98% match to a sequence in a database constructed by extracting P6-loop sequences from the EMBL Nucleotide Sequence Database (available at http://www.ebi.ac.uk/embl/) by using the software ecoPCR ([7] available at http://www.grenoble.prabi.fr/trac/ecoPCR). For the *c-h* primer pair, we used the same taxonomic reference library of arctic and boreal vascular plant species, supplemented with a new library containing 450 arctic and boreal bryophyte species (see Appendix 2).

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Appendix 2: Bryophyte reference library

Table S1. Taxonomic content of the Arctic-boreal bryophyte reference library Version 1.0 with sequences of the short P6 loop of the *trn*L plastid region (available from the Dryad Digital Repository, http://datadryad.org/). Column "lib_refN" refers to the reference number in the library.

Division/Order/Family	Genus	Species		lib_refN
Bryophyta				
Andreaeales				
Andreaeaceae	*Andreaea*	*alpestris*	(Thed.) Schimp.	ch_671
		alpina	Hedw.	ch_672
		blyttii	Schimp.	ch_673
		crassinervia	Bruch	ch_010
		nivalis	Hook.	ch_675
		obovata	Thed.	ch_676
		rothii	F.Web. & D.Mohr	ch_677
		rupestris	Hedw.	ch_514
		rupestris	Hedw.	ch_678
		sp.		ch_513
Bryales				
Aulacomniaceae	*Aulacomnium*	*palustre*	(Hedw.) Schwaegr.	ch_638
		palustre	(Hedw.) Schwaegr.	ch_520
		turgidum	(Wahlenb.) Schwaegr.	ch_521
Bartramiaceae	*Bartramia*	*halleriana*	Hedw.	ch_689
		ithyphylla	Brid.	ch_1147
		pomiformis	Hedw.	ch_1021
		sp.		ch_033
	Conostomum	*tetragonum*	(Hedw.) Lindb.	ch_1148
		tetragonum	(Hedw.) Lindb.	ch_512
	Philonotis	*fontana*	(Hedw.) Brid	ch_853
		tomentella	Molendo	ch_854
	Plagiopus	*oederianus*	(Sw.) H.A.Crum & L.E.Anderson	ch_289
Bryaceae	*Bryum*	*algovicum*	Müll.Hal.	ch_053
		arcticum	(R.Br.) Bruch & Schimp.	ch_702
		argenteum	Hedw.	ch_1024
		calophyllum	R.Br.	ch_058
		capillare	Hedw.	ch_703
		cryophilum	Mårtensson	ch_535
		cryophilum	Mårtensson	ch_704
		cyclophyllum	(Schwägr.) Bruch & Schimp.	ch_061
		elegans	Nees	ch_1159
		elegans	Nees	ch_62
		pallens	Swartz	ch_540
		pseudotriquetrum	(Hedw.) Gaertn., B. Mey. & Scherb.	ch_1026
		salinum	Limpricht	ch_541

		weigelii	Spreng.	ch_710
		wrightii	Sull. & Lesq.	ch_711
		sp.		ch_1157
	Plagiobryum	*demissum*	(Hook.) Lindb.	ch_855
		zierii	(Hedw.) Lindb.	ch_1168
Catoscopiaceae	*Catoscopium*	*nigritum*	(Hedw.) Brid.	ch_1029
Mniaceae	*Cinclidium*	*arcticum*	(Bruch & Schimp.) Schimp.	ch_552
		subrotundum	Lindb.	ch_647
		stygium	Sw.	ch_092
	Cyrtomnium	*hymenophylloides*	(Huebener) T.J.Kop.	ch_1175
		hymenophylloides	(Huebener) T.J.Kop.	ch_733
	Mielichhoferia	*mielichhoferiana*	(Funck) Loeske	ch_1182
		mielichhoferiana	(Funck) Loeske	ch_1183
	Mnium	*ambiguum*	H.Müll.	ch_1189
		blyttii	Bruch & Schimp.	ch_1192
		blyttii	Bruch & Schimp.	ch_255
		hornum	Hedw.	ch_1193
		marginatum	(Dicks.) P.Beauv.	ch_1191
		marginatum	(Dicks.) P.Beauv.	ch_833
		spinosum	(Voit) Schwägr.	ch_834
		stellare	Hedw.	ch_1195
		thomsonii	Schimp.	ch_260
		sp.		ch_842
	Plagiomnium	*affine*	T.J.Kop.	ch_1197
		cuspidatum	T.J.Kop.	ch_468
		elatum	T.J.Kop.	ch_485
		ellipticum	T.J.Kop.	ch_1059
		undulatum	(Hedw.) T.J.Kop.	ch_1201
		sp.		ch_1246
	Pohlia	*cruda*	Lindb.	ch_1184
		cruda	Lindb.	ch_595
		drummondii	(Müll.Hal.) A.L.Andrews	ch_1185
		drummondii	(Müll.Hal.) A.L.Andrews	ch_596
		filum	(Schimp.) Mårt.	ch_864
		nutans	(Hedw.) Lindb.	ch_706
		nutans	(Hedw.) Lindb.	ch_865
		wahlenbergii	(F.Web. & D.Mohr) A.L.Andrews	ch_866
	Pseudobryum	*cinclidioides*	(Huebener) T.J.Kop.	ch_1202
	Rhodobryum	*roseum*	(Hedw.) Limpr.	ch_1180
		roseum	(Hedw.) Limpr.	ch_887
	Rhizomnium	*andrewsianum*	T. J. Kop.	ch_591
		magnifolium	(Horik.) T.J.Kop.	ch_1177
		pseudopunctuatum	T.J.Kop.	ch_1178
		punctatum	T.J.Kop.	ch_1179
Buxbaumiales				
Buxbaumiaceae	*Buxbaumia*	*aphylla*	Hedw.	ch_1205

		viridis	(DC.) Moug. & Nestl.	ch_712
Dicranales				
Dicranaceae	*Dicranella*	*crispa*	(Hedw.) Schimp.	ch_1209
		heteromalla	(Hedw.) Schimp.	ch_1211
		schreberiana	(Hedw.) Crum & Anderson	ch_739
	Dicranum	*angustum*	Lindb.	ch_741
		bonjeanii	De Not.	ch_128
		brevifolium	(Lindb.) Lindb.	ch_1214
		drummondii	Müll.Hal.	ch_1216
		flexicaule	Brid.	ch_1219
		flexicaule	Brid.	ch_745
		fragilifolium	Lindb.	ch_1220
		groenlandicum	Brid.	ch_558
		groenlandicum	Brid.	ch_747
		leioneuron	Kindb.	ch_1227
		majus	Sm.	ch_1038
		montanum	Hedw.	ch_1230
		polysetum	Sw.	ch_1232
		scoparium	Hedw.	ch_1233
		spadiceum	J.E.Zett.	ch_143
		spurium	Hedw.	ch_1234
		sp1.		ch_751
		sp2.		ch_112
	Paraleucobryum	*enerve*	(Thed.) Loeske	ch_1235
		longifolium	(Hedw.) Loeske	ch_1236
Ditrichaceae	*Ceratodon*	*purpureus*	(Hedw.) Brid.	ch_1262
		sp.		ch_550
	Distichium	*capillaceum*	(Hedw.) Bruch & Schimp.	ch_1239
		inclinatum	(Hedw.) Bruch & Schimp.	ch_725
	Ditrichum	*gracile*	(Mitt.) Kuntze	ch_1240
		flexicaule	Hampe	ch_559
	Saelania	*glaucescens*	(Hedw.) Broth.	ch_322
Fissidentaceae	*Fissidens*	*adianthoides*	Hedw.	ch_173
		bryoides	Hedw.	ch_772
		exilis	Hedw.	ch_176
		osmundoides	Hedw.	ch_1045
		polyphyllus	(Bruch & Schimp.) T.J.Kop.	ch_776
		taxifolius	Hedw.	ch_777
Leucobryaceae	*Campylopus*	*atrovirens*	De Not.	ch_1028
		brevipilus	Bruch & Schimp.	ch_719
		subulatus	Schimp.	ch_1254
		subulatus	Schimp.	ch_88
	Dicranodontium	*denudatum*	(Brid.) Britton	ch_124
	Leucobryum	*glaucum*	(Hedw.) Ångstr.	ch_1255
Rhabdoweisiaceae	*Amphidium*	*lapponicum*	(Hedw.) Schimp.	ch_511
		lapponicum	(Hedw.) Schimp.	ch_670

		mougeotii	(Bruch & Schimp.) Schimp.	ch_1132
	Arctoa	*fulvella*	(Dicks.) Bruch & Schimp.	ch_1256
		hyperborea	(Dicks.) Bruch & Schimp.	ch_026
	Cnestrum	*schisti*	(F.Web. & D.Mohr) I.Hagen	ch_1257
	Cynodontium	*bruntonii*	(Sm.) Bruch & Schimp.	ch_106
		bruntonii	(Sm.) Bruch & Schimp.	ch_1259
		fallax	Limpr.	ch_1260
		jenneri	(Schimp.) Stirt.	ch_109
		polycarpon	(Hedw.) Schimp.	ch_730
		strumiferum	(Hedw.) Lindb.	ch_1263
		strumiferum	(Hedw.) Lindb.	ch_731
	Dichodontium	*pellucidum*	(Hedw.) Schimp.	ch_735
	Dicranoweisia	*cirrata*	Milde	ch_125
		crispula	Milde	ch_740
	Kiaeria	*blyttii*	(Schimp.) Broth.	ch_822
		glacialis	(Berggr.) I.Hagen	ch_1275
		starkei	(F.Web. & D.Mohr) I.Hagen	ch_1054
	Oncophorus	*virens*	(Hedw.) Brid.	ch_1276
		wallenbergii	Brid.	ch_577
	Rhabdoweisia	*crispata*	(Dicks.) Lindb.	ch_1280
		crispata	(Dicks.) Lindb.	ch_883
Diphysciales				
Diphysciaceae	*Diphyscium*	*foliosum*	(Hedw.) D.Mohr	ch_1281
Encalyptales				
Encalyptaceae	*Encalypta*	*affinis*	Hedw.	ch_163
		alpina	Smith	ch_1041
		brevicollis	(Bruch & Schimp.) Ångstr.	ch_1042
		ciliata	Hedw.	ch_765
		longicollis	Bruch	ch_1044
		longicollis	Bruch	ch_1284
		mutica	I.Hagen	ch_167
		rhaptocarpa	Schwägr.	ch_1285
		streptocarpa	Hedw.	ch_169
Funariales				
Funariaceae	*Funaria*	*arctica*	Kindberg	ch_570
		hygrometrica	Hedw.	ch_1288
Grimmiales				
Grimmiaceae	*Coscinodon*	*cribrosus*	(Hedw.) Spruce	ch_1290
	Grimmia	*ramondii*	(Lam. & DC.) Margad.	ch_1040
	Grimmia	*alpestris*	(Web. & Mohr)Schleich.	ch_1292
		anodon	Bruch & Schimp.	ch_1293
		decipiens	(Schultz) Lindb.	ch_1294
		donniana	Sm.	ch_785
		elongata	Kaulf.	ch_786
		funalis	(Schwägr.) Bruch & Schimp.	ch_787

		hartmanii	Schimp.	ch_1298
		incurva	Schwägr.	ch_789
		laevigata	(Brid.) Brid.	ch_1300
		montana	Bruch & Schimp.	ch_1046
		montana	Bruch & Schimp.	ch_791
		ovalis	(Hedw.) Lindb.	ch_792
		pulvinata	(Hedw.) Sm.	ch_1305
		torquata	Drummond	ch_515
		sp.		ch_1047
	Racomitrium	*aciculare*	(Hedw.) Brid.	ch_1306
		canescens	(Hedw.) Brid.	ch_611
		canescens	(Hedw.) Brid.	ch_879
		fasciculare	(Hedw.) Brid.	ch_313
		heterostichum agg.	(Hedw.) Brid.	ch_1309
		lanuginosum	(Hedw.) Brid.	ch_659
		lanuginosum	(Hedw.) Brid.	ch_881
		microcarpum	(Hedw.) Brid.	ch_1310
		sp1.		ch_612
		sp2.		ch_203
	Schistidium	*agassizii*	Sull. & Lesq.	ch_1312
		apocarpum	(Hedw.) Bruch & Schimp.	ch_1313
		frisvollianum	H.H.Blom	ch_1314
		papillosum	Culm.	ch_1316
		poeltii	H.H.Blom	ch_893
Seligeriaceae	*Blindia*	*acuta*	(Hedw.) Bruch & Schimp.	ch_035
	Seligeria	*donniana*	(Sm.) Müll.Hal.	ch_1318
Hedwigiales				
Hedwigiaceae	*Hedwigia*	*ciliata*	P.Beauv.	ch_1048
		stellata	Hedenäs	ch_1320
Hookeriales				
Hookeriaceae	*Hookeria*	*lucens*	(Hedw.) Sm.	ch_1321
Hypnales				
Amblystegiaceae	*Amblystegium*	*fluviatile*	(Hedw.) Loeske	ch_1131
		serpens	(Hedw.) Schimp.	ch_1130
	Campyliadelphus	*sommerfeltii*	(Myrin) Hedenäs	ch_081
		polygamus	(Schimp.) Kanda	ch_1330
	Campylium	*stellatum*	(Hedw.) Lange	ch_653
	Campylophyllum	*calcareum*	(Crundwell & Nyholm) Hedenäs	ch_1327
		calcareum	(Crundwell & Nyholm) Hedenäs	ch_1328
		sommerfeltii	(Myrin) Hedenäs	ch_081
	Cratoneuron	*filicinum*	(Hedw.) Spruce	ch_1033
	Drepanocladus	*aduncus*	(Hedw.) Warnst.	ch_1333
		aduncus	(Hedw.) Warnst.	ch_763
		capillifolius	(Warnst.) Warnst.	ch_160
		sendtneri	(H.Müll.) Warnst.	ch_161

		sp1.		ch_546
		sp2.		ch_560
	Hygrohypnum	*alpestre*	(Hedw.) Loeske	ch_212
		alpestre	(Hedw.) Loeske	ch_804
		cochlearifolium	(Venturi) Broth.	ch_1337
		duriusculum	(De Not.) D.W.Jamieson	ch_1338
		eugyrium	(Schimp.) Broth.	ch_1339
		eugyrium	(Schimp.) Broth.	ch_216
		luridum	Jennings	ch_1340
		molle	(Hedw.) Loeske	ch_1343
		montanum	(Lindb.) Broth.	ch_807
		norvegicum	(Schimp.) J.J.Amann	ch_220
		ochraceum	(Wilson) Loeske	ch_1050
		polare	(Lindb.) Loeske	ch_222
		smithii	(Sw.) Broth.	ch_1345
	Palustriella	*falcata*	(Brid.) Hedenäs	ch_1347
		falcata	(Brid.) Hedenäs	ch_850
		sp.		ch_1039
	Pseudocalliergon	*angustifolium*	Hedenäs	ch_1349
		brevifolium	(Lindb.) Hedenäs	ch_1348
		trifarium	(F.Weber & D.Mohr) Loeske	ch_561
		sp.		ch_544
		turgescens	(T.Jensen) Loeske	ch_621
	Sanionia	*orthothecioides*	Loeske	ch_618
		uncinata	Loeske	ch_617
	Scorpidium	*cossonii*	Hedenäs	ch_563
		revolvens	(Sw. Rubers	ch_564
		revolvens	(Sw. Rubers	ch_897
		scorpioides	(Hedw.) Limpr.	ch_898
	Tomentypnum	*nitens*	(Hedw.) Loeske	ch_629
	Vittia	sp.		ch_797
Amblystegiaceae				ch_620
Anomodontaceae	*Anomodon*	*attenuatus*	(Hedw.) Huebener	ch_1136
		attenuatus	(Hedw.) Huebener	ch_680
		longifolius	(Brid.) Hartm.	ch_681
		rugelii	(Müll.Hal.) Keissl.	ch_020
		viticulosus	(Hedw.) Hook. & Taylor	ch_1139
Brachytheciaceae	*Brachytheciastrum*	*collinum*	(Müll. Hal.) Ignatov & Huttunen	ch_1353
		collinum	(Müll. Hal.) Ignatov & Huttunen	ch_1354
		trachypodium	(Brid.) Ignatov & Huttunen	ch_046
	Brachythecium	*albicans*	Schimp.	ch_530
		coruscum	I. Hagen	ch_531
		erythrorrhizon	Schimp.	ch_693
		glareosum	(Spruce) Schimp.	ch_041
		mildeanum	(Schimp.) Milde	ch_694
		rivulare	Schimp.	ch_1355

		rutabulum	(Hedw.) Schimp.	ch_1356
		salebrosum	(Web. & Mohr) Schimp.	ch_1023
		turgidum	(Hartm.) Kindb.	ch_697
		sp.		ch_529
	Cirriphyllum	*cirrosum*	(Schwägr.) Grout	ch_1358
		crassinervium	(Wilson) Loeske & M.Fleisch.	ch_723
		piliferum	(Hedw.) Grout	ch_724
	Eurhynchium	*angustirete*	(Broth.) T.J.Kop.	ch_769
		striatum	(Hedw.) Schimp.	ch_770
	Homalothecium	*sericeum*	(Hedw.) Schimp.	ch_1361
	Pseudoscleropodium	*purum*	(Hedw.) M.Fleisch.	ch_1362
	Rhynchostegium	*murale*	(Hedw.) Schimp.	ch_1364
	Sciuro-hypnum	*populeum*	(Hedw.) Ignatov & Huttunen	ch_1322
		reflexum	(Starke) Ignatov & Huttunen	ch_895
		reflexum	(Starke) Ignatov & Huttunen	ch_1022
		starkei agg.	(Brid.) Ignatov & Huttunen	ch_1324
Calliergonaceae	*Calliergon*	*cordifolium*	(Hedw.) Kindb.	ch_1365
		giganteum	(Schimp.) Kindb.	ch_1027
		richardsonii	(Mitt.) Kindb.	ch_715
	Hamatocaulis	*vernicosus*	(Mitt.) Hedenäs	ch_1367
	Loeskypnum	*badium*	(Hartm.) Paul	ch_1369
	Straminergon	*stramineum*	Hedenäs	ch_364
	Warnstorfia	*fluitans*	(Hedw.) Loeske	ch_924
		tundrae	(Arnell) Loeske	ch_1370
Calliergonaceae				ch_722
Climaciaceae	*Climacium*	*dendroides*	(Hedw.) F.Web. & D.Mohr	ch_1371
Fontinalaceae	*Fontinalis*	*antipyretica*	Hedw.	ch_1373
		dalecarlica	Schimp.	ch_779
		hypnoides	Hartm.	ch_780
		squamosa	Hedw.	ch_781
Hylocomiaceae	*Hylocomiastrum*	*pyrenaicum*	(Spruce) M.Fleisch.	ch_1051
		umbratum	(Hedw.) M.Fleisch.	ch_1374
	Hylocomium	*splendens*	Schimp.	ch_574
		splendens	Schimp.	ch_639
	Loeskeobryum	*brevirostre*	(Brid.) Broth.	ch_829
	Pleurozium	*schreberi*	(Brid.) Mitt.	ch_1375
	Rhytidiadelphus	*loreus*	(Hedw.) Warnst.	ch_641
		squarrosus	(Hedw.) Warnst.	ch_319
		triquetrus	(Hedw.) Warnst.	ch_889
Hypnaceae	*Calliergonella*	*cuspidata*	Loeske	ch_1377
	Campylophyllum	*halleri*	(Hedw.) M.Fleisch.	ch_1378
	Ctenidium	*molluscum*	(Hedw.) Mitt.	ch_105
	Hypnum	*callichroum*	Brid.	ch_813
		cupressiforme	Hedw.	ch_1380
		jutlandicum	Holmen & E.Warncke	ch_815
		procerrimum	Molendo	ch_816

		revolutum	(Mitt.) Lindb.	ch_1053
	Isopterygiopsis	*pulchella*	(Hedw.) Z. Iwats.	ch_576
	Ptilium	*crista-castrensis*	(Hedw.) De Not.	ch_645
Lembophyllaceae	*Isothecium*	*alopecuroides*	(Dubois) Isov.	ch_820
		myosuroides	Brid.	ch_821
Leskeaceae	*Lescuraea*	*radicosa*	(Mitt.) Mönk.	ch_1383
	Leskea	*polycarpa*	Hedw.	ch_1386
	Pseudoleskeella	*nervosa*	(Brid.) Nyholm	ch_873
Leucodontaceae	*Antitrichia*	*curtipendula*	(Hedw.) Brid.	ch_1140
	Leucodon	*sciuroides*	(Hedw.) Schwägr.	ch_828
Neckeraceae	*Homalia*	*trichomanoides*	(Hedw.) Brid.	ch_1049
	Neckera	*besseri*	(Lobarz.) Jur.	ch_263
		complanata	(Hedw.) Huebener	ch_837
		crispa	Hedw.	ch_1387
		oligocarpa	Bruch	ch_839
	Thamnobryum	*alopecurum*	(Hedw.) Nieuwl.	ch_1388
Plagiotheciaceae	*Isopterygiopsis*	*pulchella*	(Hedw.) Z.Iwats.	ch_1392
	Myurella	*julacea*	(Schwägr.) Schimp.	ch_261
		sp.		ch_583
	Orthothecium	*chryseum*	(Schwägr.) Schimp.	ch_1395
		intricatum	(Hartm.) Schimp.	ch_272
		lapponicum	(Schimp.) C.Hartm.	ch_844
		rufescens	(Brid.) Schimp.	ch_845
		strictum	Lorentz	ch_1398
	Plagiothecium	*denticulatum*	(Hedw.) Schimp.	ch_1427
		laetum	Schimp.	ch_1428
		undulatum	(Hedw.) Schimp.	ch_497
	Platydictya	*jungermannioides*	H.Crum	ch_858
Pterigynandraceae	*Heterocladium*	*dimorphum*	(Brid.) Schimp.	ch_799
	Pterigynandrum	*filiforme*	Hedw.	ch_1421
		filiforme	Hedw.	ch_309
Rhytidiaceae	*Rhytidium*	*rugosum*	(Hedw.) Kindb.	ch_1420
Thuidiaceae	*Abietinella*	*abietina*	(Hedw.) M.Fleisch.	ch_1019
	Helodium	*blandowii*	(F.Web. & D.Mohr) Warnst.	ch_614
	Thuidium	*recognitum*	(Hedw.) Lindb.	ch_507
		tamariscinum	(Hedw.) Schimp.	ch_916
Orthotrichales				
Orthotrichaceae	*Orthotrichum*	*affine*	Brid.	ch_847
		alpestre	Bruch & Schimp.	ch_277
		pylaisii	Brid.	ch_588
		rupestre	Schwägr.	ch_1057
		speciosum	Nees	ch_849
		sp.		ch_666
	Ulota	*phyllantha*	Brid.	ch_664
	Zygodon	*rupestris*	Lorentz	ch_1422
		rupestris	Lorentz	ch_926

		virdissimus	(Dicks.) Brid.	ch_510
Polytrichales				
Polytrichaceae	*Atrichum*	*undulatum*	(Hedw.) P.Beauv.	ch_1400
	Oligotrichum	*hercynicum*	(Hedw.) Lam. & DC.	ch_1401
	Pogonatum	*urnigerum*	(Hedw.) P.Beauv.	ch_593
		dentatum	(Brid.) Brid.	ch_861
		sp.		ch_863
	Polytrichastrum	*sexangulare*	Brid.	ch_604
	Polytrichum	*commune*	Hedw.	ch_600
		commune	Hedw.	ch_867
		hyperboreum	R.Br.	ch_1406
		hyperboreum	R.Br.	ch_601
		jensenii	I.Hagen	ch_602
		juniperinum	Hedw.	ch_599
		strictum	Brid.	ch_605
	Psilopilum	*cavifolium*	(Wilson) I.Hagen	ch_307
		laevigatum	(Wahlenb.) Lindb.	ch_609
Pottiales				
Pottiaceae	*Aloina*	*brevirostris*	(Hook. & Grev.) Kindb.	ch_1127
	Anoectangium	*aestivum*	(Hedw.) Mitt.	ch_679
	Bryoerythrophyllum	*ferruginascens*	(Stirt.) Giacom.	ch_698
		recurvirostrum	(Hedw.) P.C.Chen	ch_1425
	Didymodon	*fallax*	(Hedw.) R.H.Zander	ch_146
		icmadophilus	(Müll.Hal.) K.Saito	ch_755
		rigidulus	Hedw.	ch_756
		sp.		ch_675
	Gymnostomum	*aeruginosum*	Sm.	ch_794
	Hymenostylium	*recurvirostrum*	(Hedw.) Dixon	ch_812
	Syntrichia	*norvegica*	F.Web.	ch_1423
		ruralis	(Hedw.) F.Weber & D.Mohr	ch_624
	Tortella	*arctica*	(Arnell) A.C. Crundwell & Nyholm	ch_1424
		fragilis	(Hook. & Wilson) Limpr.	ch_631
		fragilis	(Hook. & Wilson) Limpr.	ch_920
		tortuosa	(Hedw.) Limpr.	ch_630
		sp.		ch_760
	Tortula	*leucostoma*	(R.Br.) Hook. & Grev.	ch_547
		mucronifolia	Schwägr.	ch_351
		muralis	Hedw.	ch_508
		subulata	Hedw.	ch_922
Sphagnales				
Sphagnaceae	*Sphagnum*	*magellanicum*	Brid.	ch_334
		russowii	Warnst.	ch_907
Splachnales				
Meesiaceae	*Amblyodon*	*dealbatus*	(Hedw.) Bruch & Schimp.	ch_089
	Leptobryum	*pyriforme*	(Hedw.) Wilson	ch_1416

	Meesia	*longiseta*	Hedw.	ch_830
		triquetra	(Richt.) Ångstr.	ch_250
		triquetra	(Richt.) Ångstr.	ch_580
		uliginosa	Hedw.	ch_1418
		uliginosa	Hedw.	ch_831
	Paludella	*squarrosa*	(Hedw.) Brid.	ch_1419
Splachnaceae	*Aplodon*	*wormskioldii*	(Hornem.) R.Br.	ch_684
	Tayloria	*splachnoides*	(Schwagr.) Hook.	ch_910
	Tetraplodon	*mnioides*	(Hedw.) Bruch & Schimp.	ch_536
		mnioides	(Hedw.) Bruch & Schimp.	ch_626
		mnioides	(Hedw.) Bruch & Schimp.	ch_914
		pallidus	I. Hagen	ch_1415
	Splachnum	*vasculosum*	Hedw.	ch_1413
		sphaericum	Hedw.	ch_649
		sp.		ch_517
Tetraphidales				
Tetraphidaceae	*Tetraphis*	*pellucida*	Hedw.	ch_913
Timmiales				
Timmiaceae	*Timmia*	*austriaca*	Hedw.	ch_628
		norvegica	J.E.Zett.	ch_918
Marchantiophyta				
Jungermanniales				
Antheliaceae	*Anthelia*	*julacea*	(L.) Dumort.	ch_931
		juratzkana	(Limpr.) Trevis.	ch_1448
Calypogeiaceae	*Calypogeia*	*muelleriana*	(Schiffn.) Müll.Frib.	ch_946
		sphagnicola	(Arnell & Perss.) Warnst. & Loeske	ch_436
		sp.		ch_473
Cephaloziaceae	*Hygrobiella*	*laxifolia*	(Hook.) Spruce	ch_965
	Nowellia	*curvifolia*	(Dicks.) Mitt.	ch_988a
	Odontoschisma	*macounii*	(Aust.) Underw.	ch_400
Cephaloziellaceae	*Cephaloziella*	*divaricata*	(Sm.) Schiffn.	ch_440
Frullaniaceae	*Frullania*	*dilatata*	(L.) Dumort.	ch_448
		fragilifolia	(Taylor) Gottsche, Lindenb. & Nees	ch_449
		tamarisci	(L.) Dumort.	ch_961
Geocalycaceae	*Chiloscyphus*	*coadunatus*	(Sw.) J.J.Engel & R.M.Schust.	ch_373
		polyanthos	(L.) Corda	ch_953
		profundus	(Nees) J.J.Engel & R.M.Schust.	ch_442
	Harpanthus	*flotovianus*	(Nees) Nees	ch_1453
Gymnomitriaceae	*Gymnomitrion*	*concinnatum*	(Lightf.) Corda	ch_962
		coralloides	Nees	ch_571
		obtusum	(Lindb.) Pearson	ch_1456
	Marsupella	*emarginata*	(Ehrh.) Dumort.	ch_1457
Herbertaceae	*Herbertus*	*stramineus*	(Dumort.) Trevis.	ch_381
Jungermanniaceae	*Jungermannia*	*atrovirens*	Dumort.	ch_966

		borealis	Damsh. & Vàna	ch_967
		exsertifolia	Steph.	ch_458
		leiantha	Grolle	ch_459
		obovata	Nees	ch_968
		sphaerocarpa	Hook.	ch_460
	Mylia	*taylorii*	(Hook.) Gray	ch_1459
	Nardia	*compressa*	(Hook.) Gray	ch_985
		geoscyphus	(De Not.) Lindb.	ch_986
Lejeuneaceae	*Cololejeunea*	*calcarea*	(Lib.) Schiffn.	ch_955
Lepidoziaceae	*Bazzania*	*tricrenata*	(Wahlenb.) Lindb.	ch_1462
		trilobata	(L.) Gray	ch_368
	Lepidozia	*pearsonii*	Spruce	ch_462
Lophocoleaceae	*Lophocolea*	*bidentata*	(L.) Dum.	ch_972
Lophoziaceae	*Anastrepta*	*orcadensis*	(Hook.) Schiffn.	ch_1463
	Anastrophyllum	*donnianum*	(Hook.) Steph.	ch_422
	Barbilophozia	*hatcheri*	(A.W.Evans) Loeske	ch_432
		kunzeana	(Huebener) Müll.Frib.	ch_433
		lycopodioides	(Wallr.) Loeske	ch_1470
		sp.		ch_1469
	Jamesoniella	*autumnalis*	(DC.) Steph.	ch_456
	Lophozia	*excisa*	(Dicks.) Dum.	ch_578
		incisa	(Schrad.) Dumort.	ch_464
		longidens	(Lindb.) Macoun	ch_975
		opacifolia	Meyl.	ch_976
		silvicola	Buch	ch_1475
		ventricosa	(Dicks.) Dumort.	ch_978
		wenzelii	(Nees) Steph.	ch_979
	Tetralophozia	*setiformis*	(Ehrh.) Schljakov	ch_1476
	Tritomaria	*polita*	(Nees) Jørg.	ch_1478
		quinquedentata	(Huds.) H.Buch	ch_1477
Plagiochilaceae	*Plagiochila*	*asplenioides*	(L.) Dumort.	ch_482
		porelloides	(Nees) Lindenb.	ch_403
Pleuroziaceae	*Pleurozia*	*purpurea*	Lindb.	ch_995
Porellaceae	*Porella*	*cordaeana*	(Huebener) Moore	ch_996
		platyphylla	(L.) Pfeiff.	ch_483
Ptilidiaceae	*Ptilidium*	*ciliare*	(L.) Hampe	ch_408
Radulaceae	*Radula*	*complanata*	(L.) Dumort.	ch_1484
Scapaniaceae	*Diplophyllum*	*taxifolium*	(Wahlenb.) Dumort.	ch_958
		albicans	(L.) Dumort.	ch_1486
	Douinia	*ovata*	(Dicks.) H.Buch	ch_1487
		ovata	(Dicks.) H.Buch	ch_928
	Scapania	*aequiloba*	(Schwägr.) Dumort.	ch_489
		calcicola	(Arnell & J.Perss.) Ingham	ch_1007
		cuspiduligera	(Nees) K. Mull.	ch_1008
		hyperborea	Joerg.	ch_1009
		irrigua	(Nees) Gott. & Al.	ch_1494

		nemorea	(L.) Dum.	ch_1490
		nimbosa	Lehm.	ch_1011
		paludicola	Loeske & Müll.Frib.	ch_1013
		scandica	(H. Arnell & Buch) Macv.	ch_1492
		uliginosa	(Lindenb.) Dumort.	ch_1015
		undulata	(L.) Dumort.	ch_1016
		sp1.		ch_977
		sp2.		ch_998
Marchantiales				
Aytoniaceae	*Asterella*	*gracilis*	(F.Web.) Underw.	ch_933
		lindenbergiana	(Nees) Arnell	ch_934
	Mannia	*pilosa*	(Hornem.) Frye & L.Clark	ch_1496
Marchantiaceae	*Marchantia*	*alpestris*	(Nees) Burgeff	ch_469
		polymorpha	L.	ch_981
	Preissia	*quadrata*	(Scop.) Nees	ch_606
Monosoleniaceae	*Peltolepis*	*quadrata*	(Saut.) Müll.Frib.	ch_1497
Ricciaceae	*Riccia*	*sorocarpa*	Bisch.	ch_1498
		sorocarpa	Bisch.	ch_1499
Conocephalaceae	*Conocephalum*	*salebrosum*	Szweyk., Buczkowska & Odrzykoski	ch_1509
Metzgeriales				
Aneuraceae	*Riccardia*	*latifrons*	(Lindb.) Lindb.	ch_1500
Metzgeriaceae	*Metzgeria*	*conjugata*	Lindb.	ch_471
		furcata	(L.) Dumort.	ch_983
Pallaviciniaceae	*Moerckia*	*blyttii*	(Mörch) Brockm.	ch_1505
		hibernica	(Hook.) Gottsche	ch_1506
Pelliaceae	*Pellia*	*endiviifolia*	(Dicks.) Dumort.	ch_992
		epiphylla	(L.) Corda.	ch_655
		neesiana	(Gottsche) Limpr.	ch_401

Appendix 3: Supplementary tables and figures

Supplementary Table S2. Primer pairs and corresponding COI-fragment used for detection of lemming genera *Lemmus* and *Dicrostonyx*.

	Forward primer	**Reverse primer**	**COI-fragment amplified (consensus sequence)**
Lemmus	TAGGRACAGCCCTAAGTATCC	CAAAYGCATGTGCAGTGACAATA	taattcgrgcagaacttggacaaccgggggccctcctaggggacgatcaaatctataacgt
Dicrostonyx	GTAGGRAMAGCCCTTAGCATTT	AATGCATGGGCTGTTACRACC	taatccggscagaacttggccaaccaggygccctactaggrgaygatcaaatctacaatgt

Supplementary Table S3. Frequency of occurrence of plant families in the winter diets of collared and brown lemmings during the winter 2010-11 on Bylot Island based on DNA metabarcoding of pellets. For vascular plants, data are based on primer pair *g-h*, for mosses on primer pair *c-h*.

Taxa	*Lemmus* (n=54)	*Dicrostonyx* (n=22)
Vascular plants		
Asteraceae	2	0
Brassicaceae	12	10
Caryophyllaceae	19	14
Cyperaceae	8	4
Equisetaceae	4	2
Fabaceae	7	6
Juncaceae	46	16
Orobanchaceae	0	1
Papaveraceae	3	0
Poaceae	45	22
Polygonaceae	23	5
Ranunculaceae	1	0
Rosaceae	13	6
Salicaceae	54	22
Saxifragaceae	19	5
Mosses		
Aulacomniaceae	49	2
Bartriamiaceae	3	0
Bryaceae	10	0
Dicranaceae	35	0
Ditrichiaceae	9	0
Grimmiaceae	15	0
Polytrichaceae	49	7
Pottiaceae	1	0
Rhabdoweisiaceae	2	0
Timmiaceae	15	1

Supplementary Figure S1. An example of a capillary electrophoresis output from QIAxcel System. Colums represent 12 different samples. Horizontal bands represent DNA fragments, numbers along the edge of columns show scale in bp length. Two band sizes can be seen along 150bp line, indicating samples of *Lemmus* (146bp, samples 1-4 and 11-12) and *Dicrostonyx* (128bp, samples 5-10).