DISSERTATION

The return of the mammoth steppe?

– Rewilding in Yakutia and the actual impact of large herbivore grazing on vegetation

By Jennifer Reinecke

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The return of the mammoth steppe?

– Rewilding in northeastern Yakutia and the actual impact of large herbivore grazing on vegetation

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Eidesstattliche Erklärung

Hiermit versichere ich, Jennifer Reinecke, dass ich die vorliegende Arbeit mit dem Titel „The return of the mammoth steppe? – rewilding in Yakutia and the actual impact of large herbivore grazing on vegetation “ ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als solche kenntlich gemacht. Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

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Vorwort

Nach Alexander von Humboldt (1807): Vorrede zur 1. Ausgabe von „Ansichten der Natur“:

„Schüchtern übergebe ich dem Publikum eine Reihe von Arbeiten, die im Angesicht großer Naturgegenstände […] in den Steppen von [Sibirien] entstanden sind. Einzelne Fragmente wurden an Ort und Stelle niedergeschrieben und nochmals nur in ein Ganzes zusammengeschmolzen. Überblick der Natur im großen, Beweis von dem Zusammenwirken der Kräfte, Erneuerung des Genusses, welchen die unmittelbare Ansicht der [Wildnis] dem fühlenden Menschen gewährt, sind die Zwecke, nach denen ich strebe. Jeder Aufsatz sollte ein in sich geschlossenes Ganzes ausmachen, in allen sollte eine und dieselbe Tendenz sich gleichmäßig aussprechen. […] Reichtum der Natur veranlasst Anhäufung einzelner Bilder, und Anhäufung stört die Ruhe und den Totaleindruck des Gemäldes. […] Mögen meine Ansichten der Natur, trotz dieser Fehler, welche ich selber leichter rügen als verbessern kann, dem Leser doch einen Teil des Genusses gewähren, welchen ein empfänglicher Sinn in der unmittelbaren Anschauung findet.“

Für meine kleine Nomadenschwester

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Chapter 1

General Introduction

1.1. Large mammal extinctions and the onset of the Anthropocene

We are currently facing a massive, human-made loss of biodiversity and ecosystem functioning, to an extent that a new era, the Anthropocene (Crutzen 2002; Bocherens 2018; Box 1), has been proclaimed. Although this so-called 6th mass extinction (Barnosky et al. 2011; Box 2) spans across all taxonomic groups, there is a tendency towards large-bodied mammals, called megafauna (Box 3), being especially affected (Koch and Barnosky 2006). The removal of large wildlife leads to cascading effects on other trophic guilds, vegetation structure, plant communities and various ecosystem functions (Estes et al. 2011; Dirzo et al. 2014; Bocherens 2018). The large-scale extinction of megafauna already started in the Quarternary and on a global scale has often been found in combination with human arrival (Haynes 2017). However, this often coincided with climate changes, so the relative role of climate change (Guthrie 2001) versus overhunting (Box 4) in the extinction of large grazers and in driving vegetation change has been much debated. Thus, there is also no general agreement on where the Holocene, or anthropogenic, extinction begins, and the Quaternary extinction event ends, or if they should be considered separate events at all (Doughty et al. 2010). Likewise, the presumed onset of the Anthropocene, could be extended many thousand years back, if humans played a major role in the massive megaherbivore extinctions and subsequent re-organization of ecosystems at the end of the Pleistocene (Doughty et al. 2010; Ellis 2018).

Box 1: Anthropocene

A new geological epoch suggested by Crutzen (2002) dating from the commencement of significant human impact on the Earth's geology and ecosystems ("the age of humans"; Ellis 2018). This includes anthropogenic impacts on biodiversity loss, shifts in species distributions, climate change, geomorphology (drainage, erosion, landscape changes) and stratigraphy (sedimentation, "technofossilization", trace elements; Ellis 2018). The onset of the Anthropocene is usually set around 1950 (Great Acceleration; Steffen et al. 2011) or 1750 (Industrial Revolution; Crutzen 2002). With increasing evidence of extensive human impact on ecosystem functioning in earlier times, the onset of the Anthropocene also has been placed as far back as 8000 - 10 000 yrs bp, (Neolithic Revolution; Ruddiman 2003), 12-50 000 yrs bp (Megafauna extinctions; e.g. Bocherens 2018) or up to 1 Mio yrs bp (Human use of fire; see Ellis 2018).

Re-wilding follows the idea of re-creating an ecological state before human influence became an overriding factor and sparks ongoing interest among both conservation scientists and practitioners (e.g. Kintisch 2015; Svenning et al. 2016). This ecological restoration strategy uses species (re-)introductions to promote self-regulating biodiverse ecosystems (Malhi et al. 2016; Svenning et al. 2016). "Pleistocene rewilding" (Donlan et al. 2006) aims at reconstructing pre-historic megafaunas (Owen-Smith 1987; Zimov et al. 1995; Vera 2009; Svenning et al. 2016). This, however, does not necessarily imply bringing back extinct herbivores, such as the mammoth, but concerns substituting the respective megaherbivores with modern conspecifics and related taxa with similar ecological functions (Donlan et al. 2006; Zimov et al. 2012a). Also called "trophic re-wilding" (Svenning et al. 2016), the approach mainly aims at restoring natural trophic niches and associated top-down cascades (Estes et al. 2011), and also includes associated herbivore behavior and related processes, such as wallowing, trampling and manuring (Svenning et al. 2016).

Many studies shed light on how megaherbivores worldwide may shape vegetation structure, ecosystem processes and landscape heterogeneity, and even trigger biome shifts in their time (e.g. Gill 2014; Malhi et al. 2016). Several authors have suggested alternative climax states for today's vegetation, if megaherbivores would still play a major role in the ecosystems. For example (Gradmann 1933; Steppenheidentheorie") and (Vera 2000; "wood-pasture theory") have proposed and promoted hypotheses on a more open vegetation than the closed forest in Europe, which is usually accepted as climax vegetation in temperate regions. For northeastern Siberia (Zimov et al. 1995, 2012a, b; Zimov 2005) developed a similar herbivore-vegetation-model, assuming that dry-cold mammoth steppe would still be the natural vegetation of northeastern Siberia today, instead of dwarfshrub tundra

Box 2: The 6th mass extinction

Also known as Holocene extinction or Anthropocene extinction, this term describes a 6th wave of global biodiversity loss in earth's history due to human action (Barnosky et al. 2011; Dirzo et al. 2014; Bartlett et al. 2016). Mass extinctions are characterized by the loss of at least 75% of species within a geologically short period of time (Barnosky et al. 2011). The current rates of rates of species losses are possibly the highest ever (Ceballos et al. 2015). Still, some authors argue that anthropogenic extinctions may have begun as early as when the first modern humans spread out of Africa about 60 000 years ago, which is supported by arrival times in Australia, New Zealand and Madagascar (Araujo et al. 2017; Haynes 2017). Others suggest a time, when hunting techniques became more efficient (Ellis 2018), in Beringia supposedly around 14000 yrs BP (Zimov et al. 2012a).

and larch taiga (see section 1.2.4).

While there is plenty of literature on the consequences of megafaunal extinctions and the potential of re-wilding, the field is mostly dominated by essays and opinion pieces (Malhi et al. 2016). Even though there is a clear need for empirical studies on the effects of large grazers on vegetation, experimental settings for systematic scientific monitoring are rare (Svenning et al. 2016). Moreover, there is strong geographic bias, with most studies focusing on North America, Europe, and oceanic islands (Svenning et al. 2016). Despite relatively clear conceptions about the fauna to be re-wilded, the intended target vegetation to be reconstructed is often not addressed specifically.

In my Thesis, I focus on re-wilding of the mammoth steppe. This ecosystem draws much attention because of its iconic name givers (e.g. Kintisch 2015), although it has been proposed that restoration would also be possible without the cloning of these extinct herbivores (Donlan et al. 2006; Zimov et al. 2012a). It is also of interest, because no zonal equivalents of its vegetation exist, although extrazonal relics have been suggested (e.g. Yurtsev 1982; Chytrý et al. 2017). It is worth taking a comprehensive look at these claims in an understudied yet promising region like Beringia.

1.2. The ”mammoth steppe”

Simply releasing large herbivores into the Siberian wild is certainly not enough to bring back an entire mammoth steppe ecosystem. It is necessary to understand the grazing ecology of prehistoric megaherbivore fauna and of modern herbivores and their surrogate potential. And it is fundamentally important to define and characterize the vegetation, the re-creation of which is intended. Quarternary vegetation history of the arctic tundra is generally less well understood than the ecology and population dynamics of the mammoth steppe fauna (Willerslev et al. 2014). Strikingly different views exist on the definition of the term “mammoth steppe”, on details of the environmental conditions, on the productivity of vegetation, on plant composition and on which modern vegetation types could be considered extant relics.

1.2.1. Definitions and concepts

The term “mammoth steppe” is widely used, as it refers to its iconic mammals, conjures up a vivid picture of the ecosystem and relates to the history of its research from a zoological viewpoint (see Guthrie 1982). Guthrie (1982, 1990) established this term for the cold palaeolithic biome of northeastern Siberia, first described by Nehring (1890), which is characterized by large megaherbivores and cold-adapted steppe vegetation. As such, he also relates the term to a landscape of cold and more or less arid vegetation of tundra and steppe (Guthrie 1982, 2001). From a palaeobotanic perspective the Pleistocene vegetation of Beringia is more often called "tundra steppe" (Hibbert 1982; Yurtsev 1982, 2001), "arctic steppe", "tundra-steppe", "steppe tundra", "loess steppe", "cold steppe" (Guthrie 1982) or "cryophytic steppe" (Lavrenko 1940). As Yurtsev (2001) points out, terms like "tundra" and "steppe" can refer to either a landscape or a specific plant community; and an intermediate formation like the tundra steppe can either mean a plant community, where cryophyitic tundra species are associated with xerophytic steppe species, or a landscape, consisting of both steppe and tundra elements. This is why Guthrie (1982) opposes terms, which only refer to the steppic character of the vegetation, and claims it is better characterized by the ecosystems iconic mammal. However, if we really want to restore an ancient ecosystem, we need to be clear about the definition and characteristics of all its components, including the vegetation.

I will use the term "mammoth steppe", when referring to the ecosystem as a whole (including vegetation, fauna and ecosystem processes) following Guthrie (1982, 1990), and to "tundra steppe" when referring to a specific vegetation type (following phytosociological classifications, e.g. Kucherov and Daniëls 2005). This leaves out Yurtesv's and Guthrie's definition of "tundra steppe" as a landscape of different tundra and steppe communities, which is a possible option for the Pleistocene setting, but not for today.

1.2.2. Environmental conditions

Beringia remained free of continental ice caps throughout the Pleistocene (Svendsen et al. 2004), even during glacial stages. It thus provided refuge to arctic flora and fauna in both glacial and interglacials (e.g. Kienast et al. 2011; Kahlke 2014). The mammoth steppe was the dominant biome of glacial stages, which overall featured cooler and drier climate than during interglacials and today (Hopkins et al. 1982). Details on climate conditions, especially regarding the growing season are, however, less consistent. There is, for example, conflicting evidence on whether summers were cooler or warmer than today, depending on the proxy used (see Guthrie 2001).

Most researchers agree that more arid macroclimatic conditions prevailed, which would explain the apparently wide distribution of typical steppe flora and fauna (Hopkins et al. 1982). However, different views exist on the driving forces behind the aridity of the biome. The earliest idea was that Pleistocene climate was simply more continental (e.g. Nehring 1890). Lowered sea-levels and glaciation of the North Atlantic created a large continental shelf with reduced flows of moisture in northeastern Siberia (Guthrie 2001). However, more important than total precipitation is its timing. Guthrie (1982, 1990) proposed a precipitation regime with little snow in winter, high amount of spring rains and a period of summer drought. He argues that the most striking feature of dry Pleistocene climate was the predominance of clear skies (Guthrie, 1982, 1990, 2001). This would result in 1) sunnier days with higher temperatures and evapotranspiration in summer; 2) more winter winds, leading to snow drift; the lack of a uniform snow cover resulting in a longer growing season (early spring) and higher moisture availability in early summer (deeper soil thaw); 3) subsequent accessibility of winter pastures to grazers would leave less insulating litter cover in spring, adding to the early onset of the season. Other zoologists claim that circulation models suggested similar precipitation but wetter soils than today; not an arid macroclimate, but higher evapotranspiration due to grazing-induced dominance of productive grasses (Zimov et al. 1995; see section 1.2.4.) would be responsible for the aridity of the mammoth steppe soil.

The soil of the mammoth steppe was dry and firm, as indicated by the number of small-hoofed large mammals (Guthrie 1982); and it must have been relatively fertile in order to support a productive vegetation that can sustain herds of large grazers. Fertile soils formed as a result of continual input of relatively nutrient-rich loess, high soil pH and high summer temperatures, which enhance nutrient turnover (Guthrie 1982, 1990). In contrast, nutrient deficiency is often the limiting factor in the arctic today (Guthrie 1982; Chapin et al. 1995). The question remains, if this is simply due to cooler summers and less loess deposition today (Guthrie 1982), or if reduced litter quality due to vegetation change and the loss of herbivores as facilitators in nutrient turnover also played a role (Chapin et al. 1995; Zimov et al. 1995; see sections 1.2.4 and 1.3.2).

1.2.3. Vegetation of the mammoth steppe

Early palaeobotanic evidence of Pleistocene vegetation mostly stems from floristics (Hulten 1937; Yurtsev 1982, 2005; Swanson 2006) and pollen analysis (Cwynar and Ritchie 1980; Hopkins et al. 1982), which indicated the simultaneous presence of steppe and tundra species during glacial times. Grass pollen dominated pollen records, hence the widely-used terminology and visual imagery of the mammoth steppe (Willerslev et al. 2014). Nutrient rich soils (see section 1.2.2.) would explain the dominance of graminoids over cryptogams (McKendrick et al. 1980), while simultaneous aridity prevented boreal taiga and tussock tundra plants to take advantage (Guthrie 1982). *Artemisia* and *Kobresia* were also important components of pollen records, and were also abundant in stomach contents of the mammoth fauna (see Walker et al. 2001; Boeskorov et al. 2011). Overall, pollen influx was relatively low, which has been interpreted as reduced vegetation cover (Cwynar and Ritchie 1980; Müller et al. 2010). Thus, first hypotheses on the character of the mammoth steppe vegetation were that of polar deserts today (Cwynar and Ritchie 1980). However, such low productive steppes could not have sustained the large numbers of herbivores, leading to a conflict of botanical and zoological indications called the "productivity paradox" (Hopkins et al. 1982).

The problem with the widely used pollen data is the low taxonomic resolution for some taxa (e.g. grasses) and the insensitivity to subtle, local variations in vegetation composition, resulting in misinterpretations (Blinnikov et al. 2011). Identifications carried out to the genus level only, bear the risk of including species of broadly different environmental niches. Also, low pollen concentrations of tundra steppe, which have been interpreted as reduced vegetation cover (Müller et al. 2010), may merely reflect a high proportion of vegetative reproduction (Blinnikov et al. 2011), e.g. under grazing (Guthrie 1982). At the same time, pollen data revealed assemblages of plant species, which do not co-occur today (Guthrie 1982, 2001). This might either indicate that no exact analogues of the Pleistocene tundra steppe survived, despite physiognomic similar vegetation types and single relic plant species (Guthrie 1982, 2001), or that resolution of pollen data is too low to reconstruct vegetation (Blinnikov et al. 2011).

Plant macrofossil analysis has the advantage of giving a local vegetation signal and being of higher taxonomic resolution for some differentially important plant taxa (Blinnikov et al. 2011). Macrofossil studies from Beringia have demonstrated local presence of productive herbs (e.g. *Alyssum obovatum*, *Silene repens* and *Linum perenne*) among grasses (e.g. *Koeleria cristata*, *Festuca*, *Poa*) (Kienast et al. 2005). Moss and lichen carpets, which are abundant components of modern vegetation, were sparse or non-existent (Guthrie 1982; Blinnikov et al. 2011). Local variability of plant assemblages depended on topography and ranged from dry to mesic (Kienast et al. 2005; Blinnikov et al. 2011). Macrofossil analysis reveals great floristic diversity at the local scale, despite rather homogenous spatial and temporal variability across Beringia (probably because few perennials were adapted to the harsh climatic and disturbance conditions) (Blinnikov et al. 2011). Recent reconstructions of arctic vegetation using DNA barcoding supported the notion that mammoth steppe was dominated by forbs, not grasses (Willerslev et al. 2014).

Despite recent progress and modern approaches to palaeovegetation reconstruction, key issues remain: the most likely composition of Pleistocene plant communities, including local variability, productivity and ecological drivers (climate versus herbivore disturbance; Blinnikov et al. 2011).

1.2.4. Megafauna and suggested ecosystem processes of the mammoth steppe

The fauna of the Beringian mammoth steppe consisted of a combination of Central Asian steppe (saiga, horses) and Arctic tundra (reindeer, musk ox, wholly mammoth, wholly rhino) faunal elements, both of which were adapted to open landscapes (Kahlke 2014). While the iconic large mammals, mammoth and rhino, went extinct at the transition to the Holocene, the surviving herbivore species retreated to the regions of their origin and today form disjunct communities (Kahlke 2014).

This community of diverse, large bodied mammals showed high dietary specialization (Guthrie 1982). Most zoologists agree that neither low temperature nor aridity limits large mammal distribution, as long as diverse plant communities allow for species co-existence (Guthrie 1982), and thus ensure food availability for all. Grazers developed in co-evolution with steppes, where they found unique ecological niches and food sources (Zherikhin 1993). High crowned teeth to open up silica-rich grasses are indications for their close adaptation (Blinnikov et al. 2011). The key herbivores of the mammoth steppe, bison, horse and mammoth, were specialized grazers; browsing specialists, like moose, were rare during high glacials, but played a larger role in interglacials (Guthrie 2001). Interestingly, both grazers and browsers occurred during the last interglacial, when mesic and dry vegetation co-existed (Guthrie 1990).

Box 3: Megafauna

Different definitions regarding the weight cut-off for Megafauna exist. It may be defined as large mammals >1000kg (Owen-Smith 1987), thus including e.g. mammoth, wolly rhino, or >100kg (e.g. Gill 2014) and thus including e.g. bison, horse, or as low as >44 kg (e.g. Stuart 2015). Following the definition of Owen-Smith (1987) megaherbivores are characterized by 1) being largely immune to non-human predation due to their size; on the other hand their size made them especially susceptible to human hunting and extinction; 2) long gut retention times, thus being able to consume woody and lower quality vegetation; 3) consumption of larger fractions of the available plant biomass; 4) a more generalist diet.

The most striking feature of the mammoth steppe fauna is the large size of many species, therefore also called megafauna (Box 3). Owen-Smith (1987) suggested that, contrary to smaller-sized herbivores, their populations would not be controlled by predation, so that they could reach saturated populations. Due to their large size and long gut retention times, they would also be able to consume more plant biomass, and digest forage of lower quality than smaller and often more specialized herbivores (Owen-Smith 1987). Consequently, megaherbivores would be able to exert top-down controls on vegetation and shape the ecosystems of their time (Owen-Smith 1987). On the other hand, group behavior among mesoherbivores can lower the size threshold, thus making them ecologically comparable to megaherbivores (Malhi et al. 2016).

Based on extrapolations from bone deposits, Zimov (2012b) has proposed an animal density of five bison, 7.5 horses, 15 reindeer, 1 mammoth and few of the more uncommon herbivores per square kilometer of mammoth steppe. This amounts to a total herbivore biomass of 10.5 tons, which by sheer mass should have significant effects on vegetation. Guthrie (2001) criticized that an estimated density of 20-30 large grazers per km^2 is probably too high and that even 1/10 of that would still have overstocked the mammoth steppe.

Assuming sufficiently high animal abundances, several herbivore-vegetation-models suggest that grazing created and maintained more open vegetation than the usually considered climax state (Gradmann 1933; Vera 2000). Zimov (Zimov et al. 1995, 2012b, a; Zimov 2005) developed a similar model, the ecosystem-hypothesis (Box 4), for northeastern Siberia. He proposes that 1) grazing and trampling of herbivores would create and maintain a dominance of fast-growing, productive grasses over inedible mosses and dwarf shrubs, which are more susceptible to disturbance; 2) higher litter quality of grasses and enhanced microbial decomposition of grazed plant biomass through herbivore gut passage would promote nutrient cycling and thus maintain high soil fertility; 3) higher evapotranspiration of re-growing grasses would cause high water consumption, leading to arid soil conditions; 4) soil insulation from moss carpets or thick, hardly decomposable litter layers would be low and soils would not be water-logged; this would deepen the active layer with relatively high microbial activity, which would further increase productivity; 5) dry and fertile soils would in turn further promote productive grasses instead of less-demanding, but slow-growing mosses and woody plants. He thus claims that cold, dry mammoth steppe would still be the natural vegetation of northeastern Siberia today, instead of wetter dwarf shrub tundra and larch taiga (Zimov et al. 1995, 2012b, a; Zimov 2005).

1.2.5. The demise of the mammoth steppe

Around 12 000 BP several large megaherbivores became extinct, others declined in numbers, or their distribution ranges shrank or shifted markedly (Guthrie 1982; Zimov et al. 2012a). These changes were accompanied by a shift to nutrient-poorer soils, while wetter ground made many habitats inaccessible to herbivores (Guthrie 1982). Reconstructions of palaeovegetation show a demise of open tundra and steppe vegetation and the appearance of low-diverse taiga and tundra wetlands with a dominance of unpalatable mosses and woody taxa (e.g. Kienast 2013) along with increased vegetation zonation (Guthrie 1982).

There are two main lines of hypotheses (but see Box 4) on the drivers behind the demise of the mammoth steppe with both its iconic large herbivores and the associated vegetation.

With the warming of the climate at the beginning of the Holocene, sea levels rose and the coast line of northern Beringia drew closer inland, thus reducing the continental character of its climate (Guthrie 2001). Guthrie (1982) proposed that seasonal changes in moisture distribution (increased snow, late summer moisture), wind and temperature were the most relevant factors. Increased moisture availability would have allowed more competitive, but slow growing and unpalatable woody plants to replace the xerophytic herb and grass vegetation. The appearance of evergreen plants and thick tussocks would have favored mesic vegetation and insulate the soil, thus decreasing nutrient availability (Guthrie 1982). According to the climate hypothesis, this climate-induced vegetation change, subsequently starved the megafauna of their fodder and led to their decline.

Most opponents of the climate hypothesis, argue that this Holocene climate warming was comparable to that of the interglacials of the Pleistocene before (Zimov et al. 2012a; Sandom et al. 2014). They believe the essential difference to these warm stages, and the more important driver for the stark vegetation changes, was not the climate, but the extinction and decline of the megafauna. A coincidence of megafauna decline and human arrival has been found worldwide (e.g. Haynes 2017). Humans were already present in Siberia at the time (earliest evidence from 35 000 BP, regular colonization probably around 14 000 BP; Hopkins et al. 1982), but just developed more efficient hunting techniques, which allowed increased hunting pressure on megaherbivores (Guthrie 1990). The survival of the mammoth on Wrangel Island until around 4000 BP in the absence of humans, provides further evidence (Zimov et al. 2012a). The functional removal of the megafauna as apex consumers led to trophic downgrading with far-reaching

Box 4: Hypotheses related to the demise of the mammoth steppe

Climate change hypothesis

This hypothesis suggests that wetter climate in the Holocene caused habitat and vegetation change, which in effect caused extinctions of megafauna due to declining forage quality and quantity (see Hopkins et al. 1982).

Overkill hypothesis

This hypothesis is also known as “Prehistoric overkill” or "Blitzkrieg"-hypothesis (Martin 1967; Martin and Klein 1984). It suggests that humans acted as new "super-predators", making megaherbivore populations susceptible to top-down-control and eventually leading to massive declines and extinctions. Worldwide evidence supporting this hypothesis comes from for similar timing of human arrival and megafauna extinctions (Haynes 2017).

Coincidence-of-factors hypothesis

It has often been suggested that both climate change and overkill could have been important drivers of megafauna decline (Stuart 2015; Gill 2014).This hypothesis suggests that only the temporal coincidence of human hunting and climate change acting at the same time could have been responsible (Martin and Klein 1984).

Keystone herbivore hypothesis

Megaherbivores are keystone species, which act as ecosystem engineers (also see Box 6). Immune to predation, they reach saturated populations and thus exert top-down control on vegetation and shape ecosystem processes and characteristics (Owen-Smith 1987).

Ecosystem hypothesis

This hypothesis is an application of the keystone-herbivore hypothesis and overkill hypothesis to the Beringian mammoth steppe (Zimov and Chupryninm 1991; Zimov et al. 2012b). It predicts that the anthropogenically driven extinction of megaherbivores led to a, theoretically reversible, shift from the Pleistocene cold steppe to contemporary tundra and taiga vegetation.

consequences on the structure and dynamics of the entire trophic system of herbivory and predation by removing large apex consumers (Gill 2006; Estes et al. 2011). According to Zimov's ecosystem hypothesis, these consequences would include a shift in competition from productive grasses to inedible woody and moss vegetation with respective effects on soil microclimate (moisture and temperature) and soil and vegetation productivity (see sections 1.2.4 and 1.3.2).

1.3. Grazing ecology

1.3.1. Effects of herbivores on vegetation

In the absence of unambiguous evidence for Pleistocene vegetation-herbivore-interactions, one has to turn to equivalent modern grazing systems and the field of rangeland ecology for further evidence (Box 5).

Early range succession models (Box 5) proposed that herbivores can continuously and reversibly drive vegetation changes (Sampson 1919; Dyksterhuis 1949), as Zimov hypothesized for the mammoth steppe. However, more recent models suggest that increasing grazing intensity can lead to alternative equilibria with irreversible transitions (Westoby et al. 1989; Box 5). These alternative stable states (Box 5) can arise from positive feedback systems between internal factors, which may have little effect until a threshold is reached that might induce dramatic shifts in ecosystems (Scheffer and Carpenter 2003). The decrease of grazing intensity with the decline of the mammoth steppe fauna and subsequent reordering of the entire ecosystem could be seen in this light.

Box 5: Rangeland theory

Theoretical framework on the effects of grazing on plant community structure and diversity. Hypotheses are either based on the assumption that vegetation-herbivore-dynamics are in equilibrium, thus stressing density-dependent biotic feedback systems; or based on the idea that both are driven by (harsh) environmental conditions and stochastic events (Vetter 2005).

1) Equilibrium (Herbivore density-depended dynamics)

- The **range succession model** (Clements 1916; Sampson 1919; Dyksterhuis 1949) assumes that vegetation changes in response to grazing are continuous and reversible.
- The model of **alternative stable states** (Scheffer & Carpenter 2003) tries to explain dramatic shifts in ecosystems, assuming gradual changes having little permanent effect until a threshold is reached, which might be difficult to reverse; alternative stable states can arise from positive feedback systems between internal factors.
- The **generalized model for grazing effects on vegetation (MSL)** (Milchunas et al. 1988; Cingolani et al. 2005) assumes different equilibrium stages depending on grazing intensity, evolutionary grazing history and site productivity of the communities.

2) Non-Equilibrium (independent dynamics, driven by abiotic factors)

- The **Non-Equilibrium model** (Ellis and Swift 1988; Vetter 2005) assumes that grazing systems under harsh conditions are governed by abiotic factors, because herbivore populations never reach densities in equilibrium with their food plants. Thus, they are thought to have negligible effects on vegetation.
- The **state-and-transition (S-T-) model** (Westoby et al. 1989; Laycock 1991) predicts that rangeland systems shift between discrete alternate stable states. These can be triggered by changes in grazing (intensity, type of herbivores; temporal patterns) or abiotic factors (e.g. fire regime, extreme weather events) or combinations of these factors.

In a global meta-analysis on plant traits (Díaz et al. 2007) found that grazing favored annuals over perennials, short over tall plants, prostate growing over erect growing plants, and rosettes over stoloniferous plants and tussock grasses (Díaz et al. 2007). However, both direction and strength of responses depended on productivity and grazing history of sites, with minimal to insignificant effects in dry systems with a long grazing history. This is line with the MSL model (Milchunas et al. 1988; Box 5), which suggests that ecosystems with a long history of grazing allow the development of species pools adapted and resilient to different grazing intensities (Cingolani et al. 2005). Weaker effects in arid systems could be due to different grazing strategies of herbivores in less dense vegetation (Vesk et al. 2004) or confounding effects linked to productivity or environmental stress (Carmona et al. 2015). For example, it has been suggested that aridity selects for similar plant traits as grazing, thus leading to convergence of traits (Quiroga et al. 2010; Carmona et al. 2015). According to this hypothesis we could either expect little influence of grazing on mammoth steppe vegetation, as a dry ecosystem with long grazing history, or strong effects, as a probably productive ecosystem. This also strongly depends on the proportionate contribution of herbivores to the aridity and productivity of the ecosystem (see sections 1.2.2, 1.2.4 and 1.3.2).

On the other hand, vegetation in extreme and highly variable climates could be more determined by the stochasticity of the environment and uncoupled from herbivore populations, according to non-equilibrium rangeland theory (Ellis and Swift 1988; Vetter 2005; Box 5). Several studies have found that climatic variability was more important than grazing in explaining vegetation composition and productivity (e.g. Wehrden et al. 2012; Wang et al. 2017). The overriding climatic factor in the respective rangelands is variability of rainfall. Projected on past and present Beringia, climatic harshness is rather defined by constant extreme conditions of long, cold winters and short summers, and not by interannual variability. Grazer populations might be driven by fluctuating mortality in winters, and, thus, might not reach critical densities to have a profound effect on vegetation. Also, strong adaptations of plant communities to harsh environmental conditions (soil aridity and/ or nutrient limitations during a short vegetative period) might leave little room for competitive release from herbivory.

The closest contemporary analogues in regard to grazing in cold climates are studies on reindeer grazing in Scandinavian taiga and tundra, and yak grazing in Tibetan alpine meadows and meadow steppes. Though precipitation may be low here, water availability is usually sufficient (less so in Eastern Tibet). Results show that grazing and trampling can have an effect in these ecosystems. Intensive grazing might lead to degradation and reduced vegetation cover (Manseau et al. 1996; Wang and Wesche 2016); while moderate grazing has been shown to reduce the litter layer (Suominen and Olofsson 2000; Virtanen 2000), increase species richness and diversity (Suominen and Olofsson 2000) and even lead to the establishment of productive grasslands on the expense of shrubs and mosses (Suominen and Olofsson 2000; Post and Pedersen 2008; Ravolainen et al. 2011). In forests, grazing can change understory microclimate and influence recruitment of tree seedlings; in effect even creating relatively stable savanna-like woodlands (Suominen and Olofsson 2000). Overall, despite harsh climatic conditions we can expect grazing to have an effect on contemporary vegetation of northeastern Yakutia.

1.3.2. Effects of herbivores on ecosystem processes

If the influence of herbivores on vegetation is especially large, they can be considered ecosystem engineers (Box 6). Studies usually address the herbivore's potential to alter habitat structure and fire regimes (e.g. Waldram et al. 2008; Cornelissen 2017); less often the effects on nutrient turnover and soil moisture availability are considered, the central aspects of Zimov's ecosystem hypothesis. Moreover, according to the MSL-model the largest grazing effect is expected at productive sites (Cingolani et al. 2005). However, the model assumes that this productivity is merely a result of abiotic resources (e.g. water and nutrient availability; Cingolani et al. 2005); it does not consider feedback systems of these resources with grazing animals.

Box 6: Ecosystem engineers

An ecosystem engineer is an organism that directly or indirectly modulates the availability of resources to other species, by causing physical state changes in biotic or abiotic materials, thus modifying, maintaining and creating habitats (Jones et al. 1994). Thus, they have extraordinary potential of high impact on the species richness and landscape-level heterogeneity of an area (Jones et al. 2014). Grazers can be considered ecosystem engineers by maintaining vegetation openness and mosaic diversity (Johnson 2009; Cornelissen 2017), changing habitats for other herbivores (Waldram et al 2008; Cornelissen 2017) and altering fire regimes (Johnson 2009; Waldram et al 2008).

Low temperatures and short summers in northeastern Siberia result in slow decomposition and nutrient cycling, hence many contemporary arctic ecosystems are nutrient limited (Shaver and Chapin 1980; Chapin and Shaver 1985). Zimov (Zimov et al. 1995, 2012b, a; Zimov 2005) proposed that large herbivores would greatly enhance nutrient cycling under these climate conditions (see section 1.2.4). Studies from reindeer grazing in Scandinavia have shown that intensive grazing and trampling can eventually lead to degradation of heathlands with reduced productivity (Manseau et al. 1996) and that moderate grazing can decrease litter quality and site productivity through selective foraging on nutritious plants (Suominen and Olofsson 2000). When resources are limited, plants with inherently slow growth are favored, which in turn favors large investments in antiherbivore defenses (Coley et al. 1985). Overstocking has also led to soil degradation in Tibetan *Kobresia*-meadows, although this ecosystem is generally well adapted to nutrient limitation and nutrient loss through grazing (Miehe et al. 2019). Experiments showed that exclusion of horse grazing can improve aboveground productivity (Wu et al. 2008). On the other hand, it has been demonstrated that grazing in Himalayan shrub steppes increases aboveground plant productivity, litter quality and plant available soil nitrogen (Bagchi and Ritchie 2010).

The second central aspect of Zimov's hypothesis is a pronounced decrease in soil moisture availability through grazing (see section1.2.2). Indeed, some studies have found a shift towards more drought-adapted vegetation (called xerophytization) in response to grazing in meadow steppes in Mongolia (Bazha et al. 2012) and southern Siberia (Kumacheva et al. 2017). It remains to be shown, whether this also has effect is also possible in northern Siberia, where radiation and evapotranspiration is lower and soil moisture generally higher.

1.4. Study area

Overall, a knowledge gap exists between the megaherbivore hypotheses of palaeoecologists, who focus mainly on palaeobotanic reconstructions of flora and megaherbivore's diet as well as on megaherbivore population dynamics; and current rangeland ecologists, who focus mainly on grazing effects in climatically unpredictable zonal steppes or on secondary grasslands in temperate regions, but less on the low productive, climatically harsh tundra and taiga zone. The "loose end" to close this knowledge gap is to study azonal and extrazonal grasslands within a matrix of current vegetation (like tundra and taiga) in a region like Beringia, where megaherbivores have been known to play a part in the ecosystem prehistorically.

1.4.1. Central and northeastern Yakutia

Sakha (Yakutia) is a republic of the Russian Federation located in northeastern Siberia and characterized by extreme climatic conditions and the lowest temperatures in the northern hemisphere. The Yana Highlands are bordered by the Verkhoyansky and Chersky Mountains. According to Popp et al. (2007) and Siegert et al. (2009), the Highland territory was not glaciated at least during the last 60 ka, whereas both the Verkhoyansky Mountains and Chersky Ridge were influenced by alpine glaciers during the Pleistocene cold stages (Glushkova et al. 2011; Stauch and Lehmkuhl 2010). Whereas today's coastal lowlands, during sea-level high-stands were periodically influenced by maritime climate, the Yana Highlands steadily remained under continental climate impact. Continental climate, e.g. warm summers and dry conditions, foster grassland vegetation and large grazing mammals. Interior Yakutia is therefore considered a refuge for tundra-steppe and mammoth fauna during the Quaternary (Yurtsev 1982; Boeskorov 2006).

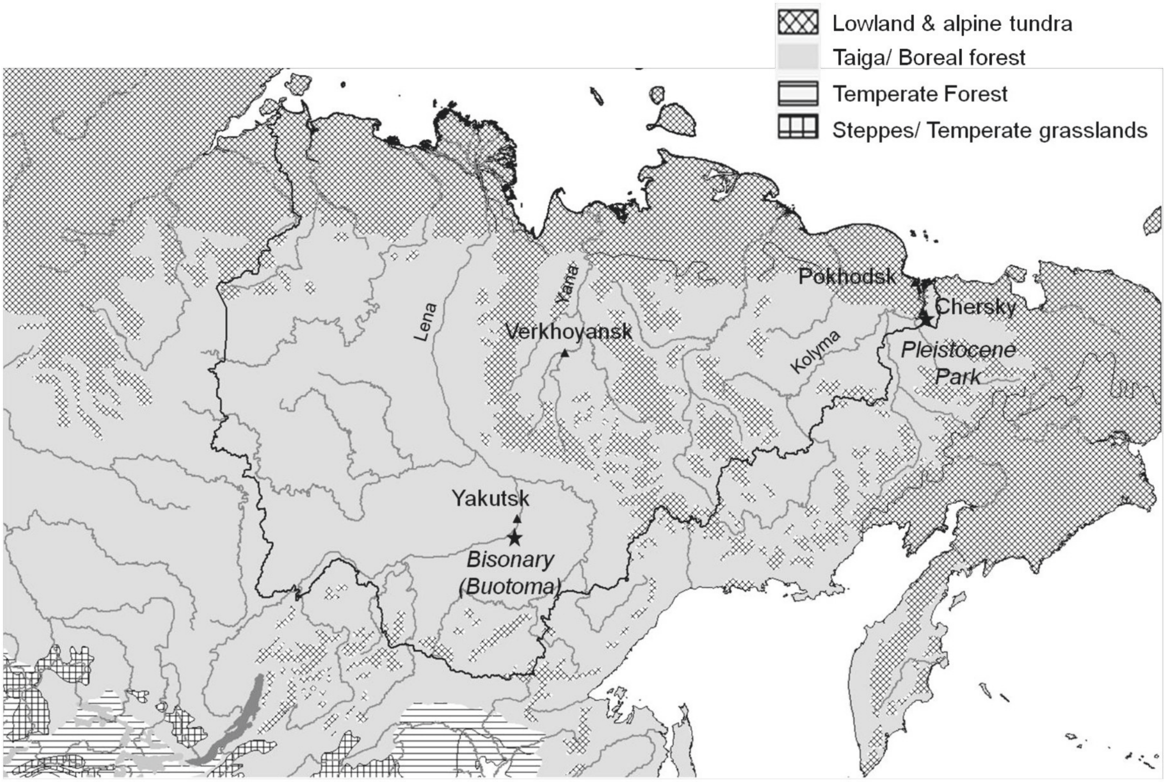

Figure 1. Map of the study area. The black line indicates the political border of the Sakha Republic (Yakutia), Russian Federation. Ecoregions according to the Nature Conservancy.

We collected data in two expeditions, to the Yana highlands in June/ July 2014 and to the lower Kolyma and middle Lena river basins in July/ August 2015. Our study region includes five locations (Figure 1): Pokhodsk and Chersky in the lower Kolyma river basin in northeastern Yakutia, Verkhoyansk in the Yana highlands, and Yakutsk and the Buotoma river confluence in the middle Lena river basin in Central Yakutia. Mean annual temperatures range from −15.4 °C at the Yana site (Worldclim; Hijmans et al. 2005; Table 1), over −12.9 °C at the Kolyma site to −9.5 °C at the Lena site, with summers being warmest at the Lena site (temperature of warmest quarter: 16.1 °C) and coolest at the Kolyma site (6.5 °C; Yana site: 12.6 °C). Mean annual precipitation is lowest at the Kolyma site (150 mm) and highest at the Lena site (271 mm; Yana site: 186 mm). Both the Lena and Yana sites are strongly continental (continentality defined as difference between max. temperature of warmest month and min. temperature of coldest month; 69

K and 71 K), while the climate at the Kolyma site is relatively less continental (50 K; Appendix A1, Figure 1.1).

Table 1. Overview on study regions.

Region	Coordinates	Mean annual temp. [°C]	Annual precipitation [mm]	main vegetation	grazing animals
Pokhodsk	69.0667° N 160.9667° E	-12.9	143	dwarfshrub and graminoid tundra; tundra steppes	free roaming reindeer
Chersky	68.7427° N 161.3508° E	-12.4	156	larch taiga; floodplain meadows; steppe slopes	"Pleistocene Park" with bison, musk ox, horse, moose; ground squirrels on steppe slopes
Verkhoyansk	67.5506° N 133.3993° E	-15.4	186	open larch taiga; floodplain meadows; steppe slopes	free roaming cattle and horses; ground squirrels
Yakutsk	62.0355° N 129.6755° E	-9.7	261	taiga; floodplain meadows; secondary grasslands and steppes	free roaming cattle and horses; ground squirrels
Buotoma	61.2394° N 128.7649° E	-9.2	284	taiga; secondary grasslands and steppes	"Bisonary" with bison; free roaming horses outside the fences

Climate data according to WorldClim (Hijmans et al. 2005).

Almost all sites are within the boreal forest zone with light taiga dominated by *Larix gmelinii* (Isaev & Timofeyev 2010). In contrast to the neighbouring, more western districts, *Pinus sylvestris* is absent there, as the Verkhoyansky mountain range seems to represent an effective migration barrier for that species. Instead, Pinus pumila is a common constituent of mountainous taiga in the Yana Highlands. The northernmost site is the Pokhodskaya Yedoma north of Chersky and lies in the tundra zone. Typical steppe vegetation (*Cleistogenetea squarrosae*) was only found at sites with special microclimatic conditions: on more or less steep, SW-exposed slopes. Thus, it was challenging to find appropriate sites across the entire study region. The number of available sites to study extrazonal steppe vegetation was especially restricted in Chersky, and all of these were out of reach of the large grazers of the "Pleistocene Park" nearby. In Pokhodsk, Verkhoyansk and Yakutsk, livestock roamed freely and grazing intensity was low to moderate and rather uniform across steppe and tundra-steppe slopes. Some more intensely grazed steppe sites were found around Yakutsk and in the outer areas of the Ust'-Buotoma Bisonary, which seemed to be the secondary vegetation after clearings of taiga forest. The small mammals inhabiting steppe slopes were usually ground squirrels (*Urocitellus parryii*).

1.4.2. Pleistocene Park and the Ust-Buotoma Bisonary

We visited two fenced grazing sites, the "Pleistocene Park" in Chersky and the "Bisonary" along the Buotoma river confluence. "Pleistocene Park" was founded in 1996 and is set in the northern taiga zone (but pastures include large areas of floodplain meadows). At the time of our study, it was grazed by one European bison (*Bison bonasus*) and three musk oxen in an inner fence (50 ha; herbivore density of 0.08 individuals/ ha) and approximately 40 horses and several moose in a larger outer fence (1600 ha; herbivore density of 0.03 individuals/ ha). Horses were also present in the inner fence from the beginning of the project until about a year previous to our study. Animals are fed in winter to secure their survival and built up high density populations. The "Bisonary" was established in 9 enclosures on 118.5 ha in 2006, and in 2014 had 35 Canadian wood bison (*Bison bison athabascae*; herbivore density of 0.29 individuals/ ha) grazing in mostly secondary meadows, steppes and larch taiga. Horses grazed freely on the meadows and steppes outside the fence, except for the steepest slopes.

1.5. Chapter outline

This Thesis consists of four chapters, which address the following main hypotheses:

- Remnants of a former more or less continuous Pleistocene mammoth steppe can be found among the extrazonal steppes of Yakutia; the plant species composition of these extrazonal steppes resembles the Pleistocene vegetation as re-constructed by palaeobotanic fossil analysis.

- Grazing in Yakutia, especially in the high densities of two wildlife parks, is able to transform vegetation: from low productive, mesic to wet moss- and dwarfshrub-dominated tundra and taiga understory vegetation to productive, relatively dry herb- and grass-dominated steppe vegetation.

The first two chapters focus on current grassland and steppe vegetation in Russia in general and in Yakutia specifically. The first chapter (CH1) highlights the biological diversity of Russia's grasslands under diverse climatic and edaphic conditions. The second chapter (CH2) focuses on the phytosociology of extrazonal steppes and other grasslands of Yakutia, and on their harsh climatic and special edaphic conditions. The third chapter (CH3) aims at a comparison of current vegetation with Pleistocene fossil remains in order to find the closest analogues of mammoth steppe vegetation. The last chapter (CH4) discusses the influence of grazing on current vegetation: grazing effects on plant species and trait composition, as well as on vegetation productivity under the given harsh climate. The findings of these chapters (CH2-5) have previously been published and references to the respective papers are given on the title page of each chapter. The discussion (CH6) is a synthesis of these chapters, setting the findings into the context of the mammoth steppe and discussing the potential of re-wilding.

CHAPTER 2

Land use of Natural and Secondary Grasslands in Russia

The content of this chapter has been published in Reinecke, J., Smelansky, I.A, Troeva, E.I., Trofimov, I. A., Trofimova, L. S. 2018. Chapter 5: Land use of natural and secondary grasslands in Russia. In: Squires, V., Dengler, J., Feng, H. & Hua, L. (Eds.), *Grasslands of the World: Diversity, Management and Conservation*, CRC Press, Boca Raton: p. 113-138.

CHAPTER 3

Extrazonal steppes and other temperate grasslands of northern Siberia

Phytosociological classification and ecological characterization

The findings of this chapter have been published in Reinecke, J., Troeva, E., Wesche, K. 2017. Extrazonal steppes and other temperate grasslands of northern Siberia – Phytosociological classification and ecological characterization. *Phytocoenologia*, 47: 167–196.

CHAPTER 4

Woodlands and steppes

Pleistocene vegetation in Yakutia’s most continental part recorded in the Batagay permafrost sequence

The findings of this chapter have been published in Ashastina, K., Kuzmina, S., Rudaya, N., Troeva, E., Schoch, W.H., Römermann, C., Reinecke, J., Otte, V., Savvinov, G., Wesche, K., Kienast, F. 2018. Woodlands and steppes: Pleistocene vegetation in Yakutia’s most continental part recorded in the Batagay permafrost sequence. *Quarternary Science Reviews*, 196:38–61.

CHAPTER 5

Grazing at the limit

Effects of large herbivore grazing on relics of presumed mammoth steppe in NE-Siberia

The findings of this chapter have been submitted as Reinecke, J., Ashastina, K., Kienast, F., Troeva, E., Wesche, K. (re-submitted). Grazing at the limit – effects of large herbivore grazing on relics of presumed mammoth steppe in NE-Siberia. Restoration Ecology, re-submitted on 15.03.2019.

Chapter 6

Synthesis – Yakutian steppes and re-wilding the mammoth steppe

6.1. Contemporary grasslands and herbivore pastures in Yakutia

Today, very little is left from the once wide-spread cold and dry mammoth steppe across northern Eurasia (Figure 1A), as a herbivore-dominated ecosystem and more or less continuous vegetation type. Extensive steppes, where herds of large herbivores still play a significant role, have retracted to the temperate zone of Southern Siberia and Mongolia (Lavrenko et al. 1991; Wesche et al. 2016). In the colder climate of the boreal taiga forest zone and (sub-) arctic tundra zone, extrazonal steppes and tundra steppes are confined to discontinuous, small islands (Figure 1B; CH3). The only other open, grass- and herb-dominated vegetation, which could nowadays provide pasture for large herbivores in Yakutia, are azonal or secondary grasslands with more mesic or wet character, e.g. along floodplains (CH2&3). However, the majority of grasslands in the forest zone are of anthropogenic origin: long-term fallows of abandoned croplands and hayfields as well as pastures resulting from deforestation and drainage of bogs or lakes (CH2). It has been suggested that traditional agriculture and livestock herding could be seen as partial ecological replacement of megaherbivores (Bocherens 2018). Semi-natural grasslands like alases and lower river terraces could be considered potential natural pastures for wild herbivores in the absence of human land use (also see section 6.3). However, irrespective of the character of these pastures, in regard to vegetation type, soil moisture and species composition, it remains unlikely that northern Siberian vegetation could currently provide enough pasture for herds of wild, large herbivores without extensive human intervention.

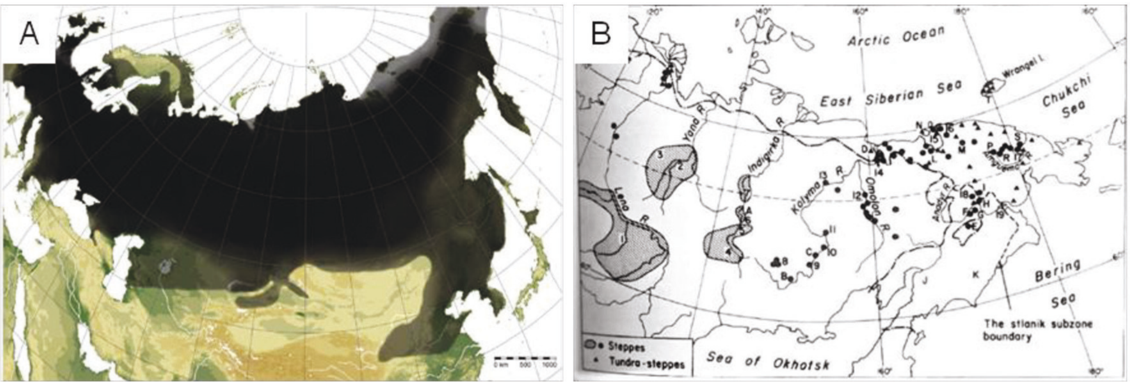

Figure 1. Extension of the mammoth steppe (based on megafauna fossil records; from Kahlke 2014) and of contemporary steppes and tundra steppes in northeastern Siberia (from Yurtsev 1982).

6.2. Contemporary steppes and tundra steppes

Steppes represent the highest share of natural grasslands in Russia, especially in Southern Siberia (CH2). Their high diversity stems from latitudinal and longitudinal zonation as well as from varying edaphic conditions (CH2). This diversity pattern is reflected, although on a much smaller scale, in Yakutia (CH3). Using a phytosociological approach we were able to demonstrate the close relationship between extrazonal steppes in Yakutia and southern Central Asian zonal steppes of the class *Cleistogenetea squarrosae*. Simply put, Yakutian steppes are largely species-poor vicariants of Eastern zonal steppes. This close affinity has also been suggested based on floristic (Yurtsev 2001) and palynological evidence (Giterman and Golubeva 1967). It indicates past connectivity and supports the idea that contemporary steppes are remnants of Pleistocene steppes, which extended far to the north during glacial periods (Yurtsev 1982; also see section 6.2.1). The results disprove the view that Yakutian steppes are merely the result of recent, accidental arrivals of broad-niched tundra and steppe species of disparate origins (see Blinnikov et al. 2011).

Following Guthrie’s (1982, 1990) hypotheses on the climate conditions of the mammoth steppe, high amounts of spring rains and very dry summer periods, one could also have suspected a close connection to West Palaearctic steppes of the class *Festuco-Brometea*. They are characterized by a vegetation peak in spring and, thus, a high share of ephemeroids in the plant communities (Lavrenko et al. 1991, Wesche et al. 2016). These steppes have also been considered potential relics of the mammoth steppe (Kienast 2002; Ermakov et al. 2014). The closer proximity of contemporary steppes to the more continental Central Asian steppes, with highest precipitation in summer (Wesche et al. 2016; CH3), as well as the lack/ low number of characteristic *Festuco-Brometea* steppe species in the palaeorecord (CH4), are evidence against Guthrie's hypothesis. He inferred high amounts of spring rains as one of the factors needed to produce abundant protein-rich spring forage for large herbivores' individual growth and for species' co-existence (Guthrie 1982). Other explanations are probably needed to explain high (spring) productivity of the mammoth steppe vegetation (see section 6.3). In general, plant communities of Central Asian steppes with summer rains are high in protein and nitrogen contents, as well (Long et al. 1999; Wesche and Ronnenberg 2010).

Both true steppes (*Stipetalia krylovii*) in Central Yakutia and meadow steppes (*Festucetalia lenensis*) occur as far as northeastern Yakutia where they are restricted to south-facing slopes (CH3). Slope steepness of steppe sites increases towards the north, compensating for a colder and wetter macroclimate (CH3). This has also been observed in Alaska (e.g. Edwards and Armbruster 1989): ultimately, soil moisture controls the lack of forest in favor of steppes on south facing bluffs in the far north. Guthrie (2001) claimed that the aridity of these slopes would be mainly due to increased radiation input of tilted surfaces and subsequently higher evapotranspiration. Likewise, the aridity of the Pleistocene mammoth steppe would be due to increased radiation because of cloudless skies. Our results, however, showed that neither heat load nor radiation were important predictors for steppe occurrence, while slope inclination was an important predictor throughout. Water run-off is obviously more important than radiation input for steppe vegetation, at least today. Thus, our results rather support the idea of lower precipitation and more arid macroclimate in the Pleistocene favoring steppe vegetation.

So called tundra steppes (*Carici rupestris-Kobresietea bellardii*) occur north of the tree line in the tundra zone, and their occurrence is more related to disturbance than to slope inclination or aspect (CH3). Despite similar physiognomy and the contribution of xerophytes, they are no steppes (*Cleistogenetea squarrosae*) in the proper phytosociological sense (CH3) and they currently have no zonal representation. On the other hand, the meadow steppe association *Astragalo-Calamagrostietum* probably represents a gradual transition of species composition from central Yakutian meadow steppes to tundra steppes (CH3). These distinctions are important to make, when trying to find modern analogues of the mammoth steppe (see section 6.2.1), and searching for the underlying environmental drivers for their species composition. For example, Yurtsev (1982) reported "steppes" from as far as the Kolyma and Anadyr river basins, which become smaller and less abundant further northeast and experience wetter climate than Central Yakutia. Determining the phytosociological units these and other so called "steppes" in northern Siberia belong to, and whether these are true *Cleistogenetea squarrosae* or actually tundra steppes sensu (Kucherov and Daniëls 2005), would help to define their status and distribution more clearly.

The species composition of both steppes and tundra steppes differs strongly on the association and community level, both among our samples as well as in comparison with other studies from northern Siberia (e.g. Mirkin et al. 1985; Kucherov and Daniëls 2005; Sinelinikova 2009). This can be attributed to the relative isolation of these microhabitats and the incomplete geographical coverage by phytosociological studies, especially of tundra steppes and hemicryophytic meadow steppes across northern Siberia. For further clarification of syntaxonomic relationships, especially regarding the lower hierarchies, it would be interesting to compare our Yakutian releves with those of other northeastern steppes, as well as southern Siberian and Mongolian steppes. A Eurasian database of steppe vegetation has been set up in cooperation with steppe vegetation ecologists of other regions within the scope of this project for a follow-up in the future.

6.2.1. Relics of the mammoth steppe?!

Very different arctic and alpine plant communities have been proposed as possible small-scale analogues of the mammoth steppe: low productive fellfields and cryoxeric steppes (Hopkins et al. 1982), such as those on Wrangel Island (Yurtsev 1982), herb- and grass-dominated slopes of pingos in Alaska (Walker et al. 1991), relatively productive vegetation between steppe and tundra in Alaska (Edwards and Armbruster 1989) and the Russian Altai (Chytrý et al. 2017), alpine steppes of the Tibetan Plateau (Guthrie 1982) and temperate grasslands of the mid-latitudes (Guthrie 1982). Even moist, calcareous sedge tundra has been suggested as the closest modern analogue due to its moderately drained and nutrient-rich character, and its importance as wildlife pasture (Walker et al.

2001). The problem with temperate grasslands as mammoth steppe analogues is their lack of cryophilic elements; alpine environments would have been unsuitable for the mammoth fauna due to their relief; and in the high arctic summers are too short for sufficiently productive vegetation (Guthrie 1982). Thus, steppe and tundra steppe vegetation in the boreal and subarctic zone seem to be the most reliable analogues.

Northern Yakutian tundra steppes, as the northernmost steppe-like vegetation type, could be considered the most likely analogues of the Pleistocene cold steppe, especially since their occurrence seems to be related to disturbance (CH3). *Kobresia* and *Artemisia*, important components of the mammoth steppe according to several paleoecological studies (Yurtsev 2001; Kienast et al. 2005), were both present in most, though not all of our tundra steppes. However, most other species of these cold-resistant communities were lacking in the palaeobotanic record (CH4).

Instead, we found a close relationship between plant assemblages of the palaeorecord and contemporary meadow steppes (*Festucetalia lenensis*; CH4). This is in line with the high proportion of forbs in the mammoth steppe vegetation, which macrofossil and environmental DNA analysis have suggested (Willerslev et al. 2014). The meadow steppe association *Astragalo-Calamagrostietum* is rather unique to northern Siberia, and represents a transition to tundra steppes on loess-like substrates (CH3). Bearing in mind that such substrates were typical for the Pleistocene environment (French 2007), these steppes are especially interesting in regard to finding the closest relics of the mammoth steppe. According to our palaeobotanic reconstructions (CH4), meadow steppes probably formed the primary vegetation of Yakutia during cold stages, but prevailed among open, coniferous woodlands during the last interglacial. Only the proportion of meadow steppe vegetation (zonal steppe with larch groves in cold stages vs. zonal larch taiga with steppe openings in warm stages) and the share of steppe species in grassland communities shifted in response to the prevailing climate conditions (CH4). Meadow steppes constitute suitable pastures for livestock, especially in winter, because of their relatively high productivity and forage quality. Given their continuity throughout the late Pleistocene, meadow steppes could potentially have supplied the base for the persistence of large herbivores (CH4).

However, our comparison of palaeovegetation with contemporary analogue steppes revealed no exact congruence of plant species composition. This could a) be due to the incomplete picture of plant communities, which macrofossil assemblages can offer; or b) the fossil record being a conglomerate of small mosaic vegetation types in close proximity, which do not exist likewise today (see next paragraph); or c) be a result of the formation of new plant communities (Gill 2014) under different environmental conditions, colonization by new plant species (Walker et al. 1991) and habitat isolation. This non-analogue mixing of typical steppe and tundra taxa in glacial biomes has also been observed in other studies (see Blinnikov et al. 2011). Thus, extrazonal meadow steppes of Yakutia strictly speaking cannot be called relics of the mammoth steppe, despite probably being the closest analogues.

The difficulty to find a modern analogue to the mammoth steppe may lie in its suggested mosaic character (Schweger and Habgood 1976; Yurtsev 1982, 2001; Kienast et al. 2005; Zanina et al. 2011). The mixed signal in our palaeorecord suggests a much more diverse and complex landscape in the Pleistocene, with different steppe, tundra steppe and meadow associations in close proximity (CH4). Similar indications for the spatial and/ or temporal mosaic of drier and moister plant communities in the mammoth steppe have also been reported by others (Willerslev et al. 2014). This kind of mosaic would also explain the preservation of local diversity across warm and cold stages (CH4), and thus support the idea of local refugia under specific edaphic and microclimatic conditions (Hulten 1937). The modern landscape of Yakutia is relatively homogenous, with medium-scale heterogeneity in vegetation (e.g. steppe patches) mainly determined by topography and microclimate. These, however, demonstrate that 1) very different vegetation types can occur in close proximity to each other, despite a common macroclimate, due to a typical micro-relief (e.g. mound and ditch vegetation of polygonal tundra or alas vegetation); 2) broad-niche species from different vegetation types make up the transition zones between them (e.g. forest steppe ecotone). Thus, given the drivers for small scale differentiation of vegetation, we could still expect similar mosaics as in the mammoth steppe today. Local disturbances created by herbivores might even be needed to create or enlarge such small-scale mosaics (see section 6.3).

In summary, we could not find unambiguous relics among contemporary plant communities, and instead support the notion that the mammoth steppe landscape consisted of a vegetation mosaic. A local mosaic of plant communities, based on topography, proximity to glaciers and coast, different soil conditions, animal disturbance and fire, is not easily resolved spatially (Blinnikov et al. 2011). Thus, the concept of a "Pleistocene tundra steppe", defined as a small-scale landscape mosaic of different tundra, tundra steppe and meadow steppe communities (Yurtsev 1982), is the most convincing image of the mammoth steppe vegetation according to our studies.

6.3. The role of grazers today - and their proposed role in the mammoth steppe

There is ongoing discussion on the two main drivers of vegetation change at the beginning of the Holocene. Advocates of the climate change versus keystone herbivores hypotheses disagree with respect to cause and effect and whether large herbivores did or did not have the capability to drive these processes. They, essentially, argue over the same processes and characteristics of vegetation, namely: aridity, disturbance, nutrient richness, snow conditions and vegetation structure. Our results from contemporary grazing in Yakutia provide some evidence on each of these points.

We attribute the occurrence of tundra steppe patches in northeastern Yakutia to frost and wind erosion (CH3). This has also been found in Chukotka, where these conditions are even more profound (Kucherov & Daniels 2005). Accordingly, soil disturbances in the mammoth steppe could be attributed to snow drift, rapid spring melt and wind/ melt water erosion, because, according to the climate hypothesis, winter winds were more prevalent in the Pleistocene (Guthrie 1982, 2001). Such disturbances could, however, just as well be ascribed to herbivore trampling. The disturbance indicators we found in meadows (annuals like *Chenopodium*), were even more common in the palaeorecord of the last interglacial: nitrophytic plants like *Urtica dioica* and ruderal plants like *Hordeum jubatum* and *Chenopodium* species (CH4). These ruderals not only indicate disturbance, but are typical for high local nutrient availability as it occurs through animal droppings. The disturbance indicators of tundra steppes (e.g. *Minuartia rubella*), were also present in the palaeorecord, but rather occur on barren soils. This is in line with Yurtsev (2001), who found that groupings of zoochoric, coenophobic ruderals and halophytes, which played a much more prominent role in the Pleistocene, are today restricted to few relic sites. This indicates a much more ubiquitous role of grazers in the past.

The most striking grazing effect was the xerophytization of mesic meadow vegetation due to intensive bison grazing under the continental macroclimate of Central Yakutia (CH4&5). Trampling and thinning out of the vegetation cover through grazing changed the microclimate (soil compaction, lower canopy cover, increased temperature and evapotranspiration), thus favoring more drought-adapted species (CH5). Lowered infiltration of water into compacted soil after trampling has also been observed in livestock pastures (Warren et al. 2010) and lichen tundra (Suominen and Olofsson 2000). Trampling compaction thus can affect drainage pathways related to microrelief (Warren et al. 2010). In a region where soil moisture and drainage are additionally influenced by soil thaw and permafrost (a drainage barrier), Guthrie (2001) argued that caribou and reindeer trampling would make tundra even wetter. The diversity of grass species adapted to moist-mesic as well as to dry conditions suggests that a variety of different habitats has probably been present in the Pleistocene tundra steppe (Kienast et al. 2005; Swanson 2006). Yurtsev's (2001) described the Pleistocene tundra steppe as a dominance of steppe, tundra steppe and dry tundra formations, with true xerophytic and cryo-xerophytic herbs extending into mesic meadows and seasonally drying-out waterbodies and shores. He also suggested a zoogenic origin of these mesic-xeric meadows (Yurtsev 2001). In correspondence, some steppe plants like *Koeleria cristata* became ubiquitous in the unique modern Indigirka forest-steppe landscape (Yurtsev 1982, 2001). Thus, if grazing can drive mesic meadows towards a more xeric species composition, similar effects could be expected in regard to other plant communities from a spectrum of steppe to tundra or forest-steppe. However, this effect was not related to an increased proportion of highly transpirating grasses in our studies, as suggested by Zimov, but more to microclimatic changes. Guthrie (2001) claimed that only clear skies with higher evapotranspiration in summer could explain increased aridity (compare to section 6.1), preventing paludification of soils and thus in effect favoring steppic plants with a quite different growth and anti-herbivory defense strategy. Now, it seems that, at least locally, grazers can also directly induce increasingly xeric conditions in plant communities by changing the microclimate.

Guthrie (2001) argued that Beringian vegetation is not unproductive due to inherently nutrient poor soils, but due to slow nutrient turnover in cold and wet soils. He claims that nutrient turnover would have been promoted in the Pleistocene by climatically determined drier and warmer soil conditions. The productivity and thus presumably enhanced decomposability of steppe vegetation, favored under this climate, in turn then would have increased nutrient turnover. Zimov and colleagues (Zimov 2005; Zimov et al. 2012b), however, link this high productivity of vegetation to a grazing-induced increase of productive grasses, as well as to the more efficient, alternative pathway of nutrient decomposition via the herbivore gut system. An increase of grasses has often been observed in present-day reindeer herder camps (see Blinnikov et al. 2011). We could not confirm this effect (CH5), even in the Pleistocene Park where Zimov tests his hypothesis experimentally. Instead we suspect selective habitat use (also see below) to explain the correlation of high grazing intensity with a high proportion of grasses in vegetation (CH5). We could also not find evidence for increased nutrient availability in grazed vegetation, except for some nutrient indicator species at few heavily grazed sites (CH5). Grazing can lead to preferential investment into aboveground biomass and increase soil nitrogen content via changes in nitrogen mineralization, abundance of soil microbes, nitrogen uptake and litter quality or plant community composition (Bagchi and Ritchie 2010). This is probably not the major driving factor for (re-)creating a productive grazing system in Yakutia, although it may be important for maintaining it. On the other hand, changes in soil nutrient availability may only take much longer to materialize than those in plant community composition. It has also been suggested that the exchange of nutrients primarily happens on a landscape scale: Megafauna have the potential to re-distribute nutrients across the landscape, because of their high food consumption, long gut retention, and large movement ranges (Malhi et al. 2016). In other grazing systems this transport of nutrients to frequently used resting places has been observed (Stumpp et al. 2006). In Yakutia this would require free roaming of large herbivores in the landscape and a specific experimental set up suitable to detect this exchange.

Snow conditions determine the availability of winter forage for large herbivores and determine the onset of spring and, thus, the duration of the growing season for plants (Guthrie 2001). *Pinus pumila* is a good indicator for winter snow conditions. It competes with steppe vegetation over dry habitats, but prefers milder winters with more snow or less wind to blow away a snow cover (Yurtsev 1982). Thus in Chukotka, where xerophytes are rare today, typical meadow steppe species thrive due to the absence of

Pinus and *Larix*. We found *Pinus pumila* close to the Batagay outcrop today, were during the last interglacial steppes resided and no *Pinus pumila* could be detected (CH4). According to Guthrie (2001) more prevalent winter winds in the last glacial would explain snow drift, lower albedo and quickly warming soils in spring, thus favoring steppe vegetation. So either wind conditions that Guthrie proposed for the last glacial must also have prevailed during the last interglacial; or the absence of snow can be related to the presence of herbivores. In order to find forage, animals would have had to scrape underneath the snow blanket. This behavior has been observed by the Zimov's in Pleistocene Park every winter in the most intensively grazed grassland patches (Zimov, pers. comm; CH5). A closed snow cover, as that over a grassland, has very high albedo, thus creating low soil temperatures. Trampling compacts snow, thus removing its soil insulation properties, exposing permafrost to extreme cold in winter and lowering soil temperatures even more (Zimov et al. 2012a). So, according to Zimov, albedo in the mammoth steppe was higher (not lower, see Guthrie 2001) and soil microclimate was colder (not warmer, see Guthrie 2001), thus producing a cold steppe, also with the assistance of large herbivores. Overall, I agree that deep snow in a wetter macroclimate would probably have been detrimental to some herbivore species (Wholly Rhino was quite sensitive to deep snow; Boeskorov et al. 2011), However, our palaeological evidence and observations of habitat use in the Pleistocene Park suggest that herbivores, by foraging underneath the snow in winter, changed albedo and soil microclimate in a way that promoted steppe and grassland vegetation. The exact processes behind this remain unclear and need to be addressed in experiments.

The main grazing effect on vegetation structure was the opening up of forests and scrub by bark stripping and crushing shrubs though bison. Debarking of stems of mature, unpalatable *Sambucus nigra* has also been found to be responsible for a major dieback of woodlands in favor of grasslands in temperate regions (Cornelissen 2017). In Scandinavia reindeer grazing has been shown to alter forest microclimate and prevent the recruitment of deciduous trees, thus contributing to the creation of open savanna-like woodlands (Suominen and Olofsson 2000). Guthrie (2001) argued that large mammals could not have been so thorough in eradicating trees, and concluded climate must have been responsible for tree absence in Beringia. Our research shows that small isles of deciduous trees survived in special microclimatic conditions in Siberia (also see Binney et al. 2009) and even in continental Yakutia (CH4). This supports the early hypothesis of Hulten

(1937), who proposed local tree refugia with mesic topo-edaphic and microclimatic conditions in cold phases. The climate of interglacials allowed abundant tree and forest growth, although these were not as ubiquitous as today. Insect assemblages of the last interglacial indicate well developed forests with thick plant litter (CH4). Nonetheless, large herbivores obviously survived in warm stages with abundant forests and bison or now extinct megaherbivores might have opened up forests and locally repressed tree growth. Herbivores can reduce the abundance of woody plants, especially at more fertile sites, where grazing impact is higher, and may even counteract shrub encroachment due to climate warming (see Bakker et al. 2016). They can halt or even reverse directional succession to woody vegetation in both wet and fertile vegetation by preventing tree seedling establishment. On the other hand, the temporary decline of herbivore numbers can create an opportunity for establishment of woody vegetation (Cornelissen 2017). In dry and nutrient-poor vegetation herbivores act by extracting and further limiting nutrients (Olff et al. 1999). *Salix* and *Populus*, the dominant shrubs and small trees at wetter sites, are palatable and rather attractive to large grazers and browsers (Olff et al. 1999). Other shrubs and dwarfshrubs defend themselves against grazing by slow, unproductive growth (Guthrie 2001) and low palatability. They are, however, not well defended when invading grasslands and surrounded by palatable plants (associational palatability; Olff et al. 1999, Cornelissen 2017). In the cold climate of Yakutia, with long regeneration times, this effect might be even more profound than in temperate regions. Overall, I consider the impact of large herbivores on vegetation structure important in both glacial as well as interglacial climates.

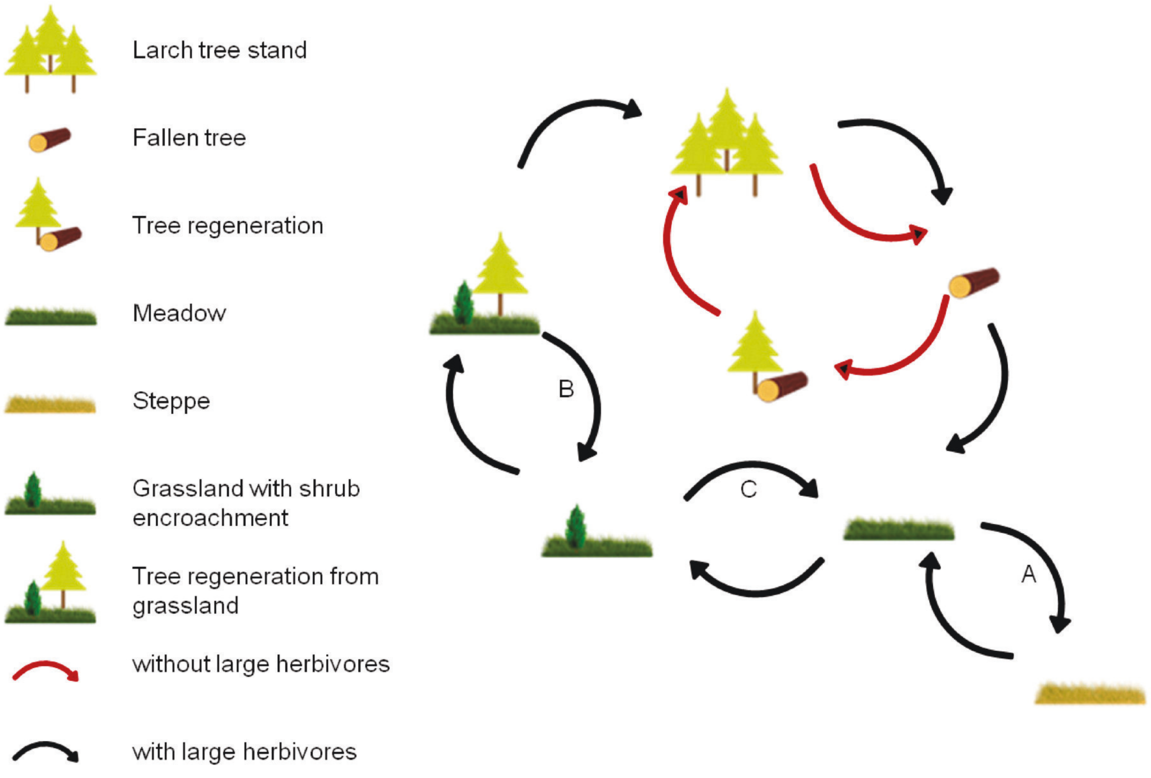

Figure 2. Patch dynamics in northern Siberia. Meadow patches are created when tree fall opens up the canopy and top soil. Herbivores maintain these patches, because they are specifically attracted to them. Steppes may form as a result of xerophytization (A) due to grazing, if the microclimate is suitable. Grasslands are maintained by large herbivores, unless shrub encroachment is higher than grazing pressure. These stages can be reversed by ecosystem engineers, which cause tree dieback (B), and browsing of shrubs (C). Adapted from Olff et al. (1999). Designed with Canva (www.canva.com).

With their ability to create local soil disturbances, to drive xerophytization, to open up vegetation canopies and possibly to increase nutrient turnover and re-distribution, large herbivores can be considered ecosystem engineers (Jones et al. 1994). As such they could be a driver behind the formation of diverse mosaic of different vegetation types (see section 6.2.1) and thus increase landscape heterogeneity (Johnson 2009). The variability of herbivore grazing pressure in space and time (due to migration routes, predation risks, water resources, unpalatable vegetation) can result in highly diverse landscapes (Bakker et al. 2016, Malhi et al. 2016). Olff et al. (1999) have described how grazing can trigger cyclic patch dynamics (Figure 2) in temperate floodplains and heathlands through alternation of facilitation and competitive displacement. In Europe there is evidence that mosaics of closed forest and wood-pasture are linked to high herbivore abundances in the last interglacial (Sandom et al. 2014). In Yakutia, open habitats during the last interglacial contained a mix of dry steppe elements with productive grasses, typical for fluctuating moisture (CH4). Facultative halophytes along seasonally retracting lake shores, where salt accumulates, attract grazers, and have been used as indicators for regularly disturbed pastures (Yurtsev 2001). Seasonally drying up frost polygons, which were even more abundant in the Pleistocene tundra steppe, provide such small-scale vegetation mosaics due to micro-topography. They would make interesting locations to further study grazing effects in Yakutia.

A herbivore-driven vegetation mosaic would explain feeding niche diversity of Pleistocene fauna (Yurtsev 2001). Analysis of stomach contents suggest that large herbivores supplemented their diets with high-protein forbs rather than specializing exclusively on grasses (Willerslev et al. 2014). Depending on the dominating vegetation, herbivores also seem to have adapted to local plant availability (Bakker et al. 2016), for example by including woody plants into their diet (Guthrie 2001; Willerslev et al. 2014). In order to explain niche diversity Guthrie, (1982) suggested several mechanisms for seasonal diversification of fodder vegetation, but did not list spatial drivers, despite mentioning topographic influences on vegetation development.

The co-existence of highly productive, grass-dominated floodplain meadows next to dry, unproductive steppes in close proximity would also help to explain the productivity paradox. Northern botanists and paleobotanists have repeatedly stressed that high levels of soil moisture are needed to provide high quality and quantity of forage to support large grazers during the Pleistocene (e.g. Cwynar and Ritchie 1980; Zimov et al. 1995, Yurtsev 2001).

Given higher mobility and more possibilities of habitat selection than in the studied parks, preferential selection of grazing sites would probably be even more pronounced. Large animals often tend to avoid steep slopes, and then concentrate in plains habitats where food quality and quantity is larger (Bakker et al. 2016). However, productive lowlands would probably be preferred in summer, and wind-swept, less snowy hilltops in winter (Yurtsev 2001).

Guthrie (2001) argued that major vegetation changes started before human over-hunting could be made responsible for extinctions, and that other large grazers would have survived up into the Holocene. He also argued that e.g. bison grazing today in Alaska would not change vegetation significantly (Guthrie 2001). Our study cannot provide evidence on the drivers of the decline of megafauna ("overkill hypothesis"). But our results show that grazers affect vegetation and point to the main pathways. These processes, if extrapolated to a landscape scale, can explain vegetation change just as well as the proposed climate changes (see chapter 6.2). Thus, we can tentatively suggest that their continuous survival (and in effect maybe also rewilding; but see section 6.4) would have had the potential to drive Holocene vegetation change into a different direction.

Guthrie (2001), defending the climate change hypothesis, might overemphasize the importance of a clear sky and strong winter winds for aridity without acknowledging the importance of spatial heterogeneity of vegetation and the participation of productive non-steppe grasslands for megaherbivore forage, as well as their potential to maintain this kind of vegetation. On the other hand, Zimov, defending the ecosystem hypothesis, might overestimate the potential of herbivores to propagate the growth of grasses and the subsequent magnitude of the xerophytization effect on vegetation on a landscape scale. He claims that modern climate would be rather arid (Zimov 2005), while not differentiating between grazing in continental Central Yakutia and the more suboceanic climate of Pleistocene Park. On the other hand, Zimov does not thoroughly discuss the potential of megaherbivores to open up shrub and forest vegetation in both of these climates.

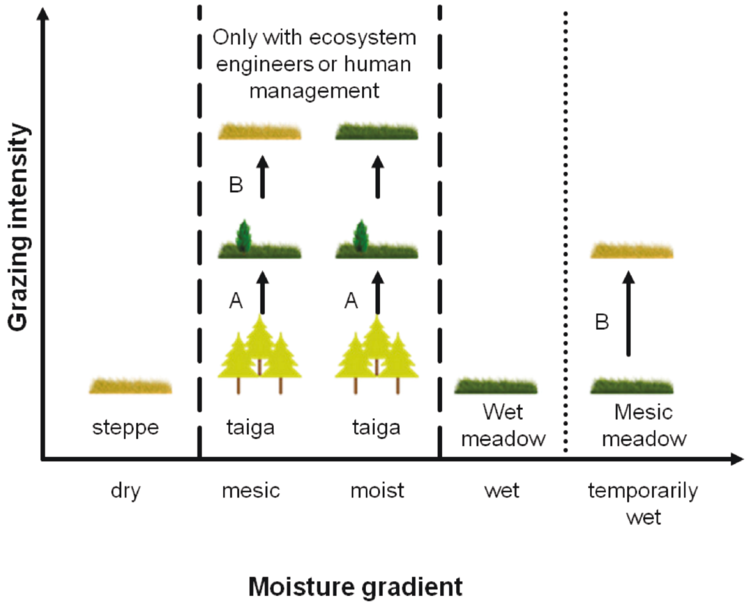

Figure 3. Grazing effects on vegetation along a moisture gradient. Taiga dominates , as long as soils are not too dry (steppe) or too wet (wet meadows). Mesic and temporarily wet meadows can transform to steppes through xerophytization (B). Taiga can only be transformed to meadows or even steppes, if trees are felled by ecosystem engineers or human management. Designed with Canva (www.canva.com).

In summary, the harsh climate of Yakutia is of overriding importance for vegetation, but there are indications that grazers are able to locally drive vegetation towards more openness, aridity and spatial heterogeneity (Figure 3). The fact that vegetation changes were larger in the more continental climate of Central Yakutia than in the suboceanic climate of northeastern Yakutia underlines the importance of the general climate conditions and thresholds for the effects of grazing on vegetation. Hypotheses on the end of the mammoth steppe often tend to overemphasize processes and effects in favor of one argument or the other. I conclude that, even with maximum grazing effects, bringing back the mammoth steppe is probably impossible, due to Holocene climate changes; but, taking current climate into account, grazing has the potential to alter and diversify contemporary vegetation.

6.4. Outlook on re-wilding

The aim of re-wilding in Yakutia was to bring back the mammoth steppe. The range succession model predicts that grazing effects are continuous and reversible and that vegetation is in equilibrium with herbivore populations (Clements 1916; Sampson 1919; Dyksterhuis 1949). Zimov's hypothesis and park management rely on this theory. According to our results, it is obviously not that easy in the case of contemporary Yakutian vegetation and the recreation of a mammoth steppe ecosystem. On the other hand, we could also not confirm the non-equilibrium model, since climate was the overriding, but not the exclusive driver of vegetation. Instead we found indications that alternative states, depending on both climate and grazing could be possible. If we assume that alternative stable states of vegetation are possible in the extreme climate of Yakutia, depending on climate and herbivores, we could imagine that re-wilding would produce a contemporary grazing system under Holocene climate conditions. Grazing ecosystems are defined and regulated by a herbivore-based food web (Frank et al. 1998). They may occur worldwide, sharing high "functional similarity", despite differences in size and structure, climate, vegetation types, plant types, animal numbers and migration patterns (Frank et al. 1998). To that end, the flora and fauna of northern Siberia should be similar to past interglacials, were forest and steppe co-existed with large herbivores in a warmer climate than during the cold, arid glacial, when mammoth steppe presided. For glacial periods Guthrie (2001) has suggested a palaeovegetation of more or less dry steppe throughout Beringia, with mesic sites only in especially damp places. The "Beringian buckle" across the Bering street with a more oceanic climate would have provided a glacial refugium for more mesic-adapted tundra, which spread across Beringia in the Holocene (Guthrie 2001). So today we could assume a similar picture: wet to mesic tundra and grasslands with (tundra) steppes at drier sites in accordance with a less continental macroclimate, but broken into small-scale vegetation mosaics through grazing (see section 6.2). Past interglacials are actually the better analogues for the current situation. The warmest interglacial (MIS 5e) had lower global ice volumes than today, and temperatures were 4-5°C above present, the treeline 600km further north (Blinnikov 2011). Climate change at the beginning of the Holocene was not more extreme from the alternations of glacial and interglacials of the Pleistocene, yet most megaherbivores survived all but this last transition (Smith et al. 2016; Haynes 2018).

Contemporary steppes are considered the most important natural grassland type in terms of conservation in most of Russia, threatened not only by intensification of land use but also by abandonment (CH2). Also, it has been suggested that some semi-natural grasslands, like alases, which are currently under land use, might originally be natural pastures of wild herbivores without human land use (Bocherens 2018**;** see chapter 6.1). All this would suggest that the occurrence of steppes (at least partly) depends on grazing, as hast been suggested for the Pleistocene mammoth steppe. Extrazonal steppes of Yakutia also are hotspots of taxonomical (Elvebakk 2005) and functional diversity (CH3) in the northern Siberian vegetation with their otherwise rather low diversity. These steppe pastures, as the closest analogues to the mammoth steppe according to our studies, however, seemed to be least affected by grazing (CH3). These results are in line with studies from Central Asia, where moist *Kobresia* meadows (Wang et al. 2018) and mesic grass and forest-steppes (Wesche and Treiber 2012) were sensitive to grazing, while arid desert-steppes were rather controlled by low precipitation. Grazing has weaker effects in arid environments, because canopy is less developed and belowground biomass is higher (Milchunas and Lauenroth 1993). In addition, adaptations to arid environments are similar to those against herbivory, for example tolerance to loss of aboveground organs, higher allocation of biomass to stem bases and roots, low digestibility of tough leaves (Milchunas and Lauenroth 1993; Quiroga et al. 2010). These results are support for the MSL model (Cingolani et al. 2005), in the way that grazing effects were larger in more productive, mesic sites (here: mesic meadows of a game park) with a short history (20 years) of intensive (bison) grazing than in dry, low productive sites like steppes. Only locally, i.e. around Yakutsk, grazing might have been responsible for maintaining large tracks of steppes, especially on lower river terraces and less steeply inclined slopes. So maybe, due to relatively low human population in Yakutia and low grazing intensity of livestock until recent times, steppes have retreated to optimal microclimatic sites, where grazing does little to affect them. Conversely, they might be dependent on grazing where sites are moist enough to trigger more competition with grassland and taiga species, such as at zonal sites of southern Siberia or in less steep, mesic habitats of Yakutia.

If current macroclimate is suboptimal for grassland and especially for steppe vegetation, the role of megaherbivores should be even more critical and important today than in the Pleistocene tundra steppe. Trees and shrubs might have a competitive advantage over grassland vegetation under current macroclimate, but the short growing season in northern Siberia limits growth rates and might make their establishment more susceptible to grazing (see section 6.3). In dwarf-shrub communities grazing reduced the warming-induced increase in aboveground plant biomass by 11-46% and mitigated the shift from grasses to dwarf shrub communities (Post and Pedersen 2008). This observation stresses the importance of herbivory for alternative vegetation states under a warming environment. The question remains, if the processes observed on the local scale are applicable at the landscape scale and sustainable over longer time scales (Figure 4). Only then does re-wilding have the potential to shift the ecosystem towards a grazing system.

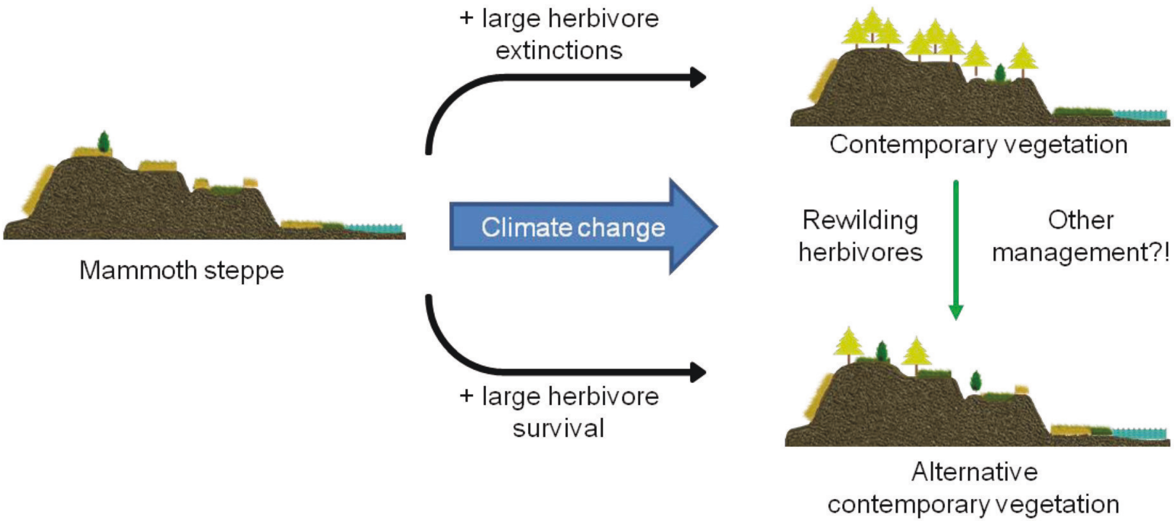

Figure 4. Landcape model of vegetation change. Climate change and the extinction of large herbivores have led to a taiga dominated vegetation; extrazonal steppes only occur on steep slopes and azonal grasslands in floodplain areas. Large herbivores could create a mosaic of taiga, grasslands and steppes, especially at topoedaphically diverse sites like permafrost polygones. The question remains, if re-wilding alone can trigger this landscape change or if more management measures have to be taken (green arrow). Inspired by Olff et al. 1999 (spatial mosaic) and Westoby et al. 1989 (state and transition diagram). Designed with Canva (www.canva.com).

In order to create that grazing system today, three main aspects have to be considered and further investigated: 1) the level of animal densities needs to be high enough to trigger changes in vegetation on a landscape scale; 2) the type of animals and composition of animal communities to be re-wilded, especially those that can be regarded ecosystem engineers; 3) other management practices, which might be needed to restore a possibly self-maintaining grazing system.

A major issue for practical re-wilding is the question of the level of animal densities needed to actually drive vegetation change. Tropical grazing systems with high primary productivity allow high total consumption rates and thus support highest herbivore densities (Frank et al. 1998). On the other hand, the consumption and conversion of plant into herbivore biomass is considered more efficient in temperate systems (Frank et al. 1998). No such data is available for arctic or boreal systems; but a tight coupling of vegetation-herbivore-interactions might me crucial for the functioning of grazing systems with a short vegetative period, relatively low primary productivity and slow growth. Grazing mostly decreases primary productivity, but seems to have a positive effect in low productive systems with a long grazing history and low consumption rates (Milchunas and Lauenroth 1993). Slower re-growth also means that a longer temporal window is open for competitive relaxation and therefore less frequent or lower levels of defoliation are necessary to achieve a similar effect as in comparatively faster growing communities (Milchunas et al. 1988). On the other hand, harsh winter conditions could have led to high mortality under suboptimal foraging conditions, so that critical densities to assert top-down controls might not have been reached. Otherwise, megaherbivores would become functionally extinct and lose their potential to alter the ecosystem (Malhi et al. 2016). Since palaeoecological estimates (like Zimovs) are unreliable, only controlled exclosure experiments with different grazing regimes can answer this question. Such experiments have not been conducted as of today.

Depending on the definition of megaherbivores (see introduction), we can argue whether any are extant in contemporary tundra and taiga ecosystems or not. Bison and horses probably are large enough to be called megaherbivores, but lack the size and behavior of the mammoth steppe's most iconic megaherbivore, the mammoth. The smaller body mass of domestic herbivores leads to different interactions with vegetation, which cannot replicate the unique impact larger, wild megaherbivores have on forest structure, such as breaking and knocking down trees, and on nutrient diffusion on the landscape scale (Smith et al. 2016). The idea of the mammoth as an ecosystem engineer is often based on comparisons with the role of the African elephant as keystone species (Jones et al. 1994) in the savannah (Haynes 2012) and in rainforests (see Malhi et al 2016). Extant elephants (and some rhinos) are generalists in both habitat and diet selection, who also feed on low nutritious bark or tall mature grasses (Owen-Smith 1987). Elephants can have a negative impact on tree recruitment even in closed canopy rainforests (see Malhi et al 2016). Most large herbivores can strongly reduce woody cover of vegetation, by feeding on saplings and debarking trees, but elephants have by far the strongest effect due to their sheer size and strength, also pushing over trees and pulling out shrubs (Bakker et al. 2016) without necessarily consuming them (Haynes 2012). Owen-Smith (1987) suggested that 1 elephant per km^2 is a high enough density to convert closed woodland to tree-coppice grassland, because saturated populations can heavily impact vegetation, when nutritional deficiencies are reached. Guthrie (2001) criticized that 1) the mammoth's feeding niche would be very different from the African elephant, because African trees and shrubs are deciduous and edible, and thus a part of the elephant's diet, while boreal woody species would be metabolically toxic; 2) the subsequently assumed avoidance of trees and shrubs by mammoths would rather promote woodlands than steppes; 3) the mammoth's tusks would not have been useful for snow shoveling, so the snow disturbance hypothesis wouldn't hold. However, the dominant shrub species in Yakutia, dwarf birch and willows are edible (1). Even unpalatable plants are consumed by large herbivores, if more palatable species grow in their vicinity (associational palatability; Olff et al. 1999) (2). Elephants also turn to woody vegetation, when their preferred grasses seasonally become less nutritious (Haynes 2012). Also crushing and trampling might still be an important factor for non-edible plant species, if they grow within or close to pastures. Tusks are not needed to create large snow disturbance (3), as bison and horses in our study have shown. Elephants also move substantial amounts of earth, and there is evidence for similar behavior from the mammoth (Haynes 2012). Overall, it remains to be investigated whether medium sized megaherbivores alone can alter an ecosystem like larger probisceans might have done. Owen-Smith (1987) has suggested that fencing in smaller herbivores might have similar effects as megaherbivores, which is also suggested by our results. Again, the importance of megaherbivores might increase under mesic environmental conditions. In South Africa the white rhino is a unique keystone species for maintaining short grass savannahs and a facilitator of other short grass grazers under mesic conditions, while smaller grazers may take over that niche in more arid regions (Waldram et al. 2008).

Just as important as the density and large size of herbivores is the species and feeding niche diversity of herbivore assemblages. Although Zimov's megaherbivore densities are probably overestimated, we probably underestimate the potential ecosystem effects even lower numbers might have. With respect to experimental approaches, I see highest potential in the creation of multispecies assemblages (also see Cornelissen 2017). The ecological impact of herbivore assemblages will depend on many factors, such as the herbivore species' foraging habits, digestive physiology, their dependence upon the availability of surface water, digging behavior, and mobility patterns (see Bocherens 2018).

Malhi et al. (2016) have pointed out, how megafauna affects the entire trophic system, changing the habitat for smaller herbivores and predators. Mammoth and bison could have opened up habitats for smaller grazers to use, enlarge and maintain grasslands of varying sward height. Interspecific competition among herbivores can lead to resource partitioning in grazing systems (Cornelissen 2017). On the other hand, generalist herbivores can facilitate more selective feeders and turn a bottom-up into a top-down controlled ecosystem (Huisman and Olff 1998). Association of smaller herbivores with megafauna can also change their role in shaping vegetation despite them being affected by predation. Species-rich herbivore assemblages in the African savannah may reduce cover of woody species by 15-95% (Bakker et al. 2016). Even ground squirrels, a common part of our steppes and once wide-spread in the mammoth steppe, might have played a larger role in conjunction with large herbivores. With the maintenance of habitats by larger herbivores and a deeper active layer due to less insulating litter, they might have played a similar role as squirrels in Alaska or prairie dogs in the USA, creating further disturbance, re-locating nutrient rich soil layers and promoting fast growing grasses and herbs (see Blinnikov et al. 2011).

A variety of feeding strategies and body size of herbivores also means an impact on a wider range of plant growth stages (Bakker et al. 2016). This might be crucial in a climate where short summers only allow slow growth and it takes time to grow beyond the “browser trap” (see Bakker et al. 2016). Guthrie (2001) claims that grazers dominated in the mammoth steppe, yet presents a figure of herbivore feeding niches, which shows relatively high amounts of woody plants in the diet of horses and musk ox. Herbivore diets also vary depending on seasonal availability of forage (e.g. Haynes 2012) and interspecific competition (Cornelissen 2017). The proportion of woody plants in the megafauna diet of the mammoth steppe is still low compared to the grazer / browser proportions in Africa; but in low latitudes with highly productive vegetation more browsers might be needed to influence the proportions of grassland to forest vegetation than at high latitudes with short summers, especially under continental aridity.

High herbivore diversity in grasslands increases competition and thus the grazing impact on other, less preferred vegetation types (Cornelissen 2017). Diversity of herbivore body size might also interact with the scale of vegetation diversity, because local effects of large herbivores can occur over much larger spatial scales than that of smaller herbivores (Olff and Ritchie 1998). The assumption that currently separated distribution ranges of mammals are due to stronger vegetation zonation (Guthrie 1982), can also be turned around, considering that multispecies assemblages are needed for creating a vegetation mosaic that enables co-existence. Unlike contemporary herbivore assemblages, the broad range of species and body sizes of late Pleistocene herbivore assemblages would probably have had stronger effects on vegetation than what we observe in studies today (Blinnikov et al. 2011; Bakker et al. 2016).

Despite all indications for small-scale herbivore-driven vegetation changes and the presumable potential of herbivores to maintain a grazing system on the landscape scale even under Holocene climate conditions, the return to a grazing system might not be simple. Species composition responds relatively fast to grazing, but changes in soil nutrient pools come rather slow (Milchunas and Lauenroth 1993). Furthermore, internal feedback systems, such as nutrient cycling processes, might have been interrupted and beyond the threshold were herbivores are able to maintain their role as ecosystem engineers (compare to alternative stable state - hypothesis; Scheffer and Carpenter 2003). It has been suggested before that the positive feedback loops between forb-rich vegetation and megafauna might have been disrupted by changed C/N-ratios through post-LGM climate warming (see Willerslev et al. 2014). Thus, the question is, whether the dominance of unproductive and inedible tundra and taiga can be disrupted by re-wilding alone, or if additional management is needed to slowly reverse processes. Wild fire, for example, is an important additional consumer of plant biomass in many ecosystems, acting similar to, but also in competition with megaherbivores (see Malhi et al. 2016). Large fires can attract grazers to feed on the regrowth of a burnt area, while grazed areas are likely to be grazed again, creating a positive feedback loop (Waldram et al. 2008). A combination of elephants and fire may maintain productive tall grasslands, while heavily grazed short grasslands, which fail to sustain fires, are more vulnerable to wood invasion (Owen-Smith 1987). As our palaeobotanic data shows, wild fires were more important during the last interglacial than today (CH4). Fire activity often increased shortly at the beginning of the Holocene when the loss of megafauna led to high fuel loads due to the standing biomass of ungrazed forage (Johnson 2009; Gill 2014). Today fire is used to open up forest, and clearings then are favorably grazed. The understory of many taiga woodlands in continental climate (e.g. middle Indigirka river basin) is more similar to steppe than to taiga understory, and these forests do not regenerate after fire and become secondary steppes (Yurtsev 1982). In the absence of grazing, a surplus of dry, ungrazed biomass incites unregulated agricultural burning to facilitate the development of steppe in former fallows (CH2). We have to investigate further, which practices are useful to drive important processes over the current limits, which might otherwise not be reached.

Chapter 7

Conclusions

It is unlikely that rewilding northern Siberia would allow us to re-create a mammoth steppe ecosystem. On the other hand, rewilding has the potential to re-install a grazing system under Holocene climate conditions and vegetation. Further research is needed to investigate the details of how this can be achieved sustainably and on a landscape scale. This requires specific experimental set ups, which are able to capture the different variables and processes. These experiments need to be carefully conducted and controlled, and should run long enough to capture long-term changes in a harsh region with many environmental constraints. Continental regions, like Central Yakutia seem to be most promising for such investigations. The direct comparison of palaeobotanic records with contemporary vegetation from the same region provides a valuable approach to reconstructing past environments and potential drivers of vegetation.

Rewilding could become a moral obligation in order to reverse the processes of human intervention, especially, if more evidence for the overkill hypothesis should emerge (e.g. Lorenzen et al. 2011, Bartlett et al. 2016, Haynes 2018). Humans would then not only be responsible for the loss of the megafauna itself, but also would also be contributors to a massive change in vegetation, the loss of landscape biodiversity and the trophic downgrading of ecosystems (Estes et al. 2011). This enormous impact could even fuel the debate on the magnitude and beginning of the Anthropocene. Even without conclusive evidence on human responsibility for megafauna extinctions, rewilding could become relevant under more practical aspects as a potential approach to mitigate climate change. Trampling of snow in winter can lead to permafrost cooling; the maintenance of grasslands through grazing lowers albedo compared to otherwise dominating forest or shrub vegetation; and the extensive root system of grasslands can increase carbon storage in the soil; thus grazing could counteract the effects of climate warming (Zimov 2005; Zimov et al. 2012), especially in the climatically sensitive subarctic region.

In any case, rewilding clearly has the potential for being a critical aspect of future management of northern Siberia. Studies can provide important contributions to this broader topic, if set up carefully and with a sensible study design. The combination of paleoecology and vegetation ecology as in the present study is a useful approach to find a baseline vegetation for rewilding.

Chapter 8

Summary

Rewilding aims at the restoration of lost ecosystems by re-introducing large herbivores. In northern Siberia, the demise of the mammoth steppe ecosystem at the end of the Pleistocene has been related to the loss of megafauna due to human overhunting. Others argue that climate change at the beginning of the Holocene has triggered the shift from dry, cold steppe vegetation to wet and low productive tundra and taiga vegetation. Despite many different opinions and ongoing discussions on the topic, few case studies are available to test the proposed hypotheses. In this thesis I try to bridge the theoretical backgrounds of palaeoecology and contemporary grazing ecology, and apply these to new data from grazed steppes and surrounding vegetation in Yakutia. This study region is suitable to shed light on the importance of grazers for the (mammoth) steppe vegetation because 1) Yakutia was dominated by mammoth steppe in Pleistocene glacials, and the extrazonal steppes of today are considered potential relics; 2) permafrost deposits in close proximity to these steppes allow palaeobotanical reconstructions of vegetation from the same area; and 3) two game parks, one in Central Yakutia, one in northeastern Yakutia, allow to study grazing impact on contemporary vegetation, specifically steppes.

The first part of the thesis focuses on current grassland and steppe vegetation in Russia in general and in Yakutia specifically. Chapter 1 highlights the biological diversity of Russia's grasslands under diverse climatic and edaphic conditions. It highlights the value of Russian steppes for nature conservation, shows that most grasslands are of agricultural origin and that cessation of land use can pose a threat to both natural and secondary grasslands. Chapter 2 focuses on the phytosociology of extrazonal steppes and other grasslands of Yakutia, and on the harsh climatic and the special edaphic conditions they inhabit. It demonstrates relationships to southern zonal steppes, despite lower species diversity and unique associations with a high contribution of alpine plants.

The second part of the thesis addresses the evidence of grazing in the palaorecord as well as effects and importance of grazing for contemporary vegetation. Chapter 3 aims at a comparison of current vegetation with Pleistocene fossil remains in order to find the closest analogues of mammoth steppe vegetation. It demonstrates that meadow steppes formed large parts of the vegetation in both cold and warm stages, only shifting in

proportions. Disturbance indicators from grazing animals were more common in the fossil record than today. Chapter 4 discusses the influence of grazing on current vegetation under the given harsh climate; on plant species and trait composition, as well as on vegetation productivity. Climate and soil conditions seem to be the most important determinants of steppe and surrounding vegetation. Large grazers like bison can alter vegetation structure and plant communities on the local scale, but do not alter composition dramatically nor do they increase vegetation productivity in the given settings.

In summary, steppes are an important part of biodiversity in Russia and specifically in Yakutia today. The extrazonal steppes of Yakutia are no direct relics of the mammoth steppe, and are not dependent on grazing. However, grazing of large herbivores, such as bison, can locally open up vegetation, and in a continental climate, drive grasslands towards a more steppic character. Further research is needed to investigate the details of these processes and how they could translate to the landscape scale.

Chapter 9

Zusammenfassung

Mit der Auswilderung von Großherbivoren wird oft das Ziel verfolgt, ein lange vergangenes Ökosystem wiederherzustellen. In Nordsibirien ist das die Mammutsteppe, deren Verlust auf die Ausrottung der Großherbivoren-Fauna durch menschliche Überjagung zurückgeführt wurde. Andererseits könnte auch der Klimawandel am Beginn des Holozäns für den Vegetationswandel von trockener, kalter Steppe zu feuchter und wenig produktiver Tundra und Taiga verantwortlich sein. Das Thema wird von verschiedenen Meinungen beherrscht und die Diskussion darüber dauert an; doch konkrete Studien, die diese Hypothesen überprüfen würden, sind selten. In meiner Dissertation versuche ich, eine Brücke zwischen Theorien aus der Paläoökologie und der rezenten Beweidungsökologie zu schlagen und diese auf die beweideten Steppen Yakutiens und deren umgebende Vegetation anzuwenden. Diese Studie liefert Erkenntnisse zur Bedeutung von Weidetieren für die (Mammut-)steppenvegetation, da 1) Yakutien in Pleistozänen Kaltzeiten von Mammutsteppe bedeckt war und die rezenten, extrazonalen Steppen als potenzielle Reliktvegetation angesehen werden; 2) Permafrostaufschlüsse in direkter Umgebung dieser Steppen die paläobotanische Rekonstruktion des selben Gebietes erlauben; und 3) zwei Wildparks, einer in Zentralyakutien, einer im Nordosten Yakutiens, die Erforschung von Beweidungseffekten auf die rezente Vegetation, vor allem Steppenvegetation, ermöglichen.

Der erste Teil meiner Dissertation bezieht sich auf die rezente Grasland- und Steppenvegetation Russlands mit Fokus auf Yakutien. Kapitel 1 stellt die biologische Vielfalt der Russischen Grasländer unter verschiedensten klimatischen und edaphischen Bedingungen heraus. Dabei steht die Bedeutung der Russischen Steppen für den Naturschutz im Fokus. Es wird deutlich, dass der Großteil der Grasländer auf landwirtschaftliche Nutzung zurückzuführen ist und dass eine Nutzungsaufgabe sowohl natürliche als auch sekundäre Grasländer bedroht. Kapitel 2 beschäftigt sich mit der Pflanzensozologie der extrazonalen Steppen und anderer Grasländer Yakutiens, sowie mit den speziellen klimatischen und edaphischen Bedingungen, unter denen sie existieren. Ich zeige die verwandtschaftlichen Beziehungen dieser Steppen mit den südlichen, zonalen Steppen, trotz ihrer geringeren Artenvielfalt und ihrer einzigartigen Assoziationen mit hohem Anteil alpiner Arten.

Der zweite Teil meiner Dissertation beschäftigt sich mit den Hinweisen auf Beweidung in paläobotanischen Rekonstruktionen der Vegetation, sowie der Bedeutung von Beweidung in der rezenten Vegetation. Kapitel 3 stellt einen Vergleich zwischen der Artenzusammensetzung Pleistozäner Pflanzenfossilien mit denen rezenter Pflanzengesellschaften an, um die Vegetation zu definieren, die der Mammutsteppe am ähnlichsten ist. Dieser Vergleich zeigt, dass Wiesensteppen sowohl in Kalt- als auch in Warmzeiten vorkamen und nur in ihrem Anteil an der Gesamtvegetation schwankten. Störungszeiger für Beweidung waren häufiger in den fossilen Pflanzenresten zu finden als in rezenten Pflanzengesellschaften. Kapitel 4 diskutiert schließlich den Einfluss von Beweidung auf die rezente Vegetation unter den gegebenen extremen Klimaverhältnissen; auf die Zusammensetzung von Arten und Artmerkmalen einer Pflanzengesellschaft, sowie auf deren Produktivität. Die klimatischen und edaphischen Bedingungen scheinen ausschlaggebend für die Steppen- und umgebende Vegetation zu sein. Großherbivoren wie das Bison können allerdings lokal Veränderungen in der Vegetationsstruktur und Pflanzengesellschaften bewirken, wenn auch, unter den gegebenen Umständen, weder Artenzusammensetzung noch Produktivität drastisch verändert wurden.

Steppen stellen einen bedeutenden Anteil der Russischen, und besonders Yakutischen, Biodiversität dar. Die extrazonalen Steppen Yakutiens sind keine unmittelbaren Relikte der Mammutsteppe und sind heute nicht auf Beweidung angewiesen. Trotzdem können Großherbivoren wie das Bison lokale Veränderungen bewirken: sie vermögen Baumbestände aufzulichten und, unter kontinentalem Klima, Wiesen hin zu einem mehr steppen-artigen Charakter zu verändern. Weitere Forschung ist nötig, um die Details der beobachteten Prozesse zu erkunden und ihre Übertragbarkeit auf die Landschaftsebene zu überprüfen.

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III. Appendix

A1 – Introduction

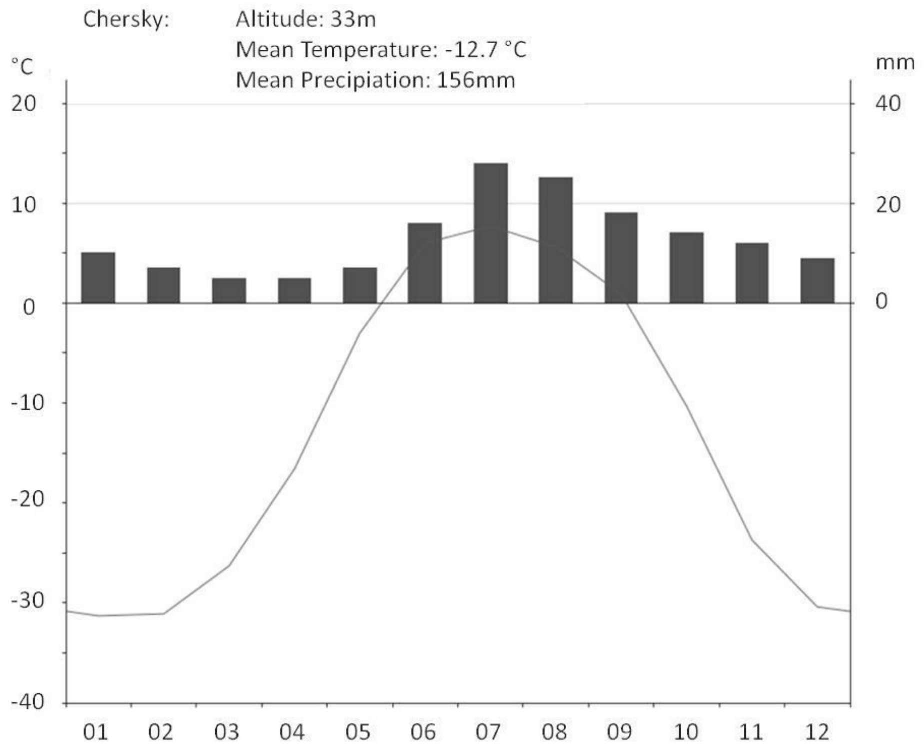

Figure 1.1 Climate diagrams of Yakutsk, Verkhoyansk and Chersky, Sakha, Russia. Climate in Yakutia is continental, characterized by very low winter temperatures and relatively high summer temperatures (Figure 1). Temperatures are less extreme in Chersky, which is closer to the Arctic Sea. Here, summer precipitation of July and August is well above the temperature curve in the climate diagram, while in Yakutsk and Verkhoyansk conditions are closer to summer droughts. Modified from climate-data.org.

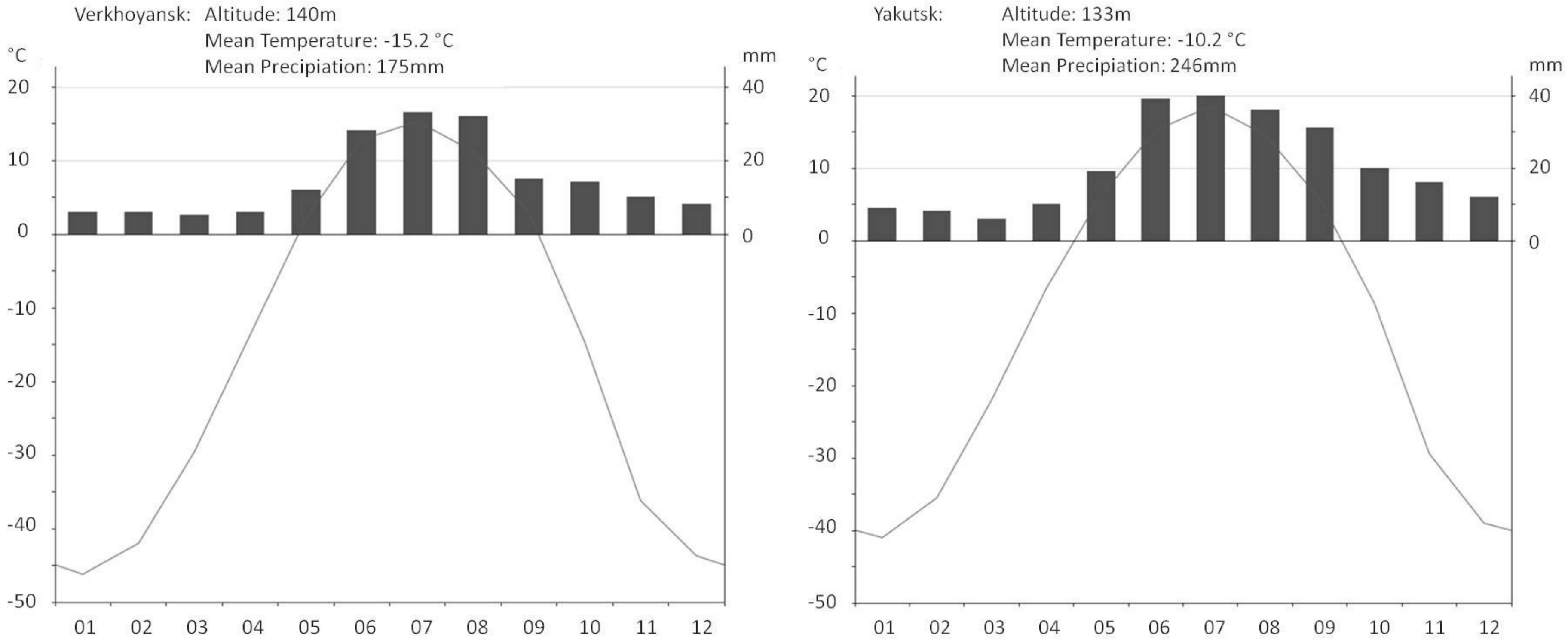

Figure 1.1 (Continued)

A2 – Chapter 2

none

A3 – Chapter 3

Table 3.1. Complete list of relevés from meadows of Calamagrostetea langsdorfii and Molinio-Arrhenatheretea; cover given in % (with r = 0.1%; + = 0,5%).

Cluster	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Releve Nr	62	73	77	78	88	97	98	99	100	101	102	126	211	27	44	162	166	172	173	174	175	176	177	178	179	180	181	188	189	191	192	193	194	201
Relevé area [m2]	10	5	10	10	10	10	10	10	10	10	10	10	10	10	10	5	10	5	10	5	5	5	10	5	5	10	5	10	10	10	10	10	10	10
Number of species	6	10	8	8	5	10	9	14	12	12	11	13	7	35	15	17	25	16	22	24	18	28	33	17	33	29	15	26	41	22	23	24	24	15
Altitude [m]	4	4	4	4	4	3	3	3	2	2	3	8	194	194	186	92	93	111	111	111	111	111	111	111	111	111	113	113	113	113	113	113	113	104
Aspect [°]	315	-	-	-	225	315	315	315	45	-	-	-	-	225	-	-	225	-	-	45	135	-	-	-	225	225	-	135	-	135	-	45	45	-
Slope [°]	1	0	0	0	2	1	1	1	1	0	0	0	0	5	0	0	2	0	0	2	6	0	0	1	2	1	0	1	4	1	0	1	1	0
Cover open ground [%]	8	2	4	2	5	25	50	15	0	25	5	2		2	10	3	0	15	15	15	10	3	2	0	5	3	1	15	3	20	10	10	20	5
Cover bare rock [%]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cover litter layer [%]	70	40	40	40	70	15	10	20	50	30	50	25	40	15	0	30	3	50	40	10	10	10	20	15	25	25	60	25	20	20	50	50	10	20
Cover shrub layer [%]	3	17	21	24	4	1	1	1	1	1	6	1	12	6	0	0	1	0	0	0	0	0	3	0	2	0	0	0	1	0	0	0	0	0
Cover herb layer [%]	20	30	36	45	33	40	40	65	41	26	36	67	33	85	70	90	115	48	58	75	90	110	110	95	100	100	50	80	90	70	60	80	70	95
Cover moss layer [%]	0	3	5	3	0	25	2	2	3	3	8	10	1	0	25	0	0	0	0	0	0	0	0	5	0	0	0	5	2	0	0	0	0	0

Table 3.1. (Continued)

Cluster	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Releve Nr	62	73	77	78	88	97	98	99	100	101	102	126	211	27	44	162	166	172	173	174	175	176	177	178	179	180	181	188	189	191	192	193	194	201
***Calamagrostetea langsdorfii, Carex cespitosa*-community**																																		
Carex cespitosa	2	.	2	4	.	2	1	+	10	2	4	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rubus arcticus	+	20	20	20	2	r	.	r	+	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Equisetum arvense	r	20	r	r	2	10	4	10	r	r	r	.	.	.	.	.	+	.	.	.	r	.	2	.	r	.	.	.	.	.	.	.	.	.
Caltha palustris	r	.	.	.	.	r	4	2	r	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Comarum palustre	.	.	.	r	.	.	.	r	+	r	r	.	2	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum angustfolium	.	.	.	.	.	.	.	.	2	r	r	4	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arctagrostis latifolia	.	r	1	+	.	.	.	30	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
***Molinio-Arrhenatheretea, Elytrigia repens-Geranium pratense*-community**																																		
Elytrigia repens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	r	40	50	10	2	r	10	r	r	30	20	40	r	10	40	10	10	r
Geranium pratense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	+	r	r	+	+	10	.	10	10	r	+	r	r	r	.	+	.
Potentilla anserina	.	.	.	.	.	.	.	.	.	.	.	.	.	10	10	.	.	.	.	4	30	4	4	10	+	.	.	20	2	.	.	4	.	30
Geum aleppicum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	+	.	r	.	.	r	2	.	r	r	.	2	10	2	.
Agrostis gigantea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	50	30	2	50	10	.	1	10	.	.	.	.	20
Trifolium repens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	30	.	.	r	r	.	2	+	.	.	.	r	r
Other species																																		
Arctagrostis spec.	.	.	.	40	30	.	.	.	.	.	20	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis spec.	.	.	.	.	.	10	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex aquatilis	.	.	.	.	.	.	.	r	20	20	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 3.1. (Continued)

Cluster	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Releve Nr	62	73	77	78	88	97	98	99	100	101	102	126	211	27	44	162	166	172	173	174	175	176	177	178	179	180	181	188	189	191	192	193	194	201
Ranunculus repens	.	.	.	.	.	+	2	10	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Calamagrostis arundinacea	.	2	.	.	.	.	r	4	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium trifidum	.	2	.	.	2	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.
Epilobium angustifolium	.	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Moehringia laterifolia	.	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spiraea spec.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis spec.	.	r	.	.	r	.	.	r	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	r	2	.	+	20	.	r	2	.	2	4	10	+	.	2	+	4	10	r
Taraxacum spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	+	r	r	.	.	.	.	.	.	r	.	.	.	.
Vicia cracca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Achillea asiatica	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	2	2	.	4	4	.	2	2	2	+	.	r	.	r	2	.
Rhinanthus serotinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	20	.	.	.	.	.	.	.	.
Plantago major	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	2	10	10	.	10	10	.	r	+	.	.	.	.	.
Hierochloe spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	r	.	r	r	.	.
Galium verum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	r	r	+	r	.	+	2	.	r	10	4	+	.	r	r	r	2	.
Sibbaldianthe bifurca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	+	r	r	4	.	.	+	.	2	4	10	20	.	40	2	10	30	.
Plantago depressa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	20	.	.	.	.	.	r	.	2	.	r	r	.	r	r
Artemisia vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	r	.	r	1	r	.	r	+	r	r	2	.
Carex spec.	r	.	.	.	.	.	r	.	.	.	.	40	.	.	.	.	.	.	.	.	2	10	.	.	.	r	.	.	2	.	r	.	.	4
Artemisia dracunculus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	r	.	.	1	2	r	.	2	2	2	r	.
Vicia spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	r	.	.	r	+	.	+	r	r	.	r	r	.
Thalictrum simplex	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	r	2	2	.	.	r	r	r	r	.	.
Scutellaria scordiifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	r	.	10	+	+	r	r	.
Astragalus inopinatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	r	.	.	.	r	.	r	.	2	+	4	2	.

Table 3.1. (Continued)

Cluster	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Releve Nr	62	73	77	78	88	97	98	99	100	101	102	126	211	227	244	162	166	172	173	174	175	176	177	178	179	180	181	188	189	191	192	193	194	201
Agrostis stolonifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50	r	2	.	+	.	.	1	2	.	.	.	.	.
Poa versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	10	r	20	+	.
Veronica longifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	r	20	.	.	.	.	.	2	.	.	.	r	.	r	.	.	.	.	.
Potentilla longifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	.	.	2	2	10	2	.
Triglochin palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	+	+	r	4	.	.	.	r	.	.	.	.	.
Potentilla conferta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	r	r	.	.	.	r	+	+	.
Thalictrum minus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	+	.	.	.	.	.	+	+	.	.	.	.	.
Heteropappus biennis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	r	+	r	.	r	.	r	r	.
Alopecurus arundinaceus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	r	r	r	.	.	.	2	.	.	.	.	.
Linaria acutiloba	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	r	r	.
Anemone sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	+	r	.	r	.	.	.	.	.
Geranium pseudosibiricum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	r	.	r	r	.	r	.	.	.	.	.	.
Rumex spec.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Hordeum brevisubulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	20
Leonurus quinquelobatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	+	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.
Rosa acicularis	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	+	.	.	.	r	.	.	.	.	.
Senecio erucifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	2	r	.	r	.	.	.	.	.	.	.	.
Tanacetum vulgare	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	1	.	r	r	.	.	r	.	r	.	.	.
Inula britannica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	.	.	r	.	.	.	+	.	.	r	r	r
Gentiana decumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	r	.	+	.	.	.	.	.	.
Campanula glomerata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	r	.	r	.	.	.	r	.	.
Silene repens	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.
Bromopsis pumpelliana	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	50	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arctagrostis arundinacea	.	.	30	.	.	.	.	.	10	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis vinealis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium boreale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	r	+	.	r	.	.	.	.	.	.	.	.	.
Glyceria arundinacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r

Table 3.1. (Continued)

Cluster	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Releve Nr	62	73	77	78	88	97	98	99	100	101	102	126	211	27	44	162	166	172	173	174	175	176	177	178	179	180	181	188	189	191	192	193	194	201
Phlomis tuberosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	r	.	.	r	r	.	.	.	.	.	.	.	.
Saussurea amara	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.	.	.	.	+	r	.
Saussurea spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Carex enervis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	80	.	.	.	.	.	.	.	.	.	2
Sanguisorba officinalis	.	.	.	.	.	.	.	.	.	.	.	.	.	30	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
Anemonidium dichotomum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Cerastium arvense	.	.	.	.	.	.	.	.	.	.	.	.	.	r	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopecurus alpinus	.	.	.	.	.	.	.	.	.	.	.	10	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex acuta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	10	.	.	.	.	.
Iris setosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	10	.	.	.	.	.
Lithosciadium multicaule	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	10	.	.	.	.	.	.	.	.	.	.	.
Carex bigelowii	.	.	.	.	.	.	.	.	.	.	.	.	.	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex duriuscula	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Poa sibirica	.	.	.	.	.	.	.	.	.	.	.	+	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum perenne	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vaccinium uliginosum	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca spec.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galatella dahurica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis palustris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	r	.	.	.	.	.
Ranunculus grandis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	r	.	.	.	.	.	.	.	.	.	.
Euphorbia esula	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia tanacetifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Chenopodium album	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Astragalus spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Epilobium palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.
Nonnea rossica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	r	.
Rumex thyrsiflorus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.
Scolochloa festucacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.

Table 3.1. (Continued)

Species with low frequency

Agrostis spec.: 62 (20); Alopecurus pratensis1: 201 (20); Beckmannia eruciformis: 189 (20); Calamagrostis purpurea: 73 (20); Alopecurus magellanicus: 99 (10); Artemisia macrantha: 166 (10); Beckmannia syzigachne: 44 (10); Calamagrostis stricta: 44 (10); Carex disticha: 27 (10); Carex rostrata: 189 (10); Hierochloe odorata: 126 (10); Puccinellia borealis: 44 (10); Puccinellia hauptiana: 44 (10); Salix glauca: 27 (4); Thalictrum foetidum: 27 (4); Poa angustifolia: 175 (2); Schoenoplectus lacustris: 178 (2); Cerastium maximum: 27 (1); Ranunculus borealis: 27 (1); Salix pyramidata: 27 (1); Carex pediformis: 27 (+); Delphinium cheilanthum: 27 (+); Equisetum fluviatile: 100 (+); Lactuca sibirica: 177 (+), 189 (r); Lappula squarrosa: 172 (+), 188 (r); Lathyrus palustris: 97 (r), 100 (+); Myosotis scorpioides: 189 (+); Pedicularis sudetica: 126 (+); Persicaria amphibia: 44 (+); Persicaria spec.: 201 (+); Plantago canescens: 27 (+); Polygonum angustifolium: 126 (+); Potentilla arenosa: 27 (+); Potentilla stipularis: 27 (+); Potentilla tanacetifolia: 172 (+), 188 (r); Rumex aquaticus: 126 (+); Saxifraga sibirica: 126 (+); Chamaedaphne calyculata: 211 (+); Alisma plantago-aquatica: 189 (r); Allium splendens: 27 (r); Anemone flavescens: 27 (r); Aquilegia parviflora: 175 (r); Artemisia jacutica: 192 (r); Carex nigra: 166 (r); Carex praecox: 162 (r); Chenopodium spec.: 172 (r); Eleocharis palustris: 44 (r); Eriophorum scheuchzeri: 126 (r); Erysimum cheiranthoides: 162 (r); Erysimum spec.: 189 (r); Helictotrichon hookeri: 27 (r); Hierochloe glabra: 27 (r); Juncus persicus: 201 (r); Lappula spec.: 173 (r); Persicaria vivipara: 27 (r); Potentilla hypoleuca: 192 (r); Ranunculus acris1: 189 (r); Ranunculus petroczenkoi: 126 (r); Rumex gmelinii: 179 (r); Salix spec.: 27 (r); Senecio dubitabilis: 188 (r); Senecio subdentatus: 173 (r); Silene samojedorum: 194 (r); Silene spec.: 188 (r); Spiraea media: 101 (r); Stellaria longipes: 180 (r); Tephroseria integrifolia: 126 (r); Thalictrum baikalense: 177 (r), 179 (r); Vaccinium vitis-idaea: 97 (r); Valeriana capitata: 73 (r); Valeriana officinalis: 166 (r), 189 (r); Aconitum barbatum: 179 (r); Sium suave: 189 (r); Stellaria spec.: 178 (r)

Table 3.2. Complete list of relevés from steppes of *Cleistogenetea squarrosae*, *Stipetalia krylovii*; cover given in % (with r = 0.1%; + = 0,5%)

Cluster	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
Releve Nr	139	154	163	164	165	167	168	170	171	200	202	140	141	142	143	144	146	147	148	149	150	151	152	155	156	157	158	159	160	161	203	204	205	206	207	208	209	210	183	184	185	197	198	199
Relevé area [m2]	5	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	8	10	10	10	10	10	5	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Number of species	30	34	30	27	34	15	22	29	13	33	35	22	19	10	11	17	18	14	25	18	23	7	11	20	16	19	22	20	24	21	24	23	28	26	23	34	21	26	22	19	11	24	27	21
Altitude [m]	105	162	93	93	93	117	117	117	117	104	104	111	111	111	111	111	199	199	199	NA	199	95	95	162	162	162	162	93	93	93	104	104	104	104	104	111	111	111	167	167	167	167	167	109
Aspect [°]	225	225	-	135	-	135	135	225	225	-	45	225	225	180	225	225	225	225	225	180	135	135	135	225	225	225	225	270	180	-	180	225	225	225	225	225	225	-	180	180	180	225	270	270
Slope [°]	1	3	0	1	0	1	1	2	1	0	4	3	3	5	10	5	5	4	4	3	20	5	1	2	10	15	5	3	18	0	6	10	2	10	10	4	15	0	15	15	20	23	18	18
Cover open ground [%]	5	1	15	20	10	70	60	40	65	20	10	8	10	60	65	50	40	40	30	45	85	75	40	40	30	40	30	30	40	30	30	50	20	10	55	15	25	25	40	55	45	20	30	20
Cover bare rock [%]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	10	0	0	0	1	2	0	0	0	0	0	0	0	30	0	0	0	0	0	5	0	0	0	20	15	0	30	10	0
Cover litter layer [%]	40	30	25	35	30	10	20	20	15	8	40	40	40	15	10	10	15	30	15	20	3	3	15	10	40	15	25	20	10	20	20	5	20	30	10	30	10	10	10	2	20	10	10	30
Cover shrub layer [%]	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	10	0	0	20	5	5
Cover herb layer [%]	60	85	60	60	75	25	25	40	25	70	60	55	45	23	20	30	40	30	65	30	13	25	50	40	40	40	50	50	20	40	50	40	55	55	35	60	60	70	30	30	38	20	50	50
Cover moss layer [%]	0	0	0	0	0	2	0	3	0	0	5	0	5	2	0	3	8	8	0	5	0	0	0	10	10	5	3	10	3	0	8	15	15	10	0	2	5	3	0	0	0	0	0	0

Table 3.2. (Continued)

Cluster	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
Releve Nr	139	154	163	164	165	167	168	170	171	200	202	140	141	142	143	144	146	147	148	149	150	151	152	155	156	157	158	159	160	161	203	204	205	206	207	208	209	210	183	184	185	197	198	199
Cleistogenetea squarrosae																																												
Veronica spicata	2	.	+	.	.	r	r	r	r	2	r	2	10	.	.	.	4	1	r	4	r	.	r	+	.	.	r	10	+	2	2	r	2	r	.	2	10	2	+	r	r	r	r	2
Artemisia commutata	2	.	r	r	.	.	4	r	r	2	r	2	10	r	+	2	10	2	r	4	2	.	.	20	2	20	10	10	2	.	.	2	2	20	4	20	10	10	4	20	r	r	+	1
Festuca lenensis	+	.	+	r	r	.	.	.	.	.	.	1	+	.	.	10	r	.	.	.	.	.	.	10	+	r	4	10	4	r	2	10	4	r	+	2	r	+	+	1	.	r	r	2
Anemone flavescens	+	+	.	4	4	.	.	+	.	.	2	.	.	.	.	r	+	.	r	.	.	.	.	r	10	r	10	+	.	.	10	r	20	+	r	r	.	10	+	r	.	.	+	r
Carex duriuscula	2	.	10	.	.	2	+	+	2	20	+	r	4	4	10	.	2	10	r	10	.	r	20	4	.	+	r	4	+	10	4	10	2	2	r	10	2	+	.	.	.	.	.	.
Stipetalia krylovii																																												
Koeleria pyramidata	4	.	10	2	r	.	.	r	r	.	r	10	10	10	2	+	2	4	4	4	r	r	20	2	+	4	4	+	2	10	r	+	r	4	2	4	4	4	.	.	.	.	.	.
Goniolimon speciosum	.	.	r	.	.	.	.	.	.	r	.	+	r	r	r	.	r	2	+	r	.	.	2	r	r	+	r	r	r	+	r	r	r	+	2	r	+	r	.	.	.	.	.	.
Stipa krylovii	2	r	.	10	r	.	.	.	.	.	.	20	4	2	r	r	4	r	r	+	2	r	r	.	.	10	+	r	r	+	r	.	.	10	2	+	4	r	.	.	30	.	.	.
Alyssum lenense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	.	.	.	.	.	.	r	+	2	+	r	2	.	r	+	+	r	2	.	r	r	r	+	r	r	4	2
***Agrostis vinealis*-community**																																												
Agrostis vinealis	20	+	+	2	4	.	+	r	.	.	2	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Linaria acutiloba	r	.	+	r	r	r	r	r	r	r	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Stipetum krylovii																																												
Astragalus angarensis	.	.	.	.	.	.	.	.	.	.	.	r	r	+	4	r	.	.	.	.	+	r	.	.	r	+	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
***Elymus reflexiaristatus*-community**																																												
Elymus reflexiaristatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	r	.	10	10	30
Crepidifolium tenuifolium	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	.	r	+	r
Nepeta multifida	.	.	.	+	4	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	+	r	2	.	+	10
Ephedra monosperma	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	r	.	.	r	4	.	.	r	r	+	.	.	r	2	.	r	r	.	r	.	.	.	+	r	2	+	+	2
Patrinia rupestis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	r
Polygala sibirica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	r	2	.

Table 3.2. (Continued)

Cluster	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
Releve Nr	139	154	163	164	165	167	168	170	171	200	202	140	141	142	143	144	146	147	148	149	150	151	152	155	156	157	158	159	160	161	203	204	205	206	207	208	209	210	183	184	185	197	198	199
Other species																																												
Psathyrostachis juncaea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa versicolor	2	r	.	10	2	2	10	10	2	r	r	1	+	.	.	.	10	2	4	+	2	.	.	r	10	2	10	.	r	+	4	4	20	10	.	r	4	20	.	1	.	r	r	+
Sibbaldianthe bifurca	r	.	20	20	.	10	4	4	10	30	2	20	r	.	.	.	2	4	4	4	2	r	10	.	.	+	+	r	4	10	2	.	2	+	+	10	r	r	.	.	.	.	.	.
Androsace septentrionalis	.	.	r	r	.	r	.	r	r	+	.	r	r	.	.	.	r	r	r	r	.	.	.	r	.	.	r	r	r	r	.	.	r	r	r	r	r	r	.	.	.	.	.	.
Galium verum	4	2	r	r	2	.	.	r	.	r	4	4	r	.	.	.	.	.	r	.	.	.	.	r	.	.	r	.	.	.	r	.	2	.	.	r	r	.	r	r	.	r	r	2
Carex pediformis	4	20	r	r	r	.	.	.	.	.	30	.	.	.	.	.	.	.	r	.	r	.	.	.	.	+	2	.	.	.	2	.	r	.	r	2	.	.	2	2	r	.	2	+
Dianthus chinensis	2	r	.	r	.	r	r	.	.	.	r	.	.	.	.	.	r	r	+	+	.	.	.	1	r	.	.	r	.	.	r	r	r	.	.	r	.	r	.	.	.	.	r	.
Thymus spec.	.	.	.	.	.	+	2	10	r	.	2	.	.	.	.	10	.	.	20	.	.	.	.	.	.	.	.	.	.	.	10	10	r	r	2	.	.	20	10	.	.	4	20	r
Heteropappus biennis	.	.	.	.	.	.	r	.	.	r	r	.	.	.	+	+	r	.	.	.	.	.	.	.	.	r	.	r	r	.	r	r	r	+	r	+	r	r	.	.	.	.	.	.
Bupleurum bicaule	.	.	.	.	.	.	.	.	.	r	+	.	r	r	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	r	r	r	2	2	+	.	.	.	.	.	.
Potentilla arenosa	.	r	.	r	.	r	+	.	.	.	r	r	.	.	.	.	.	.	.	r	.	.	.	+	.	.	r	+	.	r	r	.	r	r	.	r	r	r	.	.	.	.	.	.
Elytrigia repens	.	.	10	2	20	.	.	+	.	2	r	.	.	.	.	2	.	.	+	.	r	.	+	.	.	.	.	.	.	.	.	+	.	.	2	.	.	r	.	.	.	.	.	.
Phlomopsis tuberosa	4	4	r	2	10	.	.	.	.	.	4	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	r	.	.	.	.	.	r	r	+
Poa pratensis	.	r	2	+	r	r	+	.	.	+	r	r	.	.	.	.	.	.	2	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Scorzonera spec.	.	.	.	.	r	.	.	.	.	.	.	.	r	.	.	r	r	r	.	.	.	.	.	r	r	.	r	.	r	.	.	.	r	r	.	.	r	r	r	r	.	.	r	r
Artemisia frigida	.	.	.	.	.	.	.	.	.	+	.	r	+	4	.	.	.	.	.	.	r	10	10	r	.	.	+	.	.	.	.	.	.	2	r	r	10	.	.	.	.	.	.	.
Agropyron cristatum	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	+	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	r	.	r	10	+	r	4	.	.	.	.	.	.
Onobrychis arenaria	4	4	.	r	4	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	r	.	.	.	10	.	.	.	.	.	.	r	r	r	.	r	.	r	.	.	.	.	.	.
Peucedanum baicalense	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	2	.	r	.	.	r	r	r	r	r	r	.	.	.	.	.	r	.	.	.	.	.	.	r	.	.
Euphorbia esula	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	2	.	r	.	.	r	.	.	.	.	.	.	.	r	r	r	r	r
Allium ramosum	.	.	.	.	.	.	.	.	.	.	r	+	+	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	r	r	.	r	r	r	r	r	.	.	.	.	.	.
Potentilla conferta	.	.	r	r	r	r	+	r	r	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	r	.	r	.	.	.	r	.	+
Thesium refactum	.	r	.	.	.	.	.	.	.	.	r	.	r	.	.	r	.	.	r	.	.	.	.	.	.	.	r	r	r	.	r	.	+	.	.	r	.	.	.	.	.	.	.	.
Astragalus spec.	.	.	.	.	.	.	r	.	.	r	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	r	r	r	.	r	r	.	.	.	.	.	.

Table 3.2. (Continued)

Cluster	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
Releve Nr	139	154	163	164	165	167	168	170	171	200	202	140	141	142	143	144	146	147	148	149	150	151	152	155	156	157	158	159	160	161	203	204	205	206	207	208	209	210	183	184	185	197	198	199
Chamaerhodos erecta	.	.	.	.	.	2	+	+	2	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	2	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon hookeri	.	2	.	.	r	.	.	.	.	.	2	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	4	.	r	.	.	r	.	.	.	.	.	.	.	.
Orostachis spinosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	r	.	.	.	.	r	.	.	.	.	+	2	.	+	r	r
Aster alpinus	r	1	.	.	.	.	.	.	.	r	r	.	r	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	r	r	.	r	.	.	.	.	.	.	.	.
Phlox sibirica	.	r	.	.	.	.	.	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	.	.	.	.	.	+	.	r	r	.
Eritrichium karavaevii	.	.	.	.	.	.	.	r	.	.	.	.	.	.	r	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	r	.	.	.	.	.	.
Artemisia tanacetifolia	2	.	r	1	10	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Draba nemorosa	.	.	+	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	r	r	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Allium splendens	.	.	.	.	.	r	r	+	.	.	.	.	.	.	r	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex supina	.	.	.	.	.	10	4	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella selowii	.	.	.	.	.	r	+	4	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla longifolia	.	2	.	.	.	.	.	2	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Spiraea media	.	.	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	10	+	.
Thalictrum minus	4	1	.	r	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bromopsis pumpelliana	.	.	.	.	4	.	.	.	.	.	2	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago depressa	.	.	.	.	.	.	.	r	.	2	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astragalus inopinatus	r	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea asiatica	.	.	+	.	r	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Allium spec.	.	+	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Plantago media	.	.	r	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa acicularis	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	.
Artemisia dracunculus	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex obtusata	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lappula squarrosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.
Leontopodium ochroleucum	.	.	.	r	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia spec.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	2	.	.	.	.	.
Vicia craccca	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Thalictrum foetidum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	r	.
Vicia spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	r	.	.
Silene jeniseensis	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.

Table 3.2. (Continued)

Cluster	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5
Releve Nr	139	154	163	164	165	167	168	170	171	200	202	140	141	142	143	144	146	147	148	149	150	151	152	155	156	157	158	159	160	161	203	204	205	206	207	208	209	210	183	184	185	197	198	199
Anemone sylvestris	.	.	r	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana decumbens	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scorzonera austriaca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia vulgaris	.	.	.	.	.	.	r	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium maximum	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dianthus repens	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Erigeron acris	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Hedysarum dasycarpum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.
Jacobaea vulgaris	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lepidium densiflorum	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex thyrsiflorus	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saussurea spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	r
Scorzonera radiata	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astragalus fruticosus	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r

Species with low frequency

Artemisia macrantha: 154 (20); Artemisia laciniata: 154 (4); Artemisia santolinifolia: 197 (4); Carex enervis: 200 (4); Artemisia jacutica: 200 (2); Astragalus danicus: 159 (2); Campanula glomerata: 154 (2); Elymus lanceolatus: 160 (2); Galatella dahurica: 165 (2); Thalictrum simplex: 200 (2); Aquilegia parviflora: 154 (+); Bromopsis spec.: 139 (+); Calamagrostis spec.: 150 (+); Elymus macrourus: 142 (+); Polygonum ochreatum: 170 (+); Puccinellia nuttalliana: 163 (+); Trifolium lupinaster: 139 (+): 202 (r); Vicia multicaulis: 198 (+); Viola mauritii: 154 (+): 208 (r); Androsace maxima: 147 (r): 150 (r); Campanula punctata: 185 (r); Carex melanocarpa: 139 (r); Elymus mutabilis: 157 (r); Erysimum spec.: 163 (r); Euphrasia hyperborea: 205 (r): 210 (r); Heteropappus spec.: 150 (r); Inula britannica: 163 (r); Lathyrus humilis: 154 (r); Leonurus quinquelobatus: 200 (r); Linum perenne: 165 (r): 207 (r); Minuartia verna: 170 (r); Patrinia sibirica: 183 (r); Plantago spec. : 154 (r): 161 (r); Poa spec.: 184 (r); Saussurea amara: 202 (r); Senecio spec.: 140 (r); Senecio subdentatus: 200 (r); Serratula marginata: 207 (r): 208 (r); Silene chamarensis: 139 (r): 149 (r); Silene repens: 170 (r): 198 (r); Silene samojedorum: 202 (r): 203 (r); Silene spec.: 165 (r); Taraxacum spec.: 170 (r): 200 (r); Veronica longifolia: 165 (r); Medicago falcata: 165 (r); Taraxacum ceratophorum: 139 (r); Botrychium lunaria: 154 (r); Erigeron spec.: 161 (r); Polygonum patulum: 206 (r)

Table 3.3. Complete list of relevés from steppes of *Cleistogenetea squarrosae*, *Festucetalia lenensis*; cover given in % (with r = 0.1%; + = 0,5%)

Cluster	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7
Releve Nr	4	5	8	9	10	12	22	24	25	33	36	37	40	41	52	53	55	56	60	1	11	16	17	18
Relevé area [m2]	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Number of species	8	34	12	31	16	8	15	11	18	15	25	17	17	18	13	19	23	15	18	22	28	30	26	30
Altitude [m]	141	194	194	194	194	194	154	218	194	244	147	147	147	186	212	212	210	210	240	174	194	309	309	154
Aspect [°]	135	180	135	180	180	180	135	225	225	135	225	225	135	135	180	180	225	225	135	135	180	135	135	90
Slope [°]	18	9	10	18	10	25	25	10	28	23	10	25	8	15	18	10	7	20	15	8	2	4	4	8
Cover open ground [%]	65	10	20	10	25	75	60	45	35	35	25	35	35	35	70	3	5	70	40	10	5	15	20	20
Cover bare rock [%]	3	15	30	30	25	5	5	3	40	30	30	30	1	30	0	0	30	5	8	0	0	20	1	30
Cover litter layer [%]	5	20	3	0	10	4	3	3	0	5	5	3	10	2	2	35	2	2	2	25	20	25	35	5
Cover shrub layer [%]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cover herb layer [%]	30	35	35	40	35	15	30	10	20	30	30	30	50	30	30	35	30	25	30	60	60	35	50	35
Cover moss layer [%]	0	20	12	20	5	0	0	5	2	0	8	1	0	5	0	30	30	0	20	2	15	5	6	10

Cluster	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9
Releve Nr	19	23	28	34	38	39	46	57	3	6	14	20	43	45	59	54	69	91	92	93	94	96	103	104
Relevé area [m2]	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Number of species	23	27	27	35	19	20	18	18	30	31	30	35	20	19	35	34	39	21	15	25	19	18	20	17
Altitude [m]	154	218	186	275	147	147	161	210	141	194	309	154	244	161	212	212	240	10	10	10	11	10	12	12
Aspect [°]	270	225	135	180	135	135	315	180	135	315	225	135	135	315	180	225	270	135	180	135	135	-	225	225
Slope [°]	15	8	5	4	15	10	25	4	8	18	7	12	8	28	3	3	4	3	25	20	25	23	23	23
Cover open ground [%]	30	5	10	2	35	25	20	25	10	10	1	8	25	40	2	1	15	70	50	15	65	25	1	1
Cover bare rock [%]	20	40	1	8	15	25	0	5	0	10	0	1	15	0	0	0	0	3	25	3	3	25	0	0
Cover litter layer [%]	15	20	5	10	15	15	20	10	10	10	10	20	3	20	20	25	1	5	1	15	5	3	60	50
Cover shrub layer [%]	0	0	0	1	0	0	1	0	0	2	7	2	0	0	1	0	1	1	3	8	2	1	6	2
Cover herb layer [%]	30	25	75	30	30	35	40	50	75	55	35	70	45	35	50	60	35	25	23	80	38	50	40	60
Cover moss layer [%]	5	10	2	44	0	5	20	10	6	15	35	0	0	5	25	16	50	3	3	6	6	0	5	3

Table 3.3. (Continued)

Cluster	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9
Releve Nr	4	5	8	9	10	12	22	24	25	33	36	37	40	41	52	53	55	56	60	1	11	16	17	18	19	23	28	34	38	39	46	57	3	6	14	20	43	45	49	54	59	61	92	93	94	96	103	104
Cleistogenetea squarrosae																																																
Veronica spicata	r	1	10	2	4	.	1	10	.	2	10	1	10	+	1	10	4	1	1	10	4	10	4	4	2	4	4	2	10	10	2	10	.	1	r	+	2	2	2	2	r	r	.	r	10	4	.	.
Artemisia commutata	20	+	+	2	4	10	4	1	1	.	+	1	2	10	10	1	r	r	4	.	1	2	r	1	2	4	2	1	r	2	2	4	4	.	.	r	+	2	+	.	r	.	.	.	.	.	.	.
Festuca lenensis	r	10	10	10	10	.	1	10	1	+	4	r	10	10	2	4	10	r	10	10	4	4	10	10	4	4	10	2	2	4	10	10	30	2	4	10	4	4	2	4	+	10	+	.	2	10	.	.
Anemone flavescens	.	2	2	10	4	.	r	10	r	10	+	r	30	4	2	4	1	r	4	10	20	1	10	10	4	4	10	4	20	10	10	4	10	10	10	4	20	2	4	10	10	.	.	.	.	.	.	.
Carex duriuscula	r	10	.	4	4	r	4	1	.	+	1	.	1	4	2	2	+	.	4	1	10	1	20	2	.	1	4	+	1	2	.	10	r	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.
Festucetalia lenensis																																																
Alyssum obovatum	.	1	2	2	2	.	.	2	4	4	1	10	.	4	1	+	+	.	2	20	+	2	1	2	2	2	r	+	1	2	.	1	2	r	1	r	r	.	.	r	.	.	.	.	.	.	.	.
Helictotrichon krylovii	.	+	r	1	.	.	.	.	.	.	1	.	.	.	.	1	1	.	r	4	1	+	1	r	+	4	+	+	r	r	.	+	1	.	.	1	.	.	2	2	.	.	.	.	.	.	.	.
Thalictrum foetidum	.	r	r	.	+	.	.	.	.	.	.	+	r	r	.	.	+	r	r	r	r	+	r	.	r	+	2	r	+	r	.	r	+	r	.	2	1	.	4	r	r	.	.	.	.	.	.	.
Saxifraga bronchialis	.	r	.	r	.	.	.	.	.	.	+	.	.	.	.	r	1	.	.	r	.	r	+	2	+	2	.	r	r	1	r	.	r	4	10	r	.	.	.	r	r	.	.	.	.	.	.	.
Selaginella sellowii	.	10	.	1	2	.	.	.	.	+	4	r	.	2	.	4	2	.	.	1	1	2	1	r	.	2	.	20	+	4	.	r	2	.	1	r	r	.	r	+	r	.	.	.	.	.	.	.
Pulsatilletum flavescentis																																																
Eritrichium villosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	+	r	+	r	r	r	.	+	+	r	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
***Tephroseris kirilowii*-community**																																																
Tephroseris kirilowii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	4	4	4	.	.	.	.	.	.	.

Table 3.3. (Continued)

Cluster	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9
Releve Nr	4	5	8	9	10	12	22	24	25	33	36	37	40	41	52	53	55	56	60	1	11	16	17	18	19	23	28	34	38	39	46	57	3	6	14	20	43	45	49	54	59	61	92	93	94	96	103	104
Astragalo-Calamagrostietum																																																
Anemone patens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	20	10	10	1	r
Eremogone tschuktschorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	4	10	2	.	.
Dracocephalum palmatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	10	r	4	4	.	.
Calamagrostis purpurascens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	4	.	.	1	1	2	r	r	.	4	10
Draba cineraea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	+	+	.	r	r	+	+	+	r	+
Thymus diversifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	2	.	4	+	.	.
Phedimus middendorfianum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	2	.	.	.
Other species																																																
Poa sect. *Stenopoa*	.	+	1	+	2	.	10	10	4	1	2	r	4	1	.	r	r	.	+	.	2	+	1	2	10	1	4	2	+	1	r	2	.	.	.	20	10	2	2	2	1	.	.	.	.	.	.	.
Carex pediformis	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	.	.	.	.	2	.	r	4	.	.	.	10	.	+	.	.	r	10	r	+	4	.	.	10	4	1	+	.	10	r	10	.	.
Aster alpinus	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	r	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.
Silene samojedorum	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	1	r	1	r	4	+	1	r	r	r	.	r	1	.	+	r	.	.	.	r	r	.	.	1	.	2	.	.
Dianthus chinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	+	.	.	.	.
Euphorbia esula	+	.	.	+	.	1	2	.	r	.	.	.	r	.	+	.	.	1	.	.	r	.	.	+	.	.	2	.	.	.	+	.	.	.	.	r	r	2	r	.	.	.	.	.	.	.	.	.
Silene repens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Bromopsis pumpelliana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	+	.	.	.	.	.	.	.	1	20
Potentilla arenosa	.	r	.	r	.	.	.	.	.	.	+	.	.	.	.	1	r	.	.	r	4	10	4	r	2	+	+	+	r	1	2	r	r	10	2	+	1	.	+	1	r	+	+	2	+	2	.	.
Carex obtusata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	10	10	.	.	.	.	.	.	.
Cerastium arvense	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	r	r	.	r	.	.	+	r	.	1	r	.	.	+	.	r	.	.	.	.	.	.	.
Androsace septentrionalis	.	r	.	r	.	.	r	r	.	r	r	r	r	r	.	.	.	.	.	+	r	r	+	r	r	.	r	r	r	r	r	.	r	r	.	r	r	+	.	.	.	r	r	+	r	+	.	r
Phlox sibirica	.	1	r	+	.	.	.	r	.	.	+	.	.	.	.	r	.	.	r	r	.	r	.	10	r	r	r	r	.	r	.	r	+	4	4	r	.	.	r	+	r	.	.	1	1	+	.	.
Potentilla tollii	.	4	20	10	2	+	.	.	10	.	10	2	.	.	.	.	10	r	r	r	.	.	r	10	.	4	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium verum	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	r	+	r	.	.	.	.	4	r	r	.	.	.	r	+	2	+	4	.	1	2	1	r	.	r	.	4	.	.

Table 3.3. (Continued)

Cluster	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9
Releve Nr	4	5	8	9	10	12	22	24	25	33	36	37	40	41	52	53	55	56	60	1	11	16	17	18	19	23	28	34	38	39	46	57	3	6	14	20	43	45	49	54	59	61	92	93	94	96	103	104
Orostachis spinosa	.	r	.	+	1	.	.	.	r	+	r	+	.	r	.	+	+	.	r	.	.	+	.	r	.	+	.	r	r	r	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia tanacetifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	r	2	+	.	.	2	.	+	2	1	.	r	.	1	+	+	.	.	.	.	.	.	.
Plantago canescens	.	.	.	.	.	.	.	.	.	.	.	.	+	.	r	.	.	.	.	.	4	.	.	r	+	.	10	r	.	.	.	.	2	.	.	+	+	.	4	2	+	.	.	.	.	.	.	.
Agropyron cristatum	4	.	.	r	.	4	1	1	1	4	.	.	1	+	+	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ephedra monosperma	.	r	.	r	.	4	+	.	2	r	r	.	.	.	.	r	r	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helictotrichon hookeri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	r	.	.	.	.	.	r	.	.	.	.	.	r	+	4	r	.	4	2	r	.	.	.	.	.	.	.
Rosa acicularis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	r	.	.	.	1	.	.	.	r	r	1	r	.	2	1	r	4	2
Thymus indigirkensis	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	r	.	.	.	+	.	r	.	.	4	.	.	.	.	r	.	1	2	r	+	.	.	.	.	.	.	.
Artemisia frigida	.	r	.	r	.	r	.	.	4	4	+	4	.	.	.	.	+	r	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla conferta	r	.	.	.	.	.	10	.	r	.	.	.	r	r	.	.	r	.	r	.	.	10	.	r	.	.	+	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.
Cerastium maximum	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	r	.	.	.	.	.	.	1	r	.	.	.	r	.	.	.	.	.	.	.	r	r
Eremogone cappilaris	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	1	r	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	+	.	.	.	.	.	.	r	+	.	4	.	.	+
Myosotis spec.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	1	.	.	.	r	.	.	.	.	.	.	.	.	+	.	.	r	+	r	.	.	.	.	.	.	.
Epilobium angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	r	.	.	.	.	r	1	.	4	10
Stellaria jacutica	.	r	.	1	.	.	.	.	.	4	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pedicularis rubens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	4	r	.	.	.	.	.	.	.
Dracocephalum spec.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	r	.	.	.	.	.	.	.	.	.	.	2	.	r	.	.	.	.	.	.	.
Hedysarum alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.	r	.	.	r	2	1	.	.	.	.	.	.	.	.	.	.
Lappula spec.	r	.	.	.	.	+	r	.	r	.	r	r	.	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria longipes	.	.	.	.	.	.	.	.	.	.	1	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Myosotis asiatica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	r	4	2
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	r	r	.	1	r	.	.	.
Poa spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r
Pedicularis spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	2	.	r	.	.
Serratula marginata	.	.	.	.	.	.	r	.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Galium boreale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	4	.
Salix spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	r	.	.	.	.	.	.	.	.	.	.	.	.

Table 3.3. (Continued)

Cluster	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9
Releve Nr	4	5	8	9	10	12	22	24	25	33	36	37	40	41	52	53	55	56	60	1	11	16	17	18	19	23	28	34	38	39	46	57	3	6	14	20	43	45	49	54	59	61	92	93	94	96	103	104
Astragalus spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Stipa krylovii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia dracunculus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	10
Potentilla sanguisorba	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	10
Vicia macrantha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	4	.	.	.	.
Arctagrostis spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	+
Eritrichium caespitosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arnica angustifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	+	.	.	.	.	.	.
Myosotis alpestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga hieraciifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
Larix gmelinii s	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.
Clausia aprica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	r	.	.	.	.	.	.	r	r	.	.	r	r	.	.	.	.	.	.	.	.
Erysimum odoratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	r	r	.	.
Erysimum spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.
Sanguisorba officinalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r
Allium splendens	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	r	r	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.
Draba hirta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.
Linum perenne	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	.	.	.	.	.	.	.
Linum komarovii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	2	.	.	.	.	.	.	.	.	.

Species with low frequency

Carex rupestris: 93 (30); Calamagrostis stricta: 45 (4); Betula fruticosa: 20 (1); Hedysarum dasycarpum: 6 (1); Oxytropis species: 18 (1); Pyrola rotundifolia: 25 (1); Silene spec.: 61 (1): 92 (r); Artemisia arctica: 61 (+); Astragalus inopinatus: 36 (r): 49 (+); Chamaerhodos erecta: 37 (+); Festuca kolymensis: 93 (+); Hedysarum vicioides: 8 (+); Phlojodicarpus villosus: 5 (+); Tephroseris integrifolia: 3 (+); Arabis species: 54 (r); Artemisa campestris: 45 (r); Castilleja rubra: 45 (r); Crucihimalaya bursifolia: 9 (r): 40 (r); Crucihimalaya mollissima: 43 (r); Empetrum nigrum: 61 (r); Equisetum scirpioides: 103 (r); Erysimum cheiranthoides: 103 (r); Festuca rubra: 45 (r); Festuca spec.: 54 (r): 103 (r); Gagea serotina: 5 (r); Galium trifidum: 92 (r); Lathyrus palustris: 104 (r); Leptopyrum fumarioides: ; Linaria vulgaris: 6 (r); Orobanche coerulescens: 22 (r): 52 (r); Poa sibirica: 6 (r); Potentilla crantzii: 103 (r); Sisymbrium polymorphum: 104 (r); Vaccinium uliginosum: 93 (r); Minuartia biflora: 55 (r); Astragalus tugarinovii: ; Castilleja pallida: 28 (r); Campanula spec.: 59 (r); Erigeron acer: 59 (r); Gentianella amarella: 49 (r); Gentianopsis barbata: 59 (r); Linaria spec.: 59 (r)

Table 3.4. Complete list of relevés from tundra steppes of *Carici-Kobresietea*; cover given in % (with r = 0.1%; + = 0,5%)

Cluster	10	10	10	10	10	10	10	10	10	10
Releve Nr	105	117	118	122	123	124	125	212	213	214
Relevé number	105	117	118	122	123	124	125	212	213	214
Relevé area [m2]	10	10	10	10	10	10	10	10	10	10
Number of species	16	13	10	19	19	31	21	23	24	21
Altitude [m]	11	22	22	11	22	11	1	11	11	11
Aspect [°]	45	315	-	315	315	-	180	105	225	195
Slope [°]	3	1	0	3	3	0	6	4	5	3
Cover open ground [%]	8	0	0	3	60	30	25	30	30	20
Cover bare rock [%]	0	0	0	0	10	0	2	0	0	0
Cover litter layer [%]	5	15	8	20	3	10	5	3	5	15
Cover shrub layer [%]	0	25	35	30	0	20	20	8	43	42
Cover herb layer [%]	90	12	3	35	30	40	43	15	30	33
Cover moss layer [%]	2	55	60	15	0	2	13	1	3	3

Table 3.4. (Continued)

Cluster **Releve Nr**	10 105	10 117	10 118	10 122	10 123	10 124	10 125	10 212	10 213	10 214
***Polemonium boreale-Hierochloe alpina*-community**										
Polemoniom boreale	30	.	.	+	10	2	2	r	+	+
Hierochloe alpina	.	+	+	2	.	+	+	r	+	+
Koeleria asiatica	10	.	.	.	2	1	2	+	+	+
Minuartia rubella	+	.	.	.	+	r	r	r	r	r
Luzula confusa	.	2	r	2	1	4	2	.	.	.
Astragalus alpinus	10	.	.	.	2	1	.	2	2	1
Stellaria longifolia	.	.	.	r	r	r	r	.	.	.
Dryas octopetala	.	2	.	30	4	20	30	.	.	.
Ledum palustre	.	1	20	2	.	+	.	2	.	.
Cassiope tetragona	.	r	r	r	.	+	.	.	.	.
Festuca brachyphylla	r	.	.	+	1	.	+	.	.	.
Pedicularis hirsuta	.	r	r	r	.	r	.	.	.	.
Other species										
Vaccinium uliginosum	.	.	2	.	.	.	.	10	20	20
Potentilla arenosa	4	.	.	.	2	r	+	.	.	.
Draba cinerea	.	.	.	.	r	r	.	r	r	r
Oxytropis czukotica	.	.	.	1	.	+	r	.	.	.
Arctous alpina	.	.	.	.	.	.	.	10	4	10
Kobresia myosuroides	.	.	.	.	.	.	.	2	10	30
Androsace septentrionalis	+	.	.	.	r	r	.	r	r	+
Clausia aprica	.	.	.	+	+	r	r	.	r	.
Silene samojedorum	2	.	.	.	r	r	.	+	r	.
Taraxacum spec.	+	.	.	r	+	+	.	.	.	.
Artemisia campestris	.	.	.	+	2	1	+	.	.	.
Carex supina	2	.	.	.	.	.	.	2	4	1
Empetrum nigrum	.	.	.	.	.	r	.	10	2	4
Poa spec.	.	r	r	r	.	.	.	.	.	.
Alopecurus alpinus	.	.	.	r	.	r	+	.	.	.
Stellaria peduncularis	.	.	.	.	.	.	.	+	+	r
Campanula rotundifolia	.	.	.	.	.	.	.	r	+	+
Carex bigelowii	.	r	2	.	.	+	.	.	.	.
Phlojodicarpus villosus	.	.	.	.	.	.	.	2	+	+

Table 3.4. (Continued)

Cluster	10	10	10	10	10	10	10	10	10	10
Releve Nr	105	117	118	122	123	124	125	212	213	214
Castilleja pseudohyperborea	.	.	.	.	.	.	.	1	1	1
Myosotis asiatica	.	.	.	.	2	+	2	.	.	.
Claytonia acuminata	.	2	.	2	.	1	.	.	.	.
Thymus ochotensis	.	.	.	.	.	.	.	2	2	2
Arctagrostis arundinacea	.	2	.	.	.	4	.	r	.	.
Castilleja rubra	.	.	.	.	.	.	.	.	r	r
Diapensia lapponica	.	.	.	r	.	r	.	.	.	.
Calamagrostis holmii	r	.	.	.	.	+	.	.	.	.
Equisetum arvense	.	.	.	.	.	.	+	.	+	.
Rumex graminifolius	.	.	.	.	r	1	r	.	.	.
Carex spec.	.	2	+	.	.	.	.	.	.	.
Carex pediformis	.	.	.	.	.	.	.	2	2	.
Poa sect. *stenopoa*	.	.	.	.	.	.	.	2	2	.
Poa versicolor	10	.	.	.	.	.	+	.	.	.

Species with low frequency

Draba hirta: 123 (r); Tephroseris integrifolia: 117 (r): 122 (r); Vaccinium vitis-idaea: 122 (r); Poa tolmatchewii: 214 (r); Bromus pumpellianus: 213 (+); Polygonum tripterocarpum: 212 (+); Festuca lenensis: 214 (0,1); Poa alpigena: 123 (0,1); Poa angustifolia: 124 (0,1); Antennaria friesiana: 125 (0,2); Armeria maritima: 124 (0,2); Catolobus pendulus: 105 (0,2); Papaver alpinum: 125 (0,2); Ranunculus pedatifidus: 105 (0,2); Arnica angustifolia: 125 (r); Eriophorum vaginatum: 117 (0,4): 118 (r); Cerastium maximum: 105 (2); Draba spec.: 125 (r)

Table 3.5 Comparative table of original diagnostic (and some constant) species of all syntaxa referred to in own classification according to the referenced publications. Species are given as characteristic for the respective class (KC), order (OC), alliance (VC), association (AC) or differential (D) and constant (const.) species. If available from the reference, the frequencies are given (in brackets).

	Troeva et al. 2010	Tüxen 1937	Mirkin et al. 1992	Mirkin in Gogoleva et al. 1987	Mirkin et al. 1985	Kucherov & Daniëls 2005
Calamagrostetea langsdorfii						
Equisetum fluviatile	KC					
Carex appendiculata	KC					
Beckmannia syzigachne	KC					
Carex juncella	KC					
Calamagrostis langsdorffii	KC					
Poa palustris	KC					
Alopecurus arundinaceus	KC					
Hordeum brevisubulatum	KC					
Caltha palustris	KC					
Acorus calamus	KC					
Ranunculus gmelinii	KC					
Ranunculus propinquus	KC					
Vicia cracca	KC					
Lathyrus pilosus	KC					
Molinio-Arrhenateretea						
Alopecurus pratensis		KC				
Poa pratensis		KC				
Ranunculus acris		KC				
Taraxacum officinale		KC				
Trifolium repens		KC				
Vicia cracca		KC				
…		KC				
Arrhenatheretalia elatioris						
Achillea millefolium		OC				
Rhinantus minor		OC				
Plantago media		D				
…		OC				

Table 3.5 (Continued)

	Troeva et al. 2010	Tüxen 1937	Mirkin et al. 1992	Mirkin in Gogoleva et al. 1987	Mirkin et al. 1985	Kucherov & Daniëls 2005
Cleistogenetea squarrosae						
Veronica incana				KC		
Koeleria cristata			KC	KC		
Stipetalia krylovii						
Psathyrostachys junceae				OC		
Stipion krylovii						
Stipetum krylovii						
Stipa krylovii				OC, VC	AC (V)	
Festuca lenensis*					AC (V)	
Poa stepposa*					AC (IV)	
Carex duriuscula*			KC	KC	AC (IV)	
Artemisia commutata*			KC	KC	AC (V)	
Festucetalia lenensis						
Festucion lenensis						
Carici duriusculae-Festucetum lenensis						
Festuca lenensis*				OC, VC, AC		
Poa stepposa				OC, VC, AC		
Pulsatillion flavescentis						
Aster alpinus				VC		
Lychnis sibirica				VC		
Dianthus versicolor				VC		
Euphorbia discolor				VC		

Table 3.5 (Continued)

	Troeva et al. 2010	Tüxen 1937	Mirkin et al. 1992	Mirkin in Gogoleva et al. 1987	Mirkin et al. 1985	Kucherov & Daniëls 2005
Pulsatillietum flavescentis						
Artemisia commutata*			KC	KC	AC (V)	
Carex duriuscula*			KC	KC	AC (IV)	
Festuca lenensis*				KC	AC (V)	
Poa stepposa*				OC	AC (V)	
Pulsatilla flavescens				OC, VC	AC (V)	
Carex pediformis				OC, VC	AC (V)	
Bromopsis korotkiji				VC, AC	AC (V)	
Aster alpinus				AC		
Lychnis sibirica				AC		
Dianthus versicolor				AC		
Euphorbia discolor				AC		
Astragalo pseudoadsurgenti-Calamagrostienion purpurascentis						
Astragalus pseudoadsurgens						AC
Aster sibiricus						AC
Astragalo pseudoadsurgenti-Calamagrostienion purpurascentis & Androsacio-Aconogonion						
Aster alpinus						const.
Dianthus repens						const.
Draba cineraea						const.
Silene repens						const.
Bromopsis pumpelliana						const.
Astragalo pseudoadsurgenti-Calamagrostienion purpurascentis & Androsacio-Aconogenion						
Potentilla nivea						const.
Calamagrostis purpurascens						const.
Poa arctostepporum						const.
Thymus oxyodontus						const.
Dracocephalum palmatum						const.
Carex obtusata						const.
Potentilla matsuokana						const.
Cerastium arvense						const.
Cnidium cnidiifolium						const.
Carex spaniocarpa						const.

Table 3.5 (Continued)

	Troeva et al. 2010	Tüxen 1937	Mirkin et al. 1992	Mirkin in Gogoleva et al. 1987	Mirkin et al. 1985	Kucherov & Daniëls 2005
Carici rupestris-Kobresietea bellardii						
Saxifraga firma						KC
Dryas punctata						KC
Carex rupestris						KC
Eremogone cappilaris						KC
Eritrichium tschuktschorum						KC
Artemisia furcata						KC
Oxytropidion nigrescentis & Androsaco arctisibiricae-Aconogonion laxmannii						
Hierochloe alpina						const.
Anemonastrum sibiricum						const.
Arctous alpina						const.
Pedicularis capitata						const.
Salix sphenophylla						const.
Kobresia myosuroides						const.
Smelowskia porsildii						const.
Hedysarum truncatum						const.
Androsaco arctisibiricae-Aconogonion laxmannii						
Oxytropis vassilczenkoi						VC
Androsace arctisibirica						VC
Aconogonon ocreatum laxmannii						VC
Agrostis kudoi						VC
Draba arctogena						VC
Helictotrichon dahuricum						VC
Oxytropidion nigrescentis, Diapensio obovatae-Dryadetum punctatae vaccinietosum microphylli (subass.), but also ocurring in Androsaco arctisibiricae-Aconogonion laxmannii						
Vaccinium uliginosum microphyllum						VC
Poa malacantha						VC
Diapensia obovata						VC
Antennaria friesiana						VC
Luzula confusa						VC
Cassiope tetragona						VC

Figure 3.1 DCA with character species of all syntaxa.

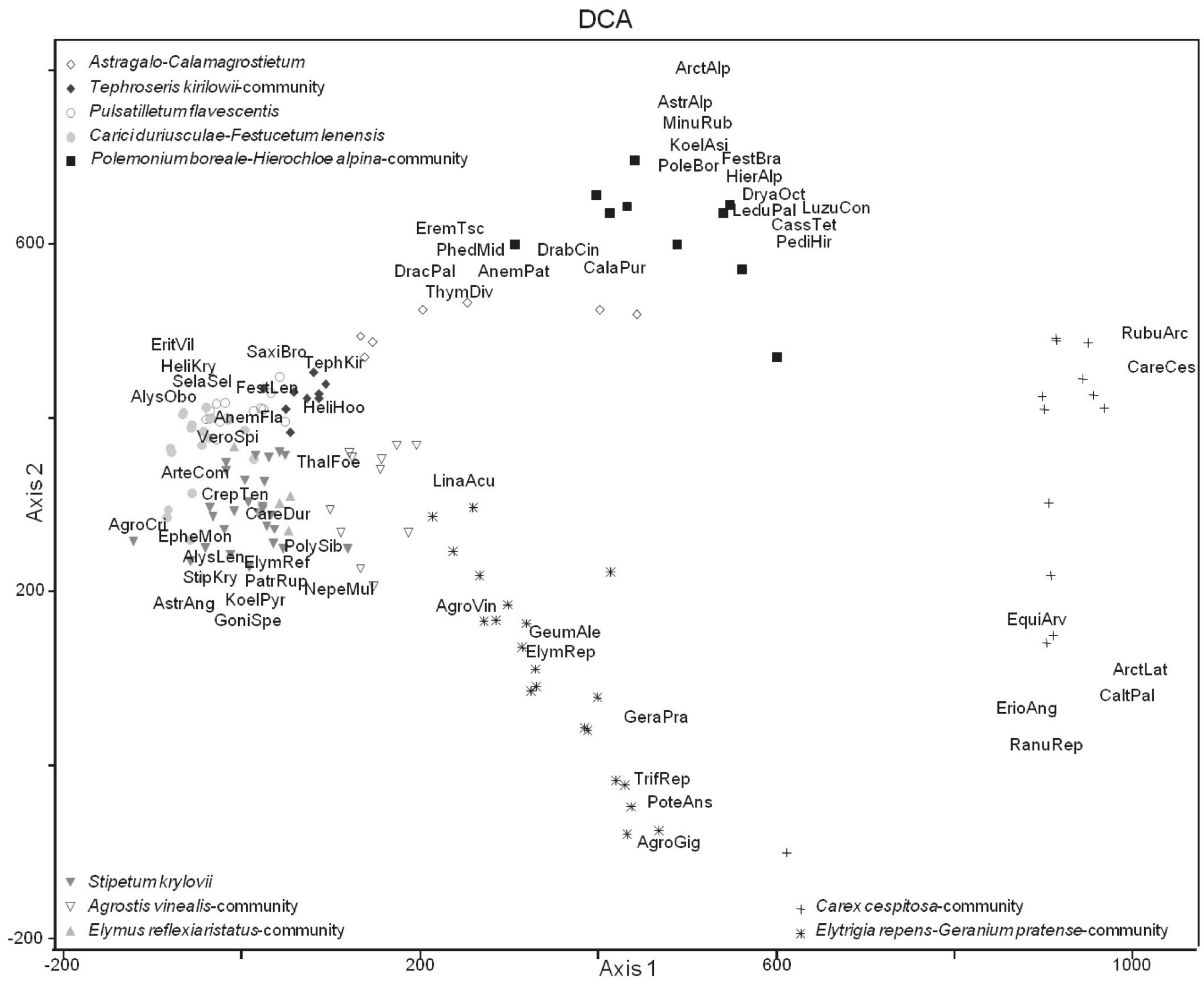

Figure 3.2 Boxplots of slope inclination and slope exposure (northerness & easterness) of all syntaxa.

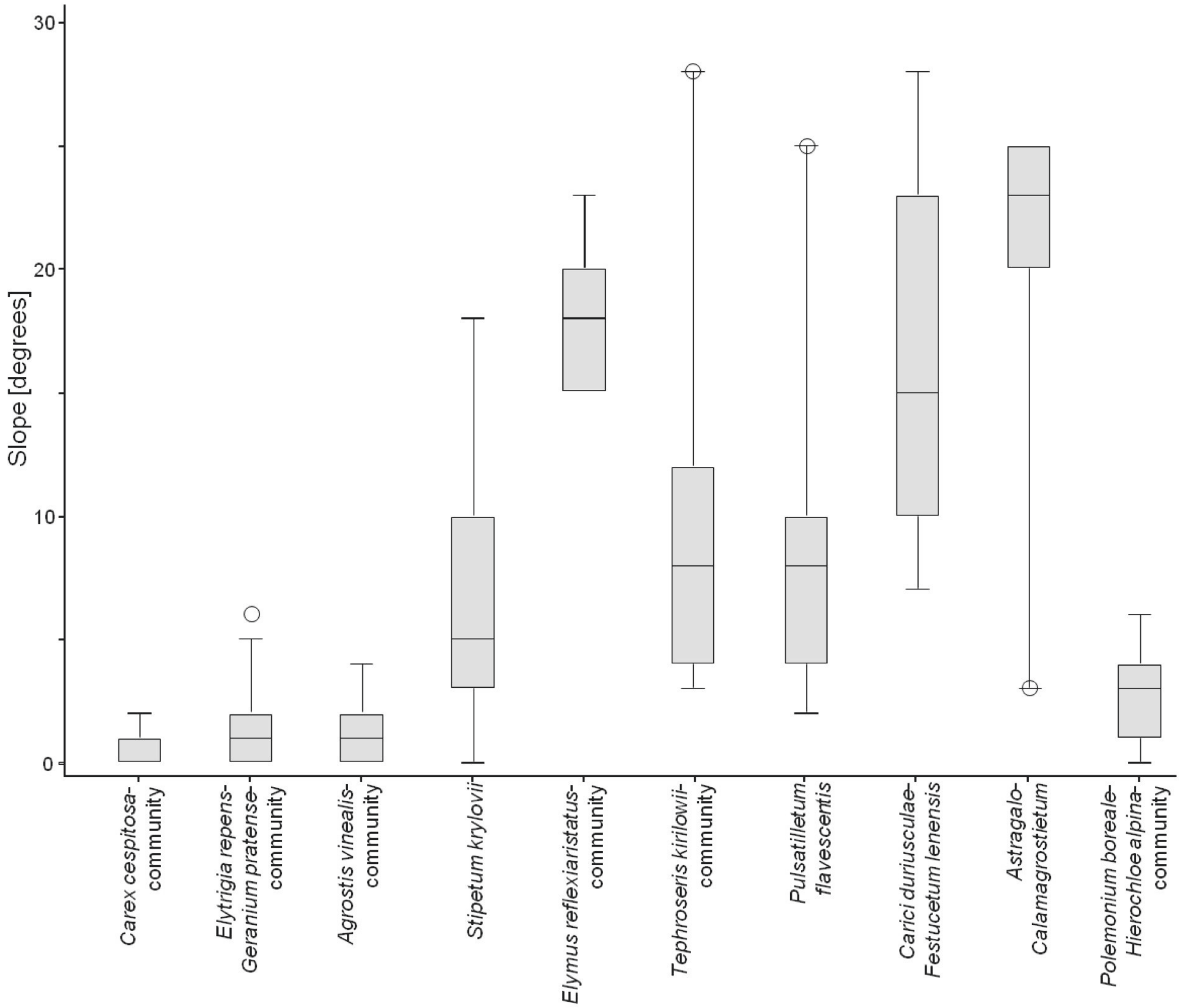

Figure 3.2 (Continued)

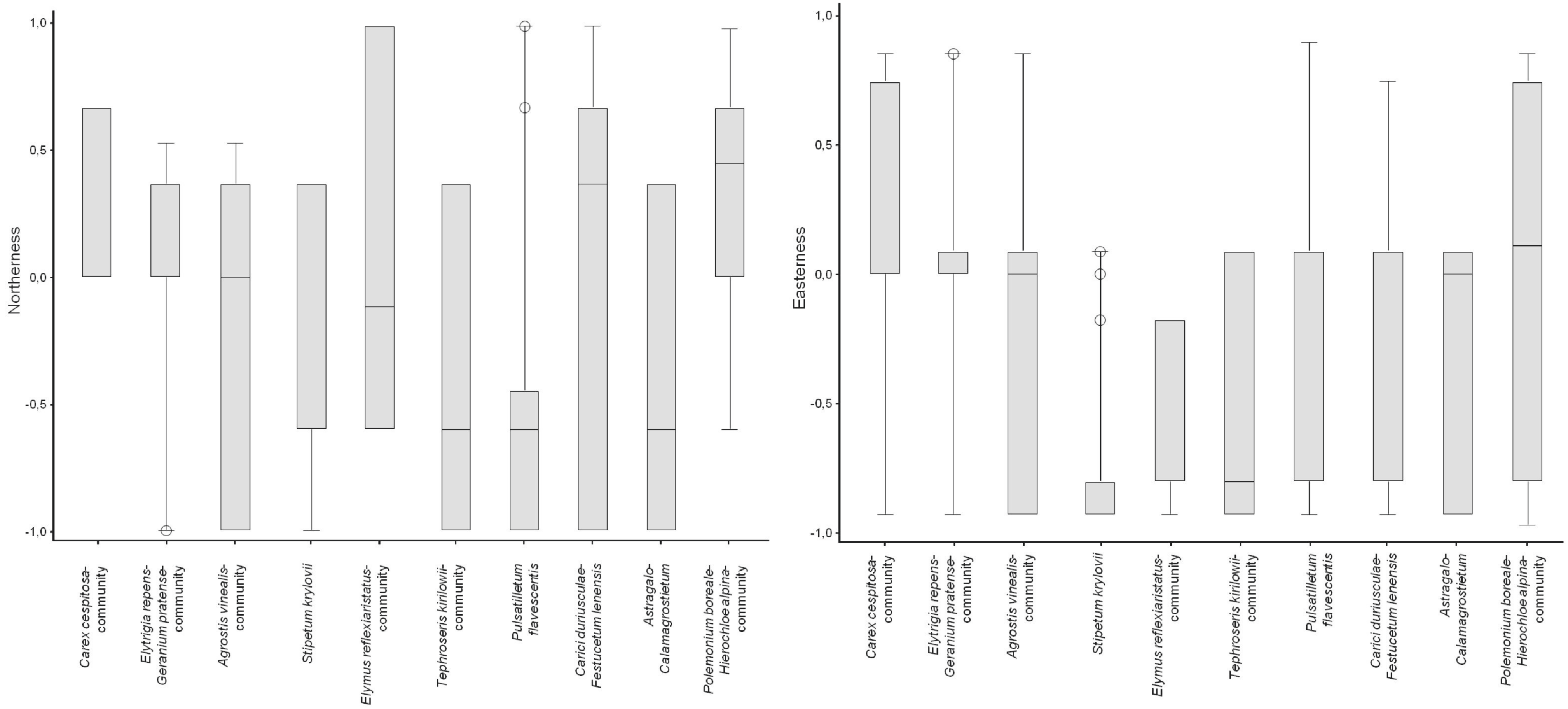

Figure 3.3 Photos of the vegetation types in the study area

Figure 3.3 A In Northern Siberia, extrazonal steppe outposts typically occur on well-drained, south-exposed slopes along river valleys. The steppes (*Cleistogenetea squarrosae*) close to Verkhoyansk (Yana river valley) belong to the order *Festucetalia lenensis*, represented by a typical association (*Pulsatilletum flavescentis*), a mesic community (*Tephroseris kirilowii* community) in moister depressions, as well as a petrophytic association (*Carici duriusculae-Festucetum lenensis*) along ridges and rocky outcrops. (Photo J. Reinecke, Jun 2014)

Figure 3.3 B Some of the northernmost Siberian steppes are found close to Chersky (Kolyma river valley), few kilometers away from the northern treeline. They represent a hemicryophytic association (*Astragalo pseudoadsurgenti-Calamagrostietum purpurascentis*) of the order *Festucetalia lenensis.* Typical species include *Dracocephalum palmatum*, *Anemone patens* and *Phlox sibirica* (Photo J. Reinecke, Jun 2015)

Figure 3.3 C North of the treeline close to Pokhodsk (Kolyma river valley), tundra steppes (class *Carici rupestris-Kobresietea bellardii*) can be found on top of pingos, small hills in the tundra landscape with better drainage than the surrounding dwarf shrub tundra. Moister stands on well developed soil like the *Polemonium boreale-Hierochloë alpina* community, are much more meadow-like in physiognomy (Photo J. Reinecke, Jun 2015)

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Figure 3.3 D True steppes of the order *Stipetalia krylovii* can be found in the environs of Yakutsk (Lena river valley); the typical association is found along most of the slopes (*Stipetum krylovii*), while meadow-like communities (*Agrostis vinealis* community) dominate in drier, often grazed and more level parts of the valley (here in the foreground). (Photo J. Reinecke, July 2015)

Figure 3.3 E Steep slopes along the Buotoma river south of Yakutsk (Lena river valley) carry a petrophytic community (*Elymus reflexiaristatus* community) of the true steppes (*Stipetalia krylovii*); the mesic meadows along the riverbank belong to the class *Molinio-Arrhenatheretea.* (Photo J. Reinecke, July 2015)

Figure 3.3 F Wet meadows of the *Carex cespitosa* community (class *Calamagrostietea langsdorfii*) are preferred pastures for the horses in the "Pleistocene Park", a grazing experiment close to Chersky (Kolyma river valley). (Photo J. Reinecke, Jun 2015)

A4 – Chapter 4

Appendix 4.1 – details on stratigraphy

Unit I represents the active layer, with a thickness varying between 1.4 and 0.85m, as measured at the end of June 2014 and is composed of fine sand. One 14C AMS age of 295 years BP from a sample directly above the permafrost table, the border to Unit II, indicates the modern origin of Unit I deposits.

Unit II consists of 30–40m thick Yedoma Ice Complex (YIC) deposits, composed of silty and, primarily, sandy sediments with a layered cryostructure and enclosed by up to 6m wide syngenetic ice wedges. The mean grain size of Unit II is fine-grained sand. The YIC deposits contain evenly distributed organic material, mainly plant detritus and vertical plant roots. Occasionally, layers and chunks with higher organic content were found, e.g. a fossilized ground squirrel nest with thick bedding of grasses, including numerous identifiable plant remains. Based on droppings preserved in the nest, it was attributed to an arctic ground squirrel (*Urocitellus parryii*, confirmed by L. Maul, Senckenberg Weimar, personal information). This ground squirrel nest was sampled in detail. Additionally, 28 samples from Unit II deposits were used for the palaeontological study. Seven AMS radiocarbon ages are available for Unit II (Table 4.1.1). An age of 33±0.5 14C ka BP was obtained from material 2.05m below the ground surface (bgs) in section A. Plant material sampled from the ground squirrel nest at 4.6m bgs in section A provided a 14C AMS date of 26±0.22 ka BP. In section C, dating of organic material at 12.5 and 14.5m bgs resulted in non-finite ages of > 48 and > 51 ka 14C BP, whereas plant material from 18.5m bgs was dated to 49±2 14C ka BP. According to the dating results and the stratigraphical interpretation, the YIC of Unit II was deposited over a long period during the last cold stage, e.g. MIS 2, 3, and 4.

Unit III is an organic layer rich in large macroscopic plant remains, including numerous branches and twigs of woody plants, situated directly below the YIC of Unit II. This horizon is detectable across the whole outcrop, mostly as a relatively thin layer about 1.5m thick, sharply delineated from the YIC and Unit IV. In places, the layer merges into accumulations of organic matter about 5m thick that are assumed to represent the fill of former trench-like depressions resembling modern gullies. Unit III was sampled in section B in the lower part of one such pocket-like accumulation below a coarse woody layer at a depth of about 43 to 44m bgs. The three samples consist largely of organic material, including numerous seeds, fruits, and plant debris in a distorted fine bedding alternating with silty fine sand beds. Radiocarbon dating of this material resulted in an non-finite age of > 44 ka BP. We assume that Unit III represents sediments from the last interglacial (MIS 5), owing to an OSL age of 142,800±25,300 a for underlying sediments from Unit IV and its position directly below last cold-stage deposits.

Unit IV is composed of horizontally layered frozen sand that is traceable without interruption over large distances along the headwall of the outcrop. This unit is about 25 m thick and in most places it reaches almost to the bottom of the exposure. In contrast to the YIC, Unit IV is not penetrated by wide ice wedges. Exposed exclusively at the headwall, Unit IV was not accessible for systematic sampling due to the danger of objects frequently falling from the > 60m high, intensely thawing and eroding, partly overhanging permafrost wall. Only one sample was collected in situ from a ridge of frozen deposits in 50m bgs for OSL dating as well as sedimentological and palaeontological analyses. According to the sedimentological characteristics of this material, Unit IV clearly differs from the overlying Units I–III in having the largest sand fraction (70 %) and the highest carbonate content 8.2 wt % within the sequence. OSL dating resulted in several non-finite minimum ages between 93.6 and 123.2 ka BP and a finite age of 142.8±25.3 ka (Table 2, Ashastina et al. 2017). Thus, unit IV probably accumulated during the late Middle Pleistocene and included the Saalian cold stage (MIS 6). This attribution is supported by data from the local Yana Geological Service, who sampled the upper part of Unit IV for detailed palynological analyses (L.Vdovina, personal communication).

Unit V represents the deepest part close to the bottom of the exposure. The main part of this unit is not exposed. The unit consists of ice-rich deposits with a layered cryostructure, embedded in syngenetic ice wedges similar to deposits of the YIC (Unit II) and is therefore assumed to be an older ice complex, probably formed during the Middle Pleistocene. Since exposed only directly at the headwall, Unit V was not accessible for sampling.

Table 4.1.1. Radiocarbon dating of the selected samples from the Batagay permafrost exposure.

Lab. No.	Sample name	Depth [m b.s.l.]	Radiocarbon ages [yr BP]	Calibrated ages 2 σ 95.4% [cal yr BP]	Description
Poz-78149	19.6/A/4/1.15	1.15	295±30	459 - 347	Plant remains
Poz-79751	19.6/A/5/2.05	2.05	33 400 ± 500		Plant remains
Poz-77152	20.6/A/1/460-472	4.6	26 180 ± 220	28 965 – 27 878	*Plantago sp., Artemisia sp.,* ground squirrel droppings
Poz-100721	20.6/A/1/460-472	4.6	140.14 ± 0.37 pMC		*Larix gmelinii*
Poz-79756	22.6/C/2/8.5	8.5	12 660 ± 50		Plant remains
Poz-79753	22.6/C/6/12.5	12.5	>48 000		Plant remains
Poz-79754	22.6/C/9/14.5	14.5	>51 000		Plant remains
Poz-79755	29.6/E/2/18.5	18.5	46 000 ± 2 000		*Papaver sp.*
Poz-78150	29.6/C/10/24.5	24.5	110.31 ± 0.37 pMC	1991AD - 2005AD	*Alnus sp., Vaccinium vitis-idea*
Poz-66024	21.6/B/3/2	44	>44 000		Plant remains

Appendix 4.2 – details on plant macrofossils

Table 4.2.1. List of identified Batagay macrofossils. Index letters identify the counted part of the plant: b – bract; c - cone/catkin; ca – capsule; cl – calyx; cr – caryopsis; cs - cone scale; cy – cypsela; f – flower; fl – floret; I – infloresconse; k – knob; l – leave; m – megaspore; mk – mericarp; n – needle; nt – nutlet; py – pyrene; s – seed; sm - sterm; sp – spiklet; v - valve of silique. Split into several depth intervals (1.1–8.5m; 9.5–18.5m; 19.5–37.5m; 38.5–50.0m). Note that species list is different for depth intervals.

	Depth, m bgs							
Plant taxa	**1.1**	**2.0**	**3.0**	**3.5**	**4.6**	**5.5**	**6.5**	**8.5**
Agropyron cristatum					3^{fl}			
Alyssum obovatum					2^{l},150^{s}			
Artemisia sp.		1^{cy}			46^{f}, 1011^{a}, 15^{fl}			1^{cy}
Betula Subgenus *Betula*								6^{Nt}
Carex duriuscula						1^{Nt}		
Chenopodium sp.			1^{s}	15^{s}				
Comastoma tenellum								
Empetrum nigrum s.l.	2^{l}				1^{l}			
Equisetum scirpoides			1^{sm}					2^{sm}
Eremogone capillaris					10^{ca}, 356^{s}			
Erigeron acris								
Eritrichium villosum					1^{s}, 10^{mk}, 45^{l}			
Festuca sp.					55^{sp}			
Juncus sp.								
Koeleria sp.					3^{fl}			
Larix gmelinii	2^{N}		1^{N}		3^{N}	5^{N}	2^{N}	
Ledum palustre								
Lepidium densiflorum								
Minuartia arctica			1^{s}					
Myosotis asiatica					1^{s}, 1^{f}, 1^{sc}			
Papaver Sect. Scapiflora				4^{s}	12^{s}	3^{s}		
Phlox sibirica					2^{sc}			
Plantago canescens					284^{s}, 800^{sc}			
Poa sp.				13^{s}	48^{fl}			
Potentilla arenosa					1^{Nt}			
Potentilla tollii								
Puccinellia sp.			1^{cr}					
Ranunculus pedatifidus subsp. *affinis*					9^{s}			
Rumex maritimus						1^{s}		
Saxifraga cf. *oppositifolia*		1^{s}						
Selaginella sibirica/rupestris	3^{m}	2^{m}						
Silene repens		1^{s}						
Silene samojedorum		2^{s}			620^{s}, 1^{cl}	1^{s}		
Smelovskia sp. (sensu Al-Shehbaz 2006)				1^{s}				
Stellaria sp.					167^{s}, 2^{cl}			
Tephroseris integrifolia					31^{s}			
Vaccinium vitis-idaea								6^{l}

Table A.2.1. (Continued)

	Depth, m bgs								
Plant taxa	**9.5**	**10.5**	**11.5**	**12.5**	**13.5**	**14.5**	**16.5**	**17.5**	**18.5**
Agropyron cristatum									
Alnus alnobetula subsp. *fruticosa*									
Alyssum obovatum						2^{s}			1^{s}
Artemisia sp.						1^{cy}			
Betula Subgenus *Betula*									
Carex duriuscula									2^{Nt}
Carex sp. *tricarpellata*								1^{Nt}	
Chenopodium prostratum									
Chenopodium suecicum									
Chenopodium sp.									
Comastoma tenellum									
Corispermum crassifolium									
Corydalis sibirica									
Descurainia sophioides									
Draba sp.									
Empetrum nigrum s.l.									
Equisetum scirpoides		1^{sm}					1^{sm}		
Eremogone capillaris						5^{s}			
Erigeron acris									
Eritrichium villosum									
Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)	1^{s}								
Festuca sp.						4^{fl}			
Frankia alni									
Hordeum jubatum									
Juncus sp.					3^{s}				
Koeleria sp.									
Larix gmelinii		1^{N}	1^{N}						
Ledum palustre				1^{l}					
Myosotis asiatica									
Papaver Sect. Scapiflora		7^{s}	1^{s}	7^{s}	6^{s}			1^{s}	250^{s}
Poa sp.					2^{fl}	10^{fl}			
Potentilla arenosa									1^{Nt}
Potentilla tollii					1^{Nt}				
Puccinellia sp.									
Puccinellia tenuiflora					2^{cr}				
Selaginella sibirica/rupestris		2^{m}			4^{m}		1^{m}		
Silene repens									
Silene samojedorum				1^{s}					127^{s}
Vaccinium vitis-idaea		1^{l}		1^{l}					2^{l}

Table A.2.1. (Continued)

	Depth, m bgs								
Plant taxa	**19.5**	**25.5**	**32.5**	**33.5**	**34.5**	**35.5**	**36.5**	**36.7**	**37.5**
Alnus alnobetula subsp. *fruticosa*									3^{cs}
Artemisia sp.								1^{cy}	
Betula Subgenus *Betula*						1^{Nt}			
Carex duriuscula	8^{Nt}								
Carex sp. *tricarpellata*									1^{Nt}
Descurainia sophioides							11^{s}	12^{s}	5^{s}
Draba sp.							2^{s}	8^{s}	
Empetrum nigrum s.l.			1^{l}						
Equisetum scirpoides	3^{sm}								
Eremogone capillaris									
Erigeron acris									
Eritrichium villosum									
Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)		1^{s}							
Festuca sp.									
Frankia alni									
Hordeum jubatum									
Juncus sp.			1^{s}	1^{s}					
Koeleria sp.									
Larix gmelinii			8^{s}, 2^{N}	1^{N}	1^{N}				
Ledum palustre									
Lepidium densiflorum							1^{v}		
Minuartia arctica									
Minuartia rubella			1^{s}						
Papaver Sect. Scapiflora	1^{s}						60^{s}		
Phlox sibirica								2^{l}	
Plantago canescens									
Poa sp.						15^{fl}	2^{fl}	5^{fl}	8^{fl}
Potentilla arenosa								4^{Nt}	
Potentilla tollii						8^{Nt}		9^{Nt}	
Puccinellia sp.									
Puccinellia tenuiflora							1^{cr}		
Saxifraga sp.			1^{s}						
Selaginella sibirica/rupestris									5^{m}
Silene repens						4^{s}	4^{s}		
Silene samojedorum									
Smelovskia sp. (sensu Al-Shehbaz 2006)							10^{s}		
Urtica dioica			1^{s}						
Vaccinium vitis-idaea				1^{l}	3^{l}				

Table A.2.1. (Continued)

	Depth, m bgs							
Plant taxa	**38.5**	**40.5**	**41.5**	**42.5**	**43.0**	**43.5**	**44.0**	**50.0**
Alnus alnobetula subsp. *fruticosa*					35^{c}, 84^{cs}	9^{sc}	153^{sc}, 55^{c}	
Alyssum obovatum								6^{s}
Artemisia sp.							4^{cy}	4^{cy}
Betula Subgenus *Betula*					8^{c}, 500^{Nt}	47^{Nt}	150^{Nt}	
Betula sp.					12^{b}, 566^{Nt}	5^{b}	8^{b}, 7^{l}, 526^{Nt}, 1^{c}	
Carex duriuscula	5^{Nt}			1^{Nt}	1^{Nt}		1^{Nt}	
Carex sp. *tricarpellata*					3^{Nt}			
Chenopodium prostratum					3^{s}			2^{s}
Chenopodium suecicum					4^{s}		2^{s}	
Chenopodium sp.					1^{s}			
Comastoma tenellum							2^{s}	
Corispermum crassifolium							1^{s}	
Corydalis sibirica					1^{s}			
Descurainia sophioides								1^{s}
Draba sp.							1^{s}	4^{s}
Equisetum scirpoides					3^{sm}	8^{sm}	9^{sm}	
Eremogone capillaris								
Erigeron acris							1^{cy}	
Eritrichium villosum								4^{s}, 19^{b}
Fabaceae tribe *Galegeae* (cf. *Oxytropis* sp.)			1^{s}					3^{s}
Festuca sp.				2^{fl}			1^{fl}	19^{fl}
Frankia alni						12	3	
Hordeum jubatum					1^{fl}			
Juncus sp.							1^{s}	
Koeleria sp.								20^{fl}
Larix gmelinii		1^{N}	1^{N}		141^{s}, 3^{N}, 41^{k}, 5^{cs}	12^{s}, 200^{N}	55^{s}, 1000^{N}	7^{N}
Ledum palustre					1^{l}			1^{l}
Minuartia verna							1^{s}	
Moehringia laterifolia					7^{s}		3^{s}	
Papaver Sect. Scapiflora			1^{s}		200^{s}		2^{s}	24^{s}
Phlox sibirica		3^{l}						
Poa sp.	1^{fl}	1^{fl}		2^{fl}	1^{fl}	1^{fl}	7^{fl}	142^{fl}
Potentilla arenosa		1^{Nt}			24^{Nt}			2^{Nt}
Potentilla tollii	2^{Nt}		41^{Nt}	6^{Nt}	14^{Nt}		11^{Nt}	4^{Nt}
Puccinellia sp.							1^{cr}	2^{cr}
Rosa acicularis					6^{Nt}	1^{Nt}	1^{Nt}	
Rubus idaea					107^{py}, 1^{f}	4^{py}	106^{py}	
Salix sp.						4^{l}		
Silene repens					2^{s}			
Silene samojedorum					1^{s}			
Sonchus arvensis					4^{cy}		1^{cy}	
Stellaria jacutica					1^{s}			
Thymus serpyllum							1^{s}	
Urtica dioica					400^{s}	1^{s}	47^{s}	

Appendix 4.3 – details on fossil pollen and spores

Table 4.3.1. List of identified pollen with counts from the Batagay permafrost exposure.

	Dephts, m bgs																		
Plant taxa	**0.2**	**4.7**	**5.5**	**8.5**	**9.5**	**12.5**	**16.5**	**18.5**	**20**	**20.5**	**22**	**32**	**32.5**	**40**	**41**	**42**	**44**	**44**	**50**
Trees and shrubs																			
Abies													1						
Alnus subg. Alnobetula								1			3	18		1					
Betula						3		4		2	16	136	9	5			1		
Larix											2								
Picea						1						1	13						
Pinaceae spp.									2		1	2	3	2					
Pinus sg Diploxylon			1			1		2			4	2	1	4		2			
Salix				1		3	2	12	2		1	1	3						
Tsuga						1													

Table 4.3.1. (Continued)

	Dephts, m bgs																	
Plant taxa	**0.2**	**4.7**	**5.5**	**8.5**	**9.5**	**12.5**	**16.5**	**18.5**	**20**	**20.5**	**22**	**32**	**32.5**	**40**	**41**	**42**	**44**	**44**	**50**
Herbs and semi shrubs																			
Amaranthaceae											3	2							
Artemisia		93	1		1	1		8	3	3	64	16	39	13	1	1		1	
Asteraceae		35	2	2		1	2	3		2	13	2	1	1	1			2	
Brassicaceae		1						4	2		2		3		1				
Caprifoliaceae subf. Valerianoideae													3						
Caryophyllaceae		165	12	1		2	2	101	1	3	59	15	20	9	1		1		
Cyperaceae		12	2	3	1	10	4	13	6	1	39	19	15	8	3	7			
Epilobium												6	6	1				1	
Ericales											1	51	173	24					
Polygonaceae														1					
Liliaceae												1	1						
Poaceae		13	1			2		5	1		7	2	1	2		1			
Ranunculaceae		1						17			7	2	3	3				1	
Rosaceae							1	1			2		2						
Saxifraga											6			1					
Thalictrum											5		1						

Table 4.3.1. (Continued)

	Dephts, m bgs																		
Plant taxa	**0.2**	**4.7**	**5.5**	**8.5**	**9.5**	**12.5**	**16.5**	**18.5**	**20**	**20.5**	**22**	**32**	**32.5**	**40**	**41**	**42**	**44**	**44**	**50**
Pollen sum		**320**	**19**	**7**	**2**	**25**	**11**	**171**	**17**	**11**	**235**	**276**	**298**	**75**	**7**	**11**	**2**	**5**	**0**
Pollen concentracions (grains/gram)	N/A	**9019**	N/A	N/A	N/A	N/A	N/A	**2394**	N/A	N/A	**6459**	**7447**	**11057**	N/A	N/A	N/A	N/A	N/A	N/A
Spores																			
Huperzia											1		1						
Lycopodium			5	1	1						2	1	2	1					
Polypodiophyta		1	3	1		3	1	3	7	2	8	1	1	1					
Selaginella rupestris	1		56	42		3	10		31	2	17	1	9	1					
Sporae redep.			1								3								
Non-pollen palynomorphs																			
Arcella																		3	
Stomata of *Pinus*													2					1	
Sordaria									11		4	5						1	
Glomus			34						22					3					130
Gelasinospora											1	1							
Mycrothyrium																		3	
Podospora												1							
Valsaria									4		3								
Zygnema											1								
Sphagnum				1		1		1					1						
Total sum		**321**	**118**	**52**	**3**	**32**	**22**	**175**	**92**	**15**	**275**	**286**	**314**	**81**	**7**	**11**	**2**	**13**	**130**

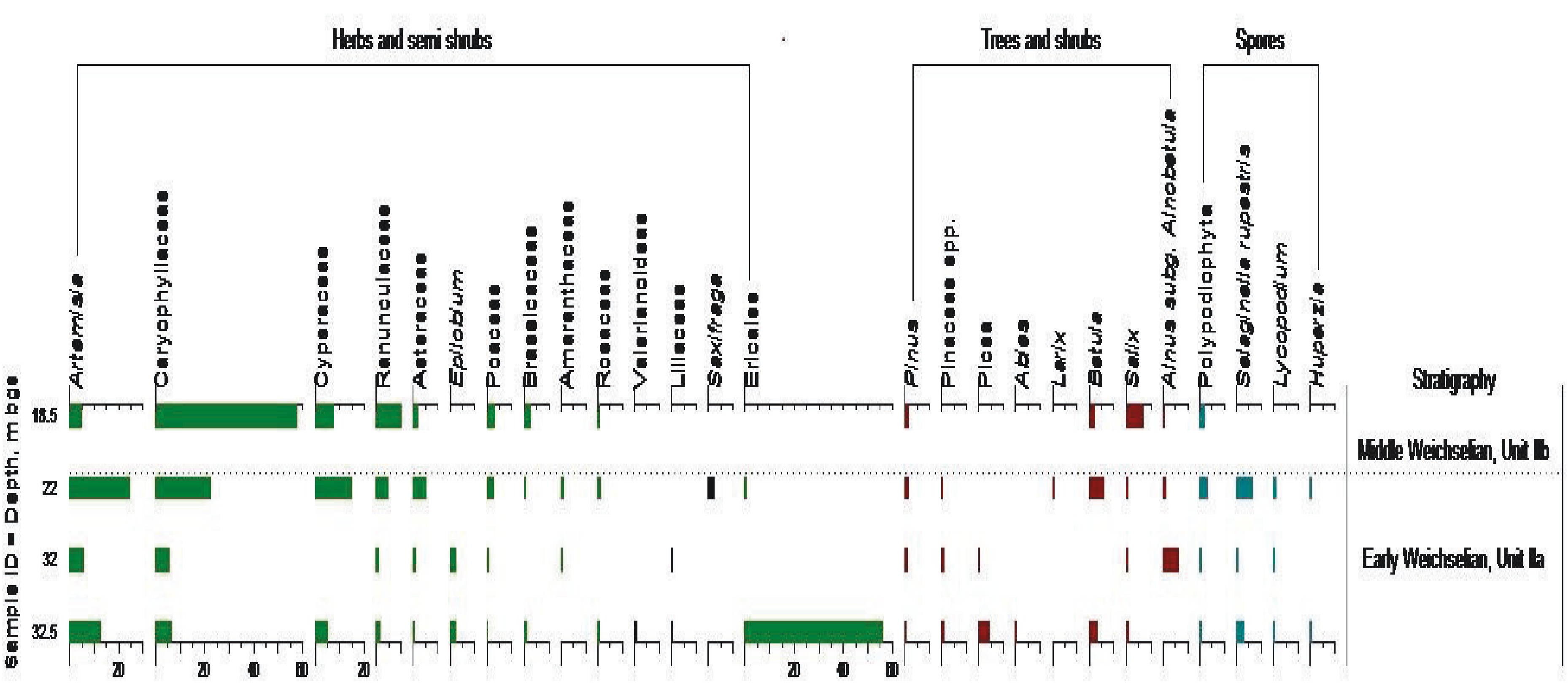

Figure 4.3.1. Pollen and spore diagram (%) illustrating four representative samples from Batagay outcrop (18.5, 22, 32, 32.5 m bgs).

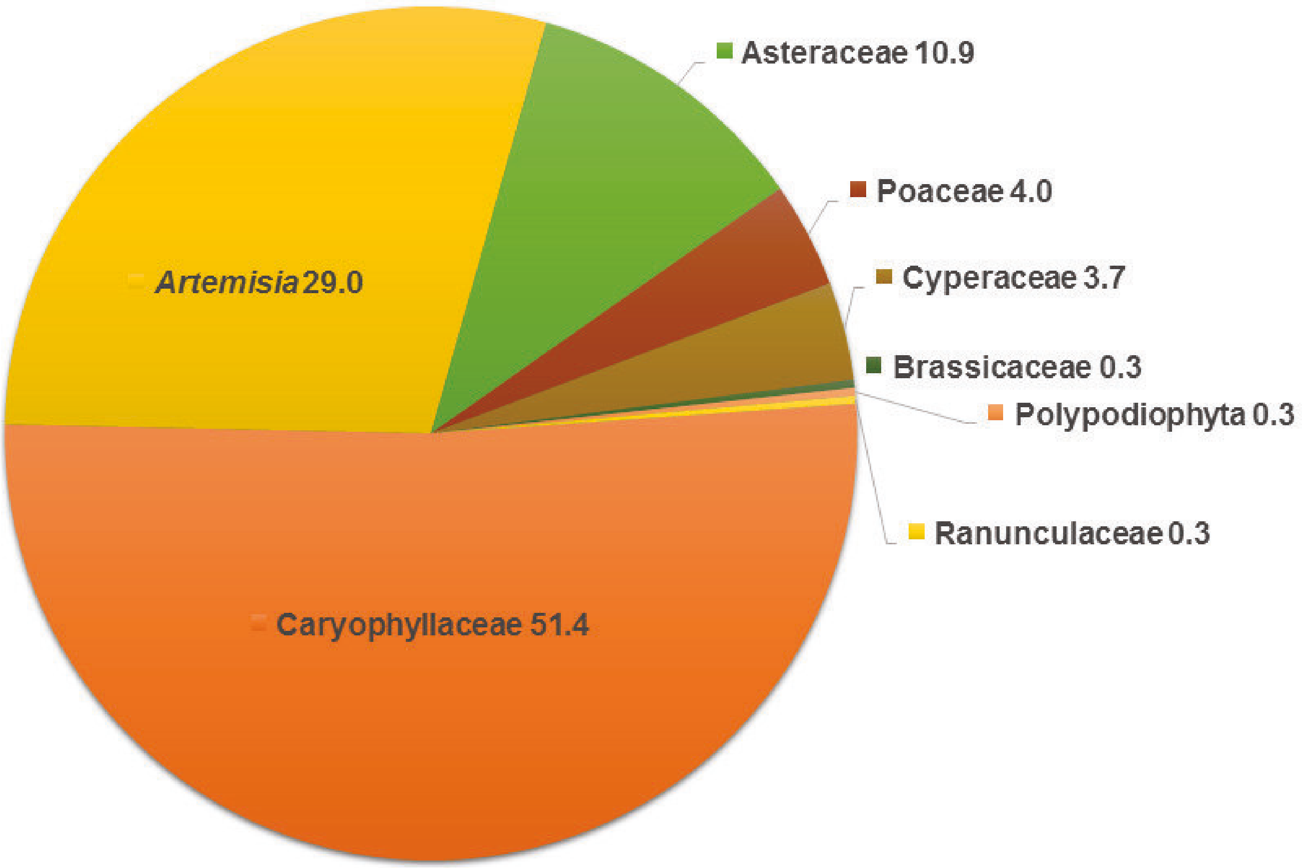

Figure 4.3.2. Pollen and spore diagram (%) illustrating palynological assemblage found in the ground squirrel nest (4.6 m bgs, 26,180±0,22 ^{14}C a BP).

Table 4.4 Abbreviations of species names used in the DCA plot.

Short	Species in modern vegetation	Species in palaeo-vegetation
AgroCri	*Agropyron cristatum*	*Agropyron cristatum*
AlysObo	*Alyssum obovatum*	*Alyssum obovatum*
ArteCom	*Artemisia commutata*	*Artemisia* sp.
ArteFri	*Artemisia frigida*	*Artemisia* sp.
BetuSpe	*Betula species*	*Betula species*
CareDur	*Carex duriuscula*	*Carex duriuscula*
ChenAlb	*Chenopodium album*	*Chenopodium sp.*
ChenSpe	*Chenopodium species*	*Chenopodium species*
EmpeNig	*Empetrum nigrum*	*Empetrum nigrum*
EquiSci	*Equisetum scirpoides*	*Equisetum scirpoides*
EremCap	*Eremogone capillaris*	*Eremogone capillaris*
ErigAce	*Erigeron acer*	*Erigeron acris*
ErigAcr	*Erigeron acris*	*Erigeron acris*
EritVil	*Eritrichium villosum*	*Eritrichium villosum*
FestLen	*Festuca lenensis*	*Festuca* sp.
KoelPyr	*Koeleria pyramidata*	*Koeleria* sp.
LariGme	*Larix gmelinii*	*Larix gmelinii*
LeduPal	*Ledum palustre*	*Ledum palustre*
LepiDen	*Lepidium densiflorum*	*Lepidium densiflorum*
MinuRub	*Minuartia rubella*	*Minuartia rubella*
MinuVer	*Minuartia verna*	*Minuartia verna*
MoehLat	*Moehringia lateriflora*	*Moehringia lateriflora*
MyosAsi	*Myosotis asiatica*	*Myosotis asiatica*
MyosSpe	*Myosotis species*	*Myosotis asiatica*
PapaAlp	*Papaver alpinum*	*Papaver Sect. Scapiflora*
PhloSib	*Phlox sibirica*	*Phlox sibirica*
PlanCan	*Plantago canescens*	*Plantago canescens*
PoaAtt	*Poa attenuata*	*Poa* sp.
PoaSib	*Poa sibirica*	*Poa* sp.
PoaSpe	*Poa species*	*Poa species*
PoteAre	*Potentilla arenosa*	*Potentilla arenosa*
PoteTol	*Potentilla tollii*	*Potentilla tollii*
PuccHau	*Puccinellia hauptiana*	*Puccinellia* sp.
RanuPed	*Ranunculus pedatifidus*	*Ranunculus pedatifidus* subsp. *affinis*
RosaAci	*Rosa acicularis*	*Rosa acicularis*
RubuIda	*Rubus idaeus*	*Rubus idaeus*
SelaSel	*Selaginella sellowii*	*Selaginella rupestris*
SileRep	*Silene repens*	*Silene repens*
SileSam	*Silene samojedorum*	*Silene samojedorum*
StelJac	*Stellaria jacutica*	*Stellaria jacutica*
TephInt	*Tephroseris integrifolia*	*Tephroseris integrifolia*
UrtiDio	*Urtica dioica*	*Urtica dioica*
VaccVit	*Vaccinium vitis-idaea*	*Vaccinium vitis-idaea*

A5 – Chapter 5

Appendix 5.1 – Details on study area and methods

Productivity of vegetation in our study regions (see Figure 5.1) ranges between 5 and 62 g/ (40x40 cm) (thus 3.1 to 38.8 g/ m² or 30-400 kg/ ha), with lowest values in the most continental Yana region. Productivity also depends much on habitat type, with meadows and wetlands being most productive and a wide range of productivity in steppes, depending on whether they belong to densely vegetated meadow steppes or sparsely vegetated typical steppes on steep slopes.

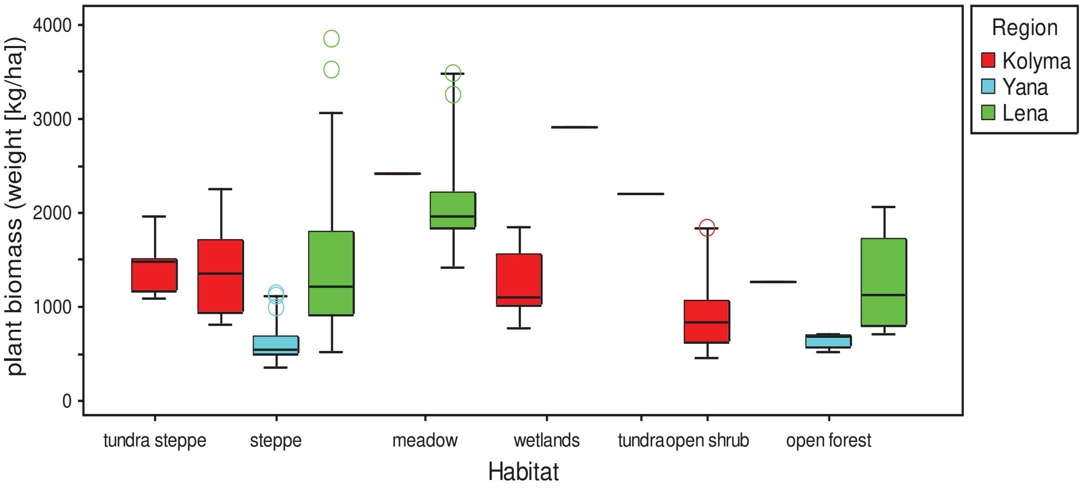

Figure 5.1. Productivity of vegetation across the study area; given as mean weight of harvested plant biomass extrapolated from subplot of 40x40 cm² per region and vegetation type.

We sampled a total of 210 vegetation plots sized 10m x 10m, across steppes and surrounding vegetation types (Table 5.1). Droppings, trails and resting places indicated regular use of study sites by grazers, but at least during our study period floodplain meadows seemed to be the preferred pastures in all regions. Scrub and forest were mostly used as resting places or were frequented during roaming between pastures, and had droppings along the way. Small clearings (from cutting, fire or tree fall) with higher herb cover were also occasionally grazed.

Table 5.1. Overview on the number of plots in each single study region per vegetation type.

	Steppe	**Meadow**	**Wetland**	**Tundra steppe**	**Tundra**	**Scrub**	**Forest**	**total**
Buotoma	10	16					7	33
Chersky	7		12			20	5	44
Verkhoyansk	41	2				2	15	60
Yakutsk	34	3					3	40
Pokhodsk			7	10	16			33
Total	92	21	19	10	16	22	30	**210**

We measured 21 grazing-related plant functional traits; (Table 5.2; following Cornelissen et al., 2003) for a subset of 92 steppe plots (Traitset 1 and 2; Table 5.3), and 13 traits for the overall set of plots (Traitset 1; Table 5.3), including other vegetation types. Traited species usually cover more than 80 % of the biomass of each plots (herb and dwarf shrub layer), except for 16 plots for which not 80 % but still the majority of species biomass was traited. We usually used the mean trait values of 5-10 individually measured plants. In order to complete and cross-check our list of traits for 217 species (92 steppe species, respectively) we added single measurements from BIOLFLOR (Kühn et al. 2004), TRY (Kattge and et al. 2011), GrassBase (Clayton et al. 2006), Flora of Siberia (Malyschev 2006), Flora of China (Brach and Song 2006), Flora of the Canadian Arctic Archipelago (Aiken et al. 2007) and Forage Plants of Mongolia (Jigjidsuren and Johnson 2003). In a few cases (<10), trait data was missing and we thus had to use nearest neighbor imputation to fill out single missing values.

Table 5.2. Functional traits and their attributes related to grazing with respective function and hypothesized mechanisms.

Trait	Attributes related to grazing	Function	Hypothesized mechanism	Reference
Above cover density (ACD)	High	Avoidance	Shoot attenuation as result of changing plant structure	McIntyre et al. 1999, Wesuls et al. 2012
Blade fragmentation	Compound	Tolerance	Lower loss of biomass per bite	Wesuls et al. 2012
Clonality	e.g. rhizomes	Tolerance	Regrowth capacity	Cornelissen et al. 2003
Defense mechanisms	Thornes, spines, hairiness, secondary compounds, leaf toughness	Avoidance	Deterrence of grazers	Cornelissen et al. 2003, Wesuls et al. 2012
Fraction belowground	High/ Low	Avoidance/ Tolerance	Re-allocation below-/ aboveground (depending on vegetation type)	Wesche et al. 2012
Growth form	Prostate, rosettes, stoloniferous	Avoidance	Buds for regrowth located close to the ground	Landsberg et al. 1999, Cornelissen et al. 2003, Díaz et al. 2007, Wesuls et al. 2012
Inflorescence height	Low (protected in foliage)	Avoidance	Spatial evasion of grazing from above	Landsberg et al. 1999
Leaf size	Small		Lower loss of biomass per bite	Landsberg et al. 1999, Díaz et al. 2001, Vesk et al. 2004
Life form	Therophytes; Chamaephytes	Avoidance	Temporal evasion of grazing and use of establishment opportunities; unpalatability	Cornelissen et al. 2003
Longevity	Annual	Avoidance	Temporal evasion of grazing; use of establishment opportunities	Díaz et al. 2001, 2007, Vesk et al. 2004
Plant type	Herbs; (Shrubs)	Avoidance	Lower palatability than grasses	Vesk et al. 2004, Díaz et al. 2007, Wesuls et al. 2012
Resprouting capacity	Low meristems, belowground storage organs	Tolerance	Regrowth capacity	Landsberg et al. 1999, Cornelissen et al. 2003
Root type	Tap root	Avoidance	Resistance to trampling	Landsberg et al. 1999
Seed mass	Small	Avoidance	High establishment potential	Vesk et al. 2004
Seed productivity	Many	Avoidance	High establishment potential	Vesk et al. 2004
Shoot diameter	Large (for woody shoots)	Tolerance	Re-allocation to side instead of high growth	Gill 2006
Shoot height	Short	Avoidance	Spatial evasion of grazing from above	Landsberg et al. 1999, Díaz et al. 2001, 2007, Cornelissen et al. 2003
SLA	High/ Low	Tolerance/ Avoidance	Fast regrowth resulting in tender leaves/ lower palatability due to leaf toughness	Díaz et al. 2001, Vesk et al. 2004, Wesuls et al. 2012
Stem/ Leaf ratio	Stemmy	Avoidance	Low palatability	Landsberg et al. 1999, Wesuls et al. 2012

Table 5.3. Overview on plant functional traits measured.

		TRAITSET 1	
abbreviation	**type**	**trait**	**value**
	Qual.	**plant type**	herb; grass; dwarfshrub
Long	**Qual.**	**Longevity**	annual; perennial
LF	**Qual.**	**life form**	hemikryptophyte; chamaephyte; phanerophyte; therophyte; other
Grow	**Qual.**	**growth form**	erect leafy; short basal; rosette; long basal; cushion; tussock; dwarf shrub; semi-basal ; tree; succulent; hemiparasites
St/L	**Qual.**	**stem/ leaf ratio**	stemmy; moderately leafy; leafy
Leaf	**Qual.**	**blade fragmentation**	broad & entire; broad & compound; long & flat; long & closed
Clon	**Qual.**	**Clonality**	none; aboveground; belowground; aboveground & belowground
Rhizome	**Qual.**	**Rhizome**	yes; no
D	**Qual.**	**Defenses**	none; thorny/ spiky; tomentous; chemical; leathery; other
Root	**Qual.**	**root type**	taproot; several main roots
ShootHeight	**Quant.**	**shoot height**	[cm]
LeafLength	**Quant.**	**leaf length**	[cm]
LeafWidth	**Quant.**	**leaf width**	[cm]
LeafRatio	**Quant.**	**leaf ratio**	[cm]
		TRAITSET 2	
	type	**trait**	**Value**
	Quant.	**Fraction belowground**	[%]
	Quant.	**Infloresence height**	[cm]
	Quant.	**Relative Infloresence**	[cm]
	Quant.	**Shoot diameter**	[cm]
	Quant.	**ACD**	[%]
	Quant.	**SLA**	[mm²/mg]
	Quant.	**Root length**	[cm]
	Qual.	**Seed productivity**	few; several; many; abundant

We collected biomass and soil samples from each vegetation plot. In grassland habitats (meadow, steppe, tundra steppe) three subplots with a size of 40 x 40 cm² were randomly selected across the vegetated area of each plot to account for spatial variability. We took one soil and one plant biomass sample per subplot in these habitats. In forest, scrub and tundra habitats, only one soil sample and no biomass samples were taken per plot. Aboveground biomass of each subplot was cut approximately 1 cm above ground using scissors, excluding dead standing biomass, and then air dried. We sampled the topsoil below the litter layer using a 100 cm^3 core cutter.

Slope inclination was estimated in the field as percent inclination. Slope aspect (N, NE, E, SE, S, SW, W, NW) was measured in the field, using a Garmin GPS (Garmin GPSMAP 64s) by walking straight downhill for a few meters until the direction was reliably given. In addition, we checked google earth maps of the location for correctness. We then derived northernness and easternness from aspect in degrees (360°; with 0°=N, 90°=E) by taking the cosine (northerness) and sine (easterness), thus transforming the degrees to a value between -1 and 1.

Heat load was calculated according to McCune (2007). This variable estimates temperatures on a land surface, based on the amount of potential direct incident radiation (DIR), which depends on latitude, slope aspect and slope inclination, while taking into account the time of the day that surface is subjected to this radiation.

The intensity of grazing by each grazing animal (bison, horse, cattle, small mammals) was based on the density of droppings (in %). Small mammals were mostly represented by ground squirrels (*Urocitellus parryii*). Droppings are considered part of a grazing effect (fertilization), apart from the actual intake of plant biomass. Other proxies, which have proven useful in other studies, for example in Mongolia and Tibet, like distance to town or water well, did not work in our setting, as livestock was not bound to settlements (except cattle to some degree). We also estimated approximate intensity of grazing in the field, but the simple index (high, medium, low) we developed from this information did also not prove useful. Instead, dung density was crucially evaluated already in the field and found to be the best approximation for grazing intensity, even when considering animal movement. Other studies have also shown that dung density is a useful indicator (e.g. Wang et al. 2018).

Macroclimatic variables (Bio 1/ 7/ 10/ 12/ 15/ 18/ 19) were extracted from WorldClim (Hijmans et al. 2005). Annual Mean Temperature (Bio 1) and Annual Mean Precipitation (Bio 12) give basic information on climate; Mean Temperature of Warmest Quarter (Bio 10) and Precipitation of Warmest Quarter (Bio 18) give information on vegetation-relevant summer conditions; and Temperature Annual Range (Bio 7) and Precipitation Seasonality (Bio 15) give information on seasonal differences in climate, thus its continentality. We used GPS coordinates of plots to extract the spatially explicit climate data from the WorldClim model.

Soil samples were initially dried in the lab for 48 hours at 40°C. Samples were then sieved using a 2 mm coarse screen, using the fine material for further analysis. We measured pH (H_2O) and electric conductivity (EC) after 1h and 24 h. We measured the C/N ratio through combustion in a CN analyzer (Vario Elementar). To assess the amount of plant available nutrients (Ca, Mg, K, P) we prepared soil extractions following the Olsen P method (Sims 2000). Nutrient contents in these extractions were measured by spectrometry (ICP-OES, Institute of Soil Science, Hannover University). Rest water was measured after drying of samples at 105°C for 24h. The carbonate content was first assessed with a quick test using 10% HCl, and samples showing a reaction were further analyzed using a calcimeter following Scheibler's method (ON L 1084-99, 1999). Rest water content was used to calibrate nutrient contents per g soil and carbonate content to correct C/N measurements.

Plant biomass was cut into pieces of 1-3 cm length using ceramic scissors and then separated about 2 (1-3; depending on amount of plant material) times using a dividing cross. A mixed sample of the biomass was then finely ground (Leuphana University of Lüneburg; Umweltanalytisches Labor, IHI Zittau, University of Dresden). C/N-ratio was analyzed using the same procedure like the soil samples. For nutrient content we decomposed the ground plant material, using microwave decomposition (samples of 2014; Umweltanalytisches Labor, IHI Zittau, University of Dresden) and pressure decomposition (samples of 2015; Lab of the Botany Department, Senckenberg Görlitz). The decomposed biomass solution was then also analyzed by spectrometry (ICP-OES, again Hannover). The measurements of the microwave decomposition were finally converted to be comparable to measurements of pressure decomposition using linear regressions.

Appendix 5.2 – Supplementary information on results

Table 5.3. Results of variation partitioning of biomass data.

		Overall		Steppes only	
Ordination method	**Environmental variable**	**variance**	**% explained**	**variance**	**% explained**
Variation Partitioning (pCCAs, Unique effects)					
	- Soil	0.19	18.7	0.10	10.0
	- Macroclimate	0.18	17.7	0.10	9.7
Variation Partitioning (pCCAs, Unique effects)					
	- Soil	0.12	12.1	0.10	10.3
	- Macroclimate	0.16	16.3	0.10	10.4
	- Microclimate	0.02	1.8	0.01	1.4
Variation Partitioning (pCCAs, Unique effects)					
	- Soil	0.15	15.5	0.11	10.7
	- Macroclimate	0.18	18.2	0.09	8.7
	- Grazing	0.02	1.6	0.01	1.3

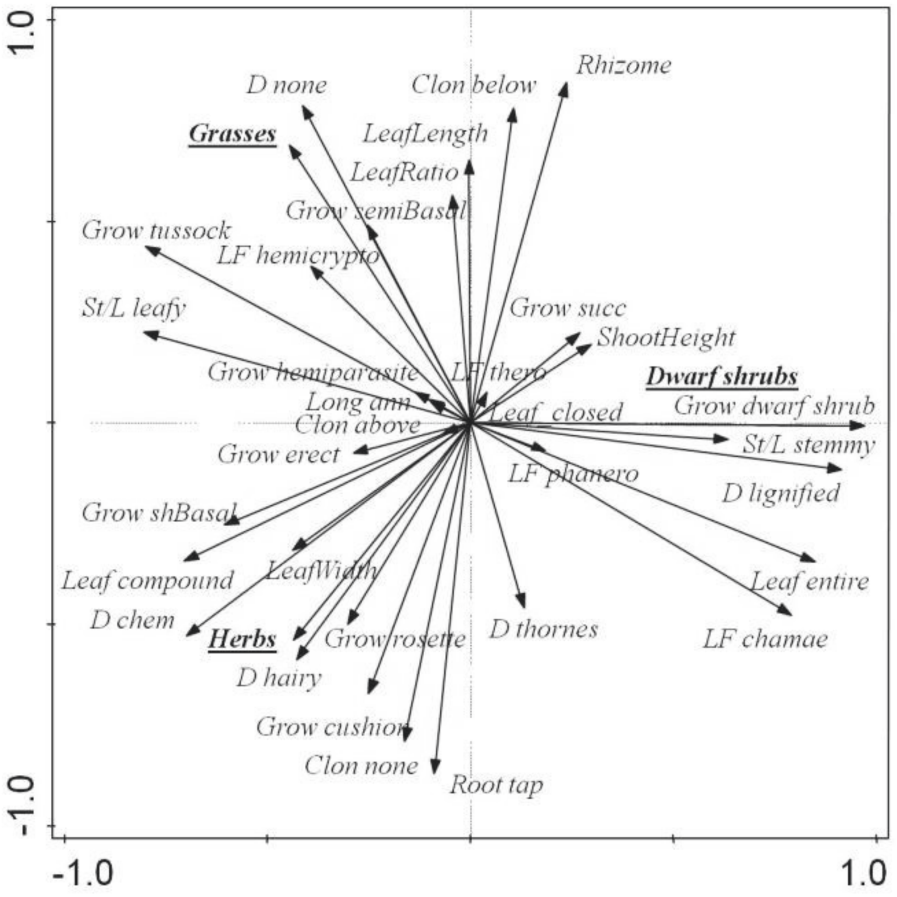

Figure 5.1. PCA of community weighted means of plant traits, which cluster around life forms dwarf shrubs, grasses and herbs (Eigenvalues: Axis1: 0.25, Axis2: 0.19).

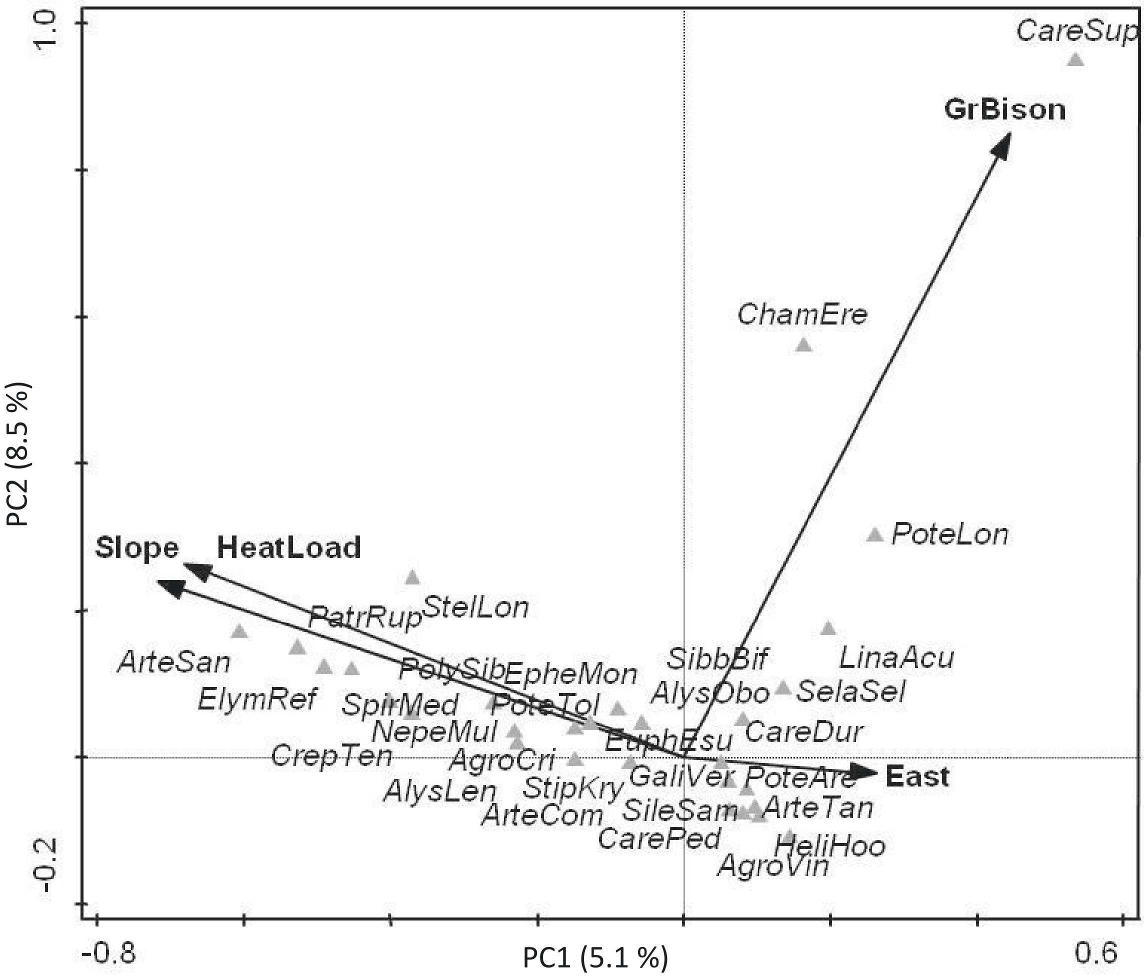

Figure 5.2. pCCa with macroclimate as co-variable and significant microclimate (slope inclination - Slope; heat load - HeatLoad; easternness - East) and grazing variables (bison - GrBison; forward selection, 499 permutations) for only steppe plots; total inertia: 3.8, Eigenvalues: Axis1: 0.20, Axis2: 0.13; %explained variance: Axis1: 5.13, Axis2: 3.32; only most abundant species used and 40 best fitted species shown; species square root-transformed

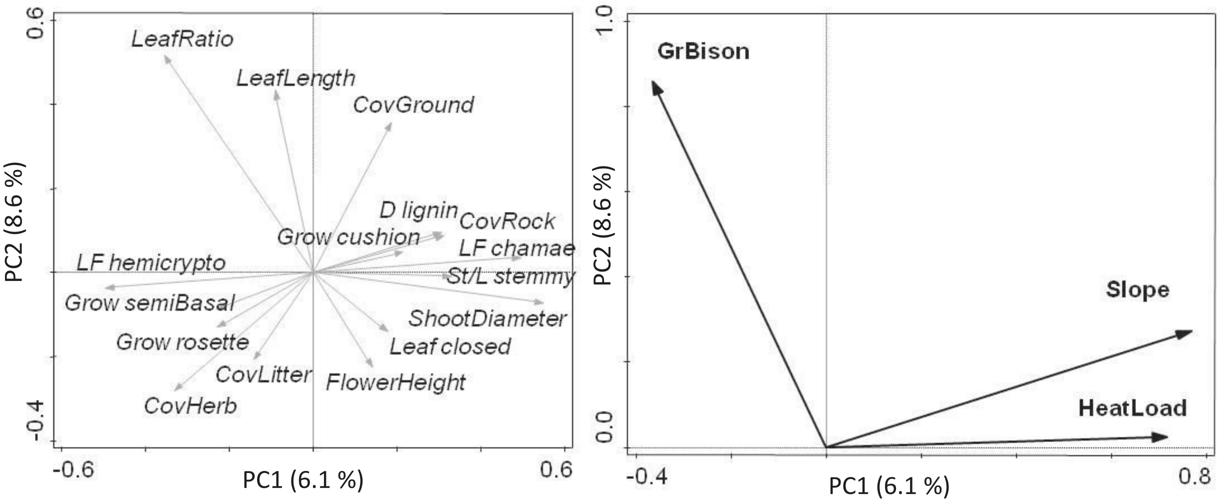

Figure 5.3. CWM-RDA (forward selection, 499 permutations) of steppe data set; total variance: 3843, explained variance: 10.0 %; Eigenvalues: Axis1: 0.05, Axis2: 0.02; %explained variance: Axis1: 6.10, Axis2: 2.47; a) CWMs (only 50 % most sig. traits, which are also confirmed by direct univariate correlation of CWMs with environmental variables, are shown), b) sig. microclimate (slope inclination (Slope); heat load (HeatLoad)) and grazing variables (bison (GrBison)).

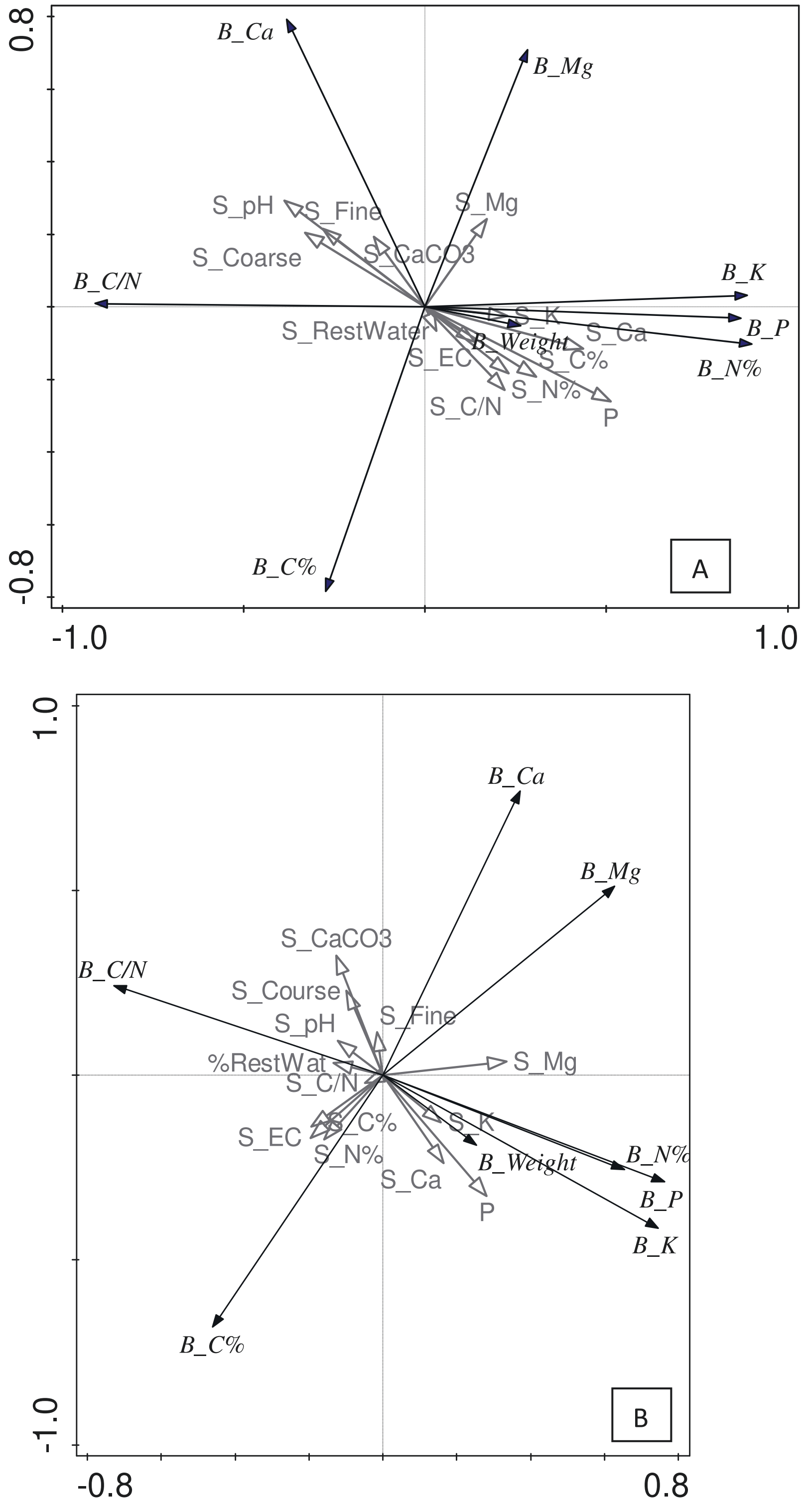

Figure 5.4. Correlation-matrix PCA of biomass variables (centered and standardized) with post hoc fitted soil variables for a) overall data; total variance: 1200, explained variance: 40.7 %, Eigenvalues: Axis1: 0.44, Axis2: 0.22; and b) for steppes; total variance: 720, explained variance: 37.5 %, Eigenvalues: Axis1: 0.36, Axis2: 0.22. See Table 1 for abbreviations.

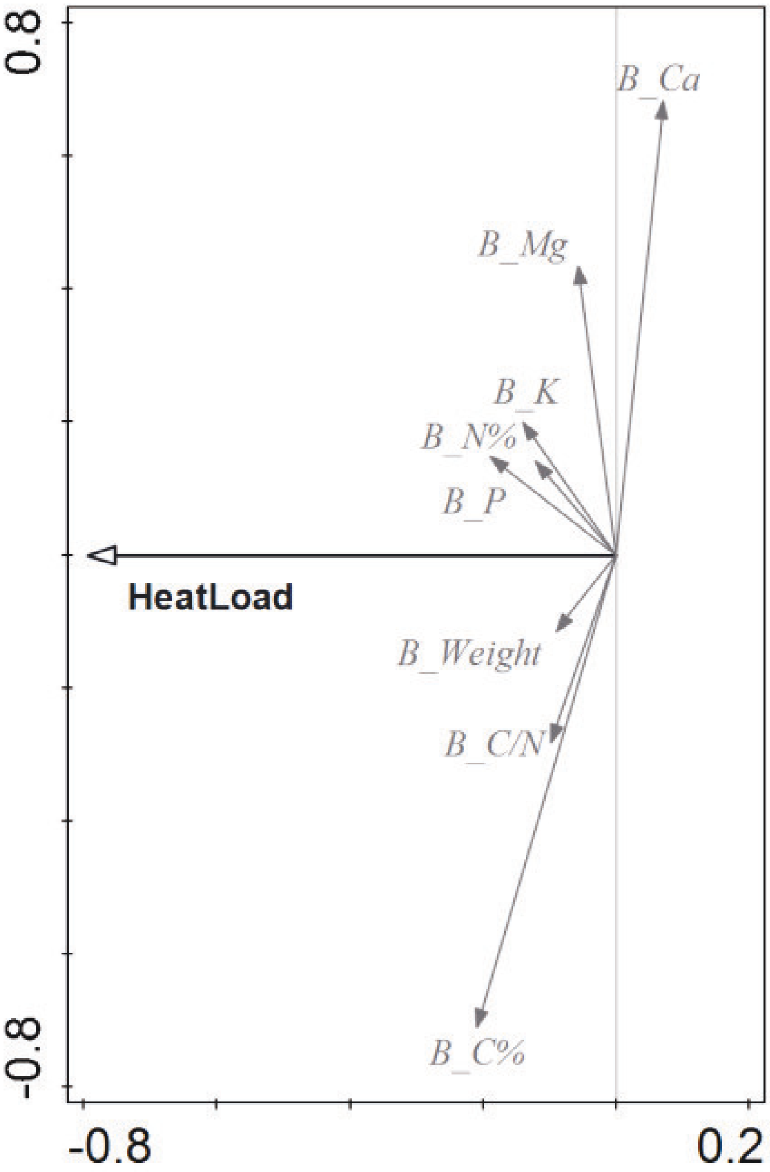

Figure 5.5. Biomass-RDA (forward selection, 499 permutations) of steppe data set, total variance: 417, explained variance: 3.0 %, Eigenvalues: Axis1: 0.02, Axis2: 0.02; %explained variance: Axis1: 3.01, Axis2: 28.78; only sig. microclimate (HeatLoad = heat load) is shown. See Table 1 for abbreviations.

IV. List of Abbreviations

Table 1. List of general abbreviations.

Abbreviation	Meaning
BP	Years before present
(p)CCA	(Partial) canonicalcorrespondence analyis
CH	Chapter
CWM	Community weighted means
DCA	Detrended Correspondence Analysis
DM	Dry matter
DNA	Deoxyribonucleic acid
FU	Fodder unit
IBA	Important Bird Area
IUCN	International Union for Conservation of Nature
LGM	Last glacial maximum
MIS	Marine isotope stages
Mt	Megaton (= 1 million tons)
NGO	Non-governmental organization
PA	Protected Area
PCA	Principal components analysis
(p)RDA	(Partial) redundancy analysis

Table 2. List of abbreviations for plant species names.

Abbreviation	Species
AchiAsi	*Achillea asiatica*
AconBar	*Aconitum barbatum*
AconSpe	*Aconitum species*
ActaRub	*Actaea rubra*
AdenSpe	*Adenophora species*
AgroCla	*Agrostis clavata*
AgroCri	*Agropyron cristatum*
AgroGig	*Agrostis gigantea*
AgroSpe	*Agrostis species*
AgroSto	*Agrostis stolonifera*
AgroVin	*Agrostis vinealis*
AlisPla	*Alisma plantago-aquatica*
AlliRam	*Allium ramosum*
AlliSpe	*Allium species*
AlliSpl	*Allium splendens*
AlopAlp	*Alopecurus alpinus*
AlopAru	*Alopecurus arundinaceus*
AlopMag	*Alopecurus magellanicus*
AlopPra	*Alopecurus pratensis*
AlysLen	*Alyssum lenense*
AlysObo	*Alyssum obovatum*
AndrMax	*Androsace maxima*
AndrPol	*Andromeda polifolia*
AndrSep	*Androsace septentrionalis*
AnemDic	*Anemonidium dichotomum*
AnemFla	*Anemone flavescens*
AnemPat	*Anemone patens*
AnemSyl	*Anemone sylvestris*
AnteFri	*Antennaria friesiana*
AquiPar	*Aquilegia parviflora*
ArabSpe	*Arabis species*
ArctAlp	*Arctous alpina*
ArctAru	*Arctagrostis arundinacea*
ArctLat	*Arctagrostis latifolia*
ArctSpe	*Arctagrostis species*
ArctUva	*Arctostaphylos uva-ursi*
ArmeMar	*Armeria maritima*
ArniAng	*Arnica angustifolia*
ArteArc	*Artemisia arctica*
ArteCam	*Artemisia campestris*
ArteCom	*Artemisia commutata*
ArteDra	*Artemisia dracunculus*
ArteFri	*Artemisia frigida*
ArteJac	*Artemisia jacutica*
ArteLac	*Artemisia laciniata*
ArteMac	*Artemisia macrantha*
ArteSan	*Artemisia santolinifolia*
ArteSpe	*Artemisia species*
ArteTan	*Artemisia tanacetifolia*
ArteVul	*Artemisia vulgaris*
AsteAlp	*Aster alpinus*
AstrAlp	*Astragalus alpinus*
AstrAng	*Astragalus angarensis*
AstrDan	*Astragalus danicus*
AstrFru	*Astragalus fruticosus*
AstrIno	*Astragalus inopinatus*
AstrSpe	*Astragalus species*
AstrTug	*Astragalus tugarinovii*
BarbStr	*Barbarea stricta*
BeckEru	*Beckmannia eruciformis*
BeckSyz	*Beckmannia syzigachne*
BotrLun	*Botrychium lunaria*
BromPum	*Bromus pumpellianus*
BromSpe	*Bromopsis species*
BuplBic	*Bupleurum bicaule*
CalaAru	*Calamagrostis arundinacea*
CalaHol	*Calamagrostis holmii*
CalaPur	*Calamagrostis purpurascens*
CalaPup	*Calamagrostis purpurea*
CalaSpe	*Calamagrostis species*
CalaStr	*Calamagrostis stricta*
CaltPal	*Caltha palustris*
CampGlo	*Campanula glomerata*
CampPun	*Campanula punctata*
CampRot	*Campanula rotundifolia*
CampSpe	*Campanula species*
CampSte	*Campanula stevenii*
CareAcu	*Carex acuta*
CareAqu	*Carex aquatilis*
CareBig	*Carex bigelowii*
CareCap	*Carex capillaris*
CareCes	*Carex cespitosa*
CareCho	*Carex chordorrhiza*
CareDis	*Carex disticha*
CareDur	*Carex duriuscula*
CareEne	*Carex enervis*
CareMel	*Carex melanocarpa*
CareNig	*Carex nigra*
CareObt	*Carex obtusata*
CarePed	*Carex pediformis*
CarePra	*Carex praecox*
CareRar	*Carex rariflora*
CareRos	*Carex rostrata*
CareRot	*Carex rotundata*
CareRup	*Carex rupestris*
CareSpe	*Carex species*
CareSup	*Carex supina*
CareVag	*Carex vaginata*
CareVan	*Carex van-heurckii*
CareWil	*Carex williamsii*
CassTet	*Cassiope tetragona*
CastPal	*Castilleja pallida*
CastPse	*Castilleja pseudohyperborea*
CastRub	*Castilleja rubra*
CatoPen	*Catolobus pendulus*
CeraArv	*Cerastium arvense*
CeraMax	*Cerastium maximum*
ChamCal	*Chamaedaphne calyculata*
ChamEre	*Chamaerhodos erecta*
ChenAlb	*Chenopodium album*
ChenSpe	*Chenopodium species*
ClauApr	*Clausia aprica*

Table 2. (Continued)

Abbreviation	Species
ClayAcu	*Claytonia acutifolia*
ClemAlp	*Clematis alpina*
CnidCni	*Cnidium cnidiifolium*
ComaPal	*Comarum palustre*
CoptLap	*Coptidium lapponicum*
CorySib	*Corydalis sibirica*
CorySpe	*Corydalis species*
CrepGme	*Crepis gmelinii*
CrepTen	*Crepidifolium tenuifolium*
CrucBur	*Crucihimalaya bursifolia*
CrucMol	*Crucihimalaya mollissima*
DelpChe	*Delphinium cheilanthum*
DelpCra	*Delphinium crassifolium*
DianChi	*Dianthus chinensis*
DianRep	*Dianthus repens*
DiapLap	*Diapensia lapponica*
DrabCin	*Draba cinerea*
DrabEsc	*Draba eschscholtzii*
DrabHir	*Draba hirta*
DrabNem	*Draba nemorosa*
DrabNiv	*Draba nivalis*
DrabSpe	*Draba species*
DrabSub	*Draba subamplexicaulis*
DracPal	*Dracocephalum palmatum*
DracSpe	*Dracocephalum species*
DryaOct	*Dryas octopetala*
EleoPal	*Eleocharis palustris*
ElymLan	*Elymus lanceolatus*
ElymMac	*Elymus macrourus*
ElymMut	*Elymus mutabilis*
ElymRef	*Elymus reflexiaristatus*
ElymRep	*Elymus repens*
EmpeNig	*Empetrum nigrum*
EpheMon	*Ephedra monosperma*
EpilAng	*Epilobium angustifolium*
EpilPal	*Epilobium palustre*
EquiFlu	*Equisetum fluviatile*
EquiPra	*Equisetum pratense*
EquiSci	*Equisetum scirpoides*
EremCap	*Eremogone capillaris*
EremTsc	*Eremogone tschuktschorum*
ErigAce	*Erigeron acer*
ErigAcr	*Erigeron acris*
ErigSpe	*Erigeron species*
ErioAng	*Eriophorum angustifolium*
ErioSch	*Eriophorum scheuchzeri*
ErioVag	*Eriophorum vaginatum*
EritCae	*Eritrichium caespitosum*
EritKar	*Eritrichium karavaevii*
EritVil	*Eritrichium villosum*
ErysChe	*Erysimum cheiranthoides*
ErysOdo	*Erysimum odoratum*
ErysSpe	*Erysimum species*
EuphEsu	*Euphorbia esula*
EuphHyp	*Euphrasia hyperborea*
FallCon	*Fallopia convolvulus*

Abbreviation	Species
FestBra	*Festuca brachyphylla*
FestJac	*Festuca jacutica*
FestKol	*Festuca kolymensis*
FestLen	*Festuca lenensis*
FestRub	*Festuca rubra*
FestSpe	*Festuca species*
FragOri	*Fragaria orientalis*
GageSer	*Gagea serotina*
GalaDah	*Galatella dahurica*
GaliBor	*Galium boreale*
GaliTri	*Galium trifidum*
GaliVer	*Galium verum*
GentAma	*Gentianella amarella*
GentBar	*Gentianopsis barbata*
GentDec	*Gentiana decumbens*
GeraPra	*Geranium pratense*
GeraPse	*Geranium pseudosibiricum*
GeumAle	*Geum aleppicum*
GlycAru	*Glyceria arundinacea*
GoniSpe	*Goniolimon speciosum*
HedyAlp	*Hedysarum alpinum*
HedyDas	*Hedysarum dasycarpum*
HedyVic	*Hedysarum vicioides*
HeliHoo	*Helictotrichon hookeri*
HeliKry	*Helictotrichon krylovii*
HeteBie	*Heteropappus biennis*
HeteSpe	*Heteropappus species*
HierAlp	*Hierochloe alpina*
HierGla	*Hierochloe glabra*
HierOdo	*Hierochloe odorata*
HierSpe	*Hieracium species*
HierSp	*Hierochloe species*
HordBre	*Hordeum brevisubulatum*
InulBri	*Inula britannica*
IrisSet	*Iris setosa*
JacoVul	*Jacobaea vulgaris*
JuncPer	*Juncus persicus*
KobrMyo	*Kobresia myosuroides*
KoelAsi	*Koeleria asiatica*
KoelPyr	*Koeleria pyramidata*
LactSib	*Lactuca sibirica*
LappSpe	*Lappula species*
LappSqu	*Lappula squarrosa*
LathHum	*Lathyrus humilis*
LathPal	*Lathyrus palustris*
leduPal	*Ledum palustre*
LeonOch	*Leontopodium ochroleucum*
LeonQui	*Leonurus quinquelobatus*
LepiDen	*Lepidium densiflorum*
LeptFum	*Leptopyrum fumarioides*
LinaAcu	*Linaria acutiloba*
LinaSpe	*Linaria species*
LinaVul	*Linaria vulgaris*
LinnBor	*Linnaea borealis*
LinuKom	*Linum komarovii*
LinuPer	*Linum perenne*

Table 2. (Continued)

Abbreviation	Species
LithMul	*Lithosciadium multicaule*
LuzuCon	*Luzula confusa*
LuzuNiv	*Luzula nivalis*
LuzuRuf	*Luzula rufescens*
LuzuSpe	*Luzula species*
MediFal	*Medicago falcata*
MenyTri	*Menyanthes trifoliata*
MinuBif	*Minuartia biflora*
MinuRub	*Minuartia rubella*
MinuStr	*Minuartia stricta*
MinuVer	*Minuartia verna*
MoehLat	*Moehringia lateriflora*
MyosAlp	*Myosotis alpestris*
MyosAsi	*Myosotis asiatica*
MyosSco	*Myosotis scorpioides*
MyosSpe	*Myosotis species*
NepeMul	*Nepeta multifida*
NoneRos	*Nonea rossica*
OnobAre	*Onobrychis arenaria*
OrobCoe	*Orobanche coerulescens*
OrosSpi	*Orostachys spinosa*
OrthSec	*Orthilia secunda*
OxytCzu	*Oxytropis czukotica*
OxytSpe	*Oxytropis species*
PapaAlp	*Papaver alpinum*
PatrRup	*Patrinia rupestris*
PatrSib	*Patrinia sibirica*
PediHir	*Pedicularis hirsuta*
PediLab	*Pedicularis labradorica*
PediLap	*Pedicularis lapponica*
PediPal	*Pedicularis palustris*
PediRub	*Pedicularis rubens*
PediSpe	*Pedicularis species*
PediSud	*Pedicularis sudetica*
PersAmp	*Persicaria amphibia*
PersSpe	*Persicaria species*
PersViv	*Persicaria vivipara*
PetaFri	*Petasites frigidus*
PeucBai	*Peucedanum baicalense*
PhedMid	*Phedimus middendorffianus*
PhloSib	*Phlox sibirica*
PhloTub	*Phlomoides tuberosa*
PhloVil	*Phlojodicarpus villosus*
PlanCan	*Plantago canescens*
PlanDep	*Plantago depressa*
PlanMaj	*Plantago major*
PlanMed	*Plantago media*
PlanSpe	*Plantago species*
PoaAlp	*Poa alpigena*
PoaAng	*Poa angustifolia*
PoaAtt	*Poa attenuata*
PoaPra	*Poa pratensis*
PoaSib	*Poa sibirica*
PoaSpe	*Poa species*
PoaTol	*Poa tolmatchewii*
PoaVer	*Poa versicolor*

Abbreviation	Species
PoleBor	*Polemonium boreale*
PolyAng	*Polygonum angustifolium*
PolyAre	*Polygonum arenastrum*
PolyOch	*Polygonum ochreatum*
PolyPat	*Polygonum patulum*
PolySib	*Polygala sibirica*
PolySpe	*Polygala species*
PolyTri	*Polygonum tripterocarpum*
PoteAns	*Potentilla anserina*
PoteAre	*Potentilla arenosa*
PoteCon	*Potentilla conferta*
PoteCra	*Potentilla crantzii*
PoteHyp	*Potentilla hypoleuca*
PoteLon	*Potentilla longifolia*
PoteNor	*Potentilla norvegica*
PoteSan	*Potentilla sanguisorba*
PoteSti	*Potentilla stipularis*
PoteTan	*Potentilla tanacetifolia*
PoteTol	*Potentilla tollii*
PsatJun	*Psathyrostachys juncea*
PuccBor	*Puccinellia borealis*
PuccHau	*Puccinellia hauptiana*
PuccNut	*Puccinellia nuttalliana*
PyroAsa	*Pyrola asarifolia*
PyroMin	*Pyrola minor*
PyroRot	*Pyrola rotundifolia*
PyroSpe	*Pyrola species*
RanuAcr	*Ranunculus acris*
RanuBor	*Ranunculus borealis*
RanuGra	*Ranunculus grandis*
RanuPed	*Ranunculus pedatifidus*
RanuPet	*Ranunculus petroczenkoi*
RanuRep	*Ranunculus repens*
RanuSpe	*Ranunculus species*
RhinSer	*Rhinanthus serotinus*
RibeTri	*Ribes triste*
RosaAci	*Rosa acicularis*
RubuArc	*Rubus arcticus*
RubuCha	*Rubus chamaemorus*
RubuIda	*Rubus idaeus*
RumeAce	*Rumex acetosella*
RumeAqu	*Rumex aquaticus*
RumeGme	*Rumex gmelinii*
RumeGra	*Rumex graminifolius*
RumeSpe	*Rumex species*
RumeThy	*Rumex thyrsiflorus*
SangOff	*Sanguisorba officinalis*
SausAlp	*Saussurea alpina*
SausAma	*Saussurea amara*
SausSpe	*Saussurea species*
SaxiBro	*Saxifraga bronchialis*
SaxiHie	*Saxifraga hieraciifolia*
SaxiPun	*Saxifraga punctata*
SaxiSib	*Saxifraga sibirica*
ScholLac	*Schoenoplectus lacustris*
ScolFes	*Scolochloa festucacea*

Table 2. (Continued)

Abbreviation	Species
ScorAus	*Scorzonera austriaca*
ScorRad	*Scorzonera radiata*
ScorSpe	*Scorzonera species*
ScutSco	*Scutellaria scordiifolia*
SelaSel	*Selaginella sellowii*
SeneDub	*Senecio dubitabilis*
SeneEru	*Senecio erucifolius*
SeneSpe	*Senecio species*
SeneSub	*Senecio subdentatus*
SerrMar	*Serratula marginata*
SibbBif	*Sibbaldianthe bifurca*
SileCha	*Silene chamarensis*
SileGra	*Silene graminifolia*
SileJen	*Silene jeniseensis*
SileLat	*Silene latifolia*
SileRep	*Silene repens*
SileSam	*Silene samojedorum*
SileSpe	*Silene species*
SisyPol	*Sisymbrium polymorphum*
SiumSua	*Sium suave*
SpirMed	*Spiraea media*
StelJac	*Stellaria jacutica*
StelLon	*Stellaria longipes*
StelSpe	*Stellaria species*
StipKry	*Stipa krylovii*
TanaVul	*Tanacetum vulgare*
TaraCer	*Taraxacum ceratophorum*
TaraLat	*Taraxacum lateritium*
TaraSpe	*Taraxacum species*
TephInt	*Tephroseris integrifolia*
TephKir	*Tephroseris kirilowii*
ThalBai	*Thalictrum baikalense*
ThalFoe	*Thalictrum foetidum*
ThalMin	*Thalictrum minus*
ThalSim	*Thalictrum simplex*
ThesRef	*Thesium refractum*
ThymDiv	*Thymus diversifolius*
ThymInd	*Thymus indigirkensis*
ThymOch	*Thymus ochotensis*
ThymRev	*Thymus reverdattoanus*
ThymSpe	*Thymus species*
TrifLup	*Trifolium lupinaster*
TrifRep	*Trifolium repens*
TrigPal	*Triglochin palustris*
TrisSpi	*Trisetum spicatum*
UnknGra	*unknown grass*
UnknSpe	*unknown species*
UrtiDio	*Urtica dioica*
UtriVul	*Utricularia vulgaris*
VaccUli	*Vaccinium uliginosum*
VaccVit	*Vaccinium vitis-idaea*
ValeCap	*Valeriana capitata*
ValeOff	*Valeriana officinalis*
VeroLon	*Veronica longifolia*
VeroSpi	*Veronica spicata*
ViciCra	*Vicia cracca*
ViciMac	*Vicia macrantha*
ViciMul	*Vicia multicaulis*
ViciSpe	*Vicia species*
ViolMau	*Viola mauritii*

Table 3. List of abbreviations for environmental variables.

Abbreviation	Environmental variable
Annu	annual
Conti	continentality
DIR	direct incident radiation
East	easterness
GrBison	intensity of bison grazing
GrHorse	intensity of horse grazing
GrSmall	intensity of small mammal grazing
HeatLoad	heat load
North	northerness
Prec	precipitation
Sais	seasonality
Slope	slope inclination [°]
Summ	summer
Temp	temperature
Wint	winter

Table 4. List of abbreviations for plant traits.

Abbreviation	Trait
Type	plant type
Long	longevity
LF	life form
Grow	growth form
St/L	stem/ leaf ratio
Leaf	blade fragmentation
Clon	clonality
Rhizome	rhizome
D	defenses
Root	root type
ShootHeight	shoot height
LeafLength	leaf length
LeafWidth	leaf width
LeafRatio	leaf ratio
Below	fraction belowground
FlowerHeight	infloresence height
RelFlowerHeight	relative infloresence height
ShootDiam	shoot diameter
ACD	above cover density
SLA	specific leaf area
RootLLength	root length
Seed	seed productivity

Table 5. List of abbreviations for biomass and soil data.

Abbreviation	Variable
CovLitter	Cover litter layer
CovHerb	Cover herb layer
CovS2	Cover dwarf shrub layer
CovGround	Cover open ground
CovRock	Cover rocks
S_	Soil variable
B_	Biomass variable
Weight	Weight
Fine	Weight of fine soil
Coarse	Weight of course soil
RestWater	Rest water content
pH	pH after 24 hours
EC	Electric conductivity after 24 hours
CaCO3	Carbonate content
C%	Percent carbon content
N%	Percent nitrogen content
C/N	Ratio of C and N
Ca	Calcium content
Mg	Sodium content
K	Potassium content
P	Phosphate content

Statement on canditates contribution to single publications.

Publication	**Contribution**
Reinecke, J., Smelansky, I.A, Troeva, E.I., Trofimov, I. A., Trofimova, L. S. 2018. Chapter 5: Land use of natural and secondary grasslands in Russia. In: Squires, V., Dengler, J., Feng, H. & Hua, L. (Eds.), *Grasslands of the World: Diversity, Management and Conservation*, CRC Press, Boca Raton: p. 113-138.	Substantial re-working of Russian translation of a raw draft; in that course extensive correspondance with co-authors and editors
Reinecke, J., Troeva, E., Wesche, K., 2017. Extrazonal steppes and other temperate grasslands of northern Siberia - Phytosociological classification and ecological characterization. *Phytocoenologia*, 47: 167–196.	Conducted the fieldwork; carried out the statistical analysis; wrote the manuscript; journal correspondance
Ashastina, K., Kuzmina, S., Rudaya, N., Troeva, E., Schoch, W.H., Römermann, C., Reinecke, J., Otte, V., Savvinov, G., Wesche, K., Kienast, F. 2018. Woodlands and steppes: Pleistocene vegetation in Yakutia's most continental part recorded in the Batagay permafrost sequence. *Quarternary Science Reviews*, 196:38–61.	Statistical analysis (DCAs) of modern vegetation; revision of manuscript
Reinecke, J., Ashastina, K., Kienast, F., Troeva, E., Wesche, K. (submitted). Grazing at the limit – effects of large herbivore grazing on relics of presumed mammoth steppe in NE-Siberia. *Restoration Ecology*, submitted on 15.03.2019.	Conducted the fieldwork; carried out the statistical analysis; wrote the manuscript; journal correspondance