1	Open	tundra persist, but arctic features decline – Vegetation changes in the
2	warn	ning Fennoscandian tundra
3	Running	g head: Open tundra persist, arctic features decline
4		
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25 Abstract

26

27	In the forest-tundra ecotone of the North Fennoscandian inland, summer and winter
28	temperatures have increased by two to three centigrades since 1965, which is expected to
29	result in major vegetation changes. To document the expected expansion of woodlands and
30	scrublands and its impact on the arctic vegetation, we repeated a vegetation transect study
31	conducted in 1976 in the Darju, spanning from woodland to a summit, 200 meters above the
32	tree line. Contrary to our expectations, tree line movement was not detected, and there was no
33	increase in willows or shrubby mountain birches, either. Nevertheless, the stability of tundra
34	was apparent. Small-sized, poorly competing arctic species had declined, lichen cover had
35	decreased, and vascular plants, especially evergreen ericoid dwarf shrubs, had gained ground.
36	The novel climate seems to favor competitive clonal species and species thriving in closed
37	vegetation, creating a community hostile for seedling establishment, but equally hostile for
38	many arctic species, too. Preventing trees and shrubs from invading the tundra is thus not
39	sufficient for conserving arctic biota in the changing climate. The only dependable cure is to
40	stop the global warming.

42 Introduction

43

44 Global warming is proceeding especially rapidly in the arctic (Overland et al., 2016; 45 Vikhamar-Schuler et al., 2016). With its total extent of 9.8 million square kilometers 46 (Virtanen et al., 2016), the arctic tundra, including its altitudinal extensions, is among the 47 world's largest biomes. The high surface albedo of these vast, open expanses plays a major 48 role in cooling down the global climate (Chapin et al., 2005; Cohen et al., 2013). Changes in 49 the arctic also influence climate patterns at lower latitudes (Sellevold et al., 2016). Moreover, 50 tundra soils are large carbon stores. If the tundra changes to forest, much of this carbon might 51 become released to the atmosphere as CO₂ because of increased rate of soil respiration 52 (Hartley et al., 2012). Whether and how rapidly the open tundra changes to woodland has 53 therefore major consequences for the rate of global warming. 54 55 Woodland and scrubland expansion is also a direct threat to plants adapted to the open tundra 56 (Pajunen et al., 2011, 2012). Warming climate can reduce arctic biodiversity by increasing the 57 intensity of plant-plant competition (Callaway et al., 2002; Sammul et al., 2006), which can 58 result in rapid habitat monopolization by the most competitive species present in the site 59 (Grime, 1973, 1979). The milder winters predicted by climate change models (Vikhamar-60 Schuler et al., 2016) will also reduce the intensity of the perturbations and stresses typical for 61 the arctic, such as frost heaving and the drought stress caused by frozen topsoil in spring 62 (Virtanen et al., 2016). The conditions on the new tundra thus created are likely to favor 63 alpine plants, adapted to an environment with mild winters and unfrozen topsoil (Billings & 64 Mooney, 1968; Virtanen et al., 2016). Also the predicted shift to moister conditions (Räisänen 65 2016) should favor alpine rather than arctic plants (Cornelissen et al., 2001). 66

67	The relevance of these challenges is verified by the recent, large scale changes from tundra to
68	woodlands, tall scrublands and to structurally novel ecosystems (Tape et al., 2006; Williams
69	& Jackson, 2007; Harsh et al., 2009; Aune et al., 2011; Macias-Fauria et al., 2012; Formica et
70	al., 2014; Fraser et al., 2014; Hagedorn et al., 2014; Mathisen et al., 2014), which have been
71	especially rapid in areas, where increasing winter temperatures or increasing winter
72	precipitation have resulted in warmer soils (Harsh et al., 2009; Hagedorn et al., 2014). The
73	spatial decline in species diversity along gradients from higher to lower latitudes and altitudes
74	within the tundra (Bruun et al., 2006; Virtanen et al., 2013) also indicates that intensification
75	of competition between tundra plants, triggered by more benign physical conditions, could
76	jeopardize arctic and alpine biodiversity.
77	
78	The main buffering mechanism recognized so far is the impact of grazing mammals, which
79	can slow down, stop or reverse the expansion of erect woody plants and tall, competitive
80	forbs (Crête & Doucet, 1998; Post & Pedersen, 2008; Olofsson et al., 2009; Aune et al., 2011;
81	Pajunen et al., 2012; Kaarlejärvi et al., 2015). The role of grazing mammals is amplified in
82	areas where they interact with folivorous insects, which have devastating outbreaks in
83	northernmost forests (Tenow, 1972; Kallio & Lehtonen, 1975; Jepsen et al., 2008, 2009),
84	because the consumption of seedlings and basal recovery sprouts by herbivorous mammals
85	can prevent the recovery of mountain birch forests (Biuw et al., 2014). Woody plants growing
86	in the tundra are also profoundly influenced by small rodents (Virtanen, 2000; Olofsson, et
87	al., 2004, 2012, 2014), which facilitates seedling establishment (Ericson, 1977). Without
88	long-term data concerning both climate and numbers and habitat use of pivotal herbivores
89	(which are sensitive to climate change, see Jepsen et al., 2008, and Cornulier et al., 2013),
90	observed vegetation changes in the forest-tundra ecotone could be hard to interpret.
91	

Most of the long term studies addressing changes in tree and shrub cover are based on remote sensing, which enables detection of changes over vast areas but does not provide information on the impacts of these changes on arctic-alpine field layer plants. Such impacts also appear to be hard to detect in the time scale typical for planned experiments and surveys (about a decade, see Pardo et al., 2013). Moreover, climate change also triggers many kinds of changes in plant-plant interactions within the tundra (Suding et al., 2015), which could either facilitate or inhibit forest advancement and shrub encroachment.

99

100 The main scope of the present study is to investigate the results of the interacting processes 101 discussed above in the North Fennoscandian inland using the unique opportunity provided by 102 detailed data on patterns in tundra and woodland vegetation from 1976. This data set covers 103 all vegetation layers from trees to terricolous lichens and bryophytes and extends from 104 mountain birch woodlands to the highest parts of a large tundra plateau, the Darju highland 105 (Fig. S1). Moreover, the sampling was designed so that local topographic gradients from 106 wind-exposed hillocks to snow accumulating depressions were equally represented at all 107 altitudes (Oksanen & Virtanen, 1995). The climate station in Karesuando, Sweden, lies only 108 39 km from Darju's highest point and provides continuous temperature and precipitation 109 records from 1879 onwards. Records on the numerical dynamics and habitat use of reindeer, 110 geometrid moths and small rodents are available for the past decades. With these background 111 data in our disposal, we have repeated the 1976 vegetation study in 2014 and analyzed 112 changes in several ecologically relevant climate parameters at Karesuando during the latest 50 113 years. Our aim is to compare vegetation patterns documented in 1976 and 2014 and to discuss 114 their possible connections with climate trends. With this approach, we hope to yield deeper 115 understanding concerning the interactions within and between different vegetation layers of 116 the tree line region in a changing climate.

117	
118	Materials and methods
119	
120	Climate
121	
122	The climate data were obtained from two weather stations of the Swedish Meteorological and
123	Hydrological Institute (SMHI) in Karesuando, station A (68°26' 33.816" N, 22° 27' 12.014" E,
124	WMO number 2-81) and station D (68° 26.526' N, 22° 27.012' E, WMO number 2-80), which
125	lay approximately 39 km southeast of Darju at 330 m.a.s.l. SMHI has published inclusive,
126	diurnal open access data of temperatures (SMHI, 2014a), precipitation (SMHI, 2014b) and
127	snow depth (SMHI, 2014c). From these three datasets, we computed annual mean
128	temperatures, annual averages for January-February temperatures, annual numbers of winter
129	days with melting temperatures (24 hrs average $> 0^{\circ}$ C) in November-April, annual
130	precipitation sums, and sums of effective temperatures (degree days >5°C), and extracted
131	annual maximum snow depths for 1964–2013. Data from 2009 had to be excluded from
132	analyses of thermal sums, annual precipitation and temperature, because of a short gap in the
133	summer record for that year. As background information, we have also reproduced the
134	Karesuando record of mean annual temperatures and annual precipitation sums based on the
135	same datasets for 1879–2008 (Fig. S2 and Fig. S3), as the source (Gustavsson et al., 2011) is
136	poorly accessible.
137	
138	The winter climate indicators were chosen on the basis of their ecological significance. Snow
139	depths and temperatures during coldest winter months determine ground temperatures, thus

- 140 influencing the risk of spring stress due to frozen topsoil after snow-melt. The number of days
- 141 with melting temperatures in winter influences the risk that plants become encapsulated in

142	solid ice when meltwater percolates to the frozen ground. The period of 50 years from 1964 to
143	2013 was chosen, because the vegetation documented in 1976 was impacted by past climatic
144	conditions.
145	
146	We analyzed climate data with linear regression analysis. There might be temporal
147	autocorrelations in data, and it is not usually desirable to use ordinary regression for time
148	series data, because the assumptions of linear regression model might be violated. However,
149	here we are interested in climate primarily as a descriptive background variable and were not
150	studying climate change per se. The fluctuations and other deviations from linear regression
151	were visualized by using smoothed averages.
152	
153	The study area
154	
155	Darju (68° 42' 41.302" N, 21° 58' 3.084" E) forms the southeastern part of a relatively flat,
156	about 50 km long and 30 km broad tundra highland, extending from the Scandinavian
157	mountains towards southeast into the North Fennoscandian inland (in northwestern Finnish
158	Lapland, referred to as Käsivarsi). The bedrock is Precambrian and nutrient-poor. The climate
159	of the area is continental and relatively dry, with mean annual average temperature of -2.3°C
160	and mean annual precipitation of 442 mm for the latest normal period (1961–1990,
161	Gustavsson et al., 2011). This highland rises very gently from surrounding woodlands; the
162	distance from the base at 450 m a.s.l. to the highest point at 730 m a.s.l. is about 10 km.
163	
164	In 1976, the woodland vegetation at the base represented dry subarctic forests types (sEMT
165	and sELiT; Hämet-Ahti, 1963), with a tree layer consisting almost exclusively of the
166	mountain birch (Betula pubescens ssp. czerepanovii), most trees being polycormic.

167	Approaching the tree line at 550 m a.s.l, the vegetation graded into lichen-dwarf birch
168	(Betula nana) tundra heaths, with the crowberry (Empetrum nigrum ssp. hermaphroditum)
169	abounding on hilltops, while in snow accumulating depressions, the purple heather
170	(Phyllodoce caerulea) and the bilberry (Vaccinium myrtillus) were co-dominants (Oksanen &
171	Virtanen, 1995). These topography-based differences were, however, modest, as compared to
172	the patterns typical for Scandinavian mountains (Nordhagen, 1927; Dahl, 1957; Oksanen &
173	Virtanen, 1995; Virtanen et al., 1999a). Climate, vegetation and flora thus joined the Darju
174	highland to the European sector of the low arctic zone, where cold, rather calm and snow poor
175	winters reduce the importance of local topography and favor the dwarf birch, adapted to
176	tolerate the drought stress caused by frozen topsoil in spring (Virtanen et al., 1999b, 2016; see
177	also de Groot et al., 1997).
178	
179	Numerical dynamics and habitat use of pivotal herbivores
180	
181	In the Käsivarsi district, reindeer numbers have fluctuated with peak numbers in 1960's and
182	1980's (Fig. S4). No linear, directional long-term trend can be seen in the data, but a change
183	from tight herd control to more extensive grazing practices since mid-1960's may have
184	gradually increased the intensity of summer grazing on Darju, which was formerly winter
185	range, but is now sporadically grazed in summer too (Käsivarren Paliskunta, 2015; sporadic
186	summer grazing verified by observations of L. Oksanen, K.E.M. Vuorinen and A. Pyykönen).
187	According to Johan Duoma Labba, (pers. comm., 2015) Darju has been primarily grazed in
188	autumn, when birch and willow leaves are no longer edible for reindeer (Skjenneberg &
189	Slagsvold, 1968). Thus, summer grazing on Darju has been lighter than in the main summer
100	

192	Small rodent (i.e. vole and lemming) dynamics in the Käsivarsi area have been characterized
193	by four to five year cycles since early 1950's, without any long-term trend (University of
194	Helsinki, 2016). Our field studies were conducted three (1976) to four (2014) years after the
195	previous peak. Major geometrid moth outbreaks have occurred in 1964–65 and 2004–05
196	(Tenow, 1972; Jepsen et al., 2008, 2009), so birch woodlands had had approximately a decade
197	to recover from the previous outbreak both in 1976 and in 2014. Thus both surveys were
198	conducted in similar phases of the rodent cycles and equally long times after latest geometric
199	moth outbreaks that are both known to have severe impacts on the vegetation. However, there
200	were some differences in the composition of the rodent community during the decades
201	preceding the two sampling occasions. During 1961–1975, the rodent community was
202	dominated by voles, while Norwegian lemmings were almost absent, except for a small peak
203	in 1970 (Lahti et al., 1976). In 2007–2008 and in 2010–2011 there were major outbreaks of
204	both vole and lemming, which were roughly synchronous over the entire northern
205	Fennoscandia and had devastating impacts on the vegetation, especially in snow-rich habitats
206	at high altitudes (Ims et al., 2011, 2014; Olofsson et al., 2012, 2014; Ruffino et al., 2016,
207	Hoset et al., 2017). The field layer vegetation was thus probably more influenced by rodents
208	in 2014 than in 1976, especially in preferred lemming habitats, even though both studies were
209	conducted several years after the last rodent peak.
210	
211	Documentation of vegetation patterns in 1976

212

In 1976, the vegetation on the southern side of Darju was studied by sampling it along 12 local topographic transects, with a 10 to 15 m distance from top to bottom. These transects were primarily sampled on moraine hillocks, but below 460 m, where the valley floor was covered by sandy soils, sampling was performed on a sand hill. The highest transect was

217	sampled at the edge of a snow accumulating depression, as no moraine hillocks were found on
218	the top plateau. The lowest woodland transect was at 450 m a.s.l., the highest tundra transect
219	was at 722 m a.s.l. The intended altitudinal difference between subsequent transects was 25
220	m, with a tolerance of \pm 10 m (Oksanen & Virtanen, 1995). Inaccuracies in the topographic
221	map available in 1976 caused minor deviations from this rule (for GPS based altitudes of
222	transects, see Table S1; for their locations, see Fig. S1). The rationale of the transect method
223	was to ensure that different parts of the snow depth gradient, created by local topography (see
224	Nordhagen, 1927; Dahl, 1957), were equally represented at all altitudes. On each sampled
225	hillock, a 15 m long rope was laid from the top to the bottom of the depression, either straight
226	southwards or obliquely towards southwest (if the distance between the top and the bottom
227	was less than 15 m). The vegetation along each transect was documented as described below.
228	
229	To obtain indices for the shading impacts of tree and shrub canopies, the presence of each tree
230	(woody plant taller than 2 m) and shrub (woody plant with height from 0.5 m to 2 m) growing
231	within a distance of 5 m from the transect line was recorded. The canopy cover of shrubs was
232	estimated in square meters, summed up and divided by 1.5 to obtain the per cent coverage of
233	shrubs along the transect. All dwarf birch, mountain birch, gray willow (Salix glauca) and
234	common juniper (Juniperus communis) individuals, which were encountered on our plots,
235	were lower than 0.5 m and were thus treated as dwarf shrubs in this context. For trees, the
236	trunk wood volume was estimated as an index of canopy cover. The height and breast height
237	diameter of each tree trunk was measured. From the values thus obtained, an estimate for the
238	amount of trunk wood in cubic meters per hectare was computed, assuming that the trunks
239	were perfect cones. The tree and shrub vegetation consisted exclusively of the mountain
240	birch.

241

242	When the goldenrod (Solidago virgaurea) had started to flower, indicating the end of the leaf
243	expansion phase for all vascular plants, the composition of the field layer along each transect
244	was documented on eight vegetation plots of 0.8 m \times 0.8 m, sampled along the east side of the
245	transect rope at distances of 2 m between adjacent plots. This was done 14.–17.7.1976. Plants
246	encountered on the plots were primarily identified to species, except that some species pairs
247	of bryophytes (e.g. Polytrichum alpinum and P. commune) were treated collectively; hepatics
248	and some lichens were identified on genus or subgenus level. The coverage of photosynthetic
249	parts of each identified taxon (i.e. species, subgenus, genus, see above) was estimated using a
250	modified Hult-Sernander-Du Rietz scale (Oksanen, 1976; Lawesson, 2000), consisting of 10
251	classes, obtained by successively halving the plot (> 50 %, 50 to 25 %, 25 to 12.5 % etc). This
252	method is reliable for estimations of relative coverages (fractions of each identified taxon out
253	of the total plant cover; Oksanen, 1976). As the classes constitute a geometric series,
254	geometric means of class limits were used as unbiased class centers when transforming
255	coverage classes to per cent coverages. The class centers correspond approximately to
256	coverage percentages of 71, 35, 18, 9, 5, 2, 1, 0.5, 0.25 and 0.125 (Oksanen, 1976).
257	
258	Repetition of the vegetation study in 2014
259	
260	We repeated the transect study described above 14.–22.8.2014, using the same methods as in
261	1976 and the same phenological indicator (flowering of the goldenrod). To avoid unnecessary
262	heterogeneity in the material, we excluded the lowest transect, where the soil difference (sand

- vs. moraine) resulted to aberrant vegetation patterns (see Oksanen & Virtanen, 1995, their
- Fig. 18(3)). The lowermost resampled transect was thus the former transect 2, at 465 m a.s.l.
- 265 The highest transect was resampled despite its aberrant local topography, because soils

(glacial till) were comparable and vegetation patterns had been similar to the patterns of other
transects (Oksanen & Virtanen, 1995, their Fig. 18(3)).

268

269 For the sake of methodological consistency, the resampling was performed using the same

taxonomic units as used in 1976, even though some of the genera identified in 1976 are now

271 outdated. Using *Barbilophozia* in the old sense was also ecologically motivated, since the

272 genus in the old sense was represented by two boreal species (*B. hatcheri* and *B.*

273 lycopodioides), whereas also arctic-alpine species are included in the revised genus. Modern

274 names are used in the results section.

275

276 The relocalization of the transects was augmented by the shallow inclination of Darju's slopes

and the shortage of moraine hillocks suitable for the sampling method. As a rule, there was

278 just one suitable hillock anywhere near the spot marked on the 1976 map, so the estimated

error in relocation was maximally 10 m in the forest and maximally 5 m at and above the tree

280 line. On the top plateau, where a rock outcrop served as a natural transect marker, the

281 relocation was even more accurate. We then marked the transects in an updated map, took

282 GPS bearings, and marked each plot permanently. The plots were also photographed. In

August 2016, when we had found the old photographs from 1976, we re-photographed

transect number 4 (the tree line transect of 1976) and its surroundings from exactly the same

spots and with the same angles as in the photographs from 1976.

286

287 Vegetation data treatment

288

As the exact locations of individual plots could not be determined, we focused on robust

290 patterns and therefore pooled all eight plots, which belonged to the same transect. To find out

291	main directions of the anticipated change in field layer vegetation, we conducted principal
292	coordinates analysis (PCoA), based on Bray-Curtis index of dissimilarity (Faith et al., 1987),
293	using the transect-specific arithmetic averages of coverage classes (1 to 10) of each identified
294	taxon as input data. As the coverage class symbols are in logarithmic relation to the
295	coverages, the procedure is equivalent of using logarithmically transformed coverage data.
296	The statistical significance of the shift of the transects with respect to the two first principal
297	axes was tested with pairwise t-tests.
298	
299	To obtain a more detailed picture on the changes in the vegetation at different altitudes, we
300	compared relative coverages in 1976 and 2014 using generalized additive models (GAM;
301	Wood, 2006). Relative coverages of taxa were obtained by first converting coverages of each
302	identified taxon to the per cent scale using the class centers. Second, we divided the coverage
303	values of these taxa by the total coverage of all taxa on the plot, to yield relative coverages,
304	which we thereafter averaged over each transect. To visualize changes in altitudinal
305	vegetation patterns, we divided plants into the following groups: lichens, mosses, hepatics,
306	graminoids, forbs, evergreen dwarf shrubs, deciduous dwarf shrubs, and the bilberry (treated
307	separately since it has deciduous leaves but also evergreen, photosynthetically active twigs,
308	which are drought sensitive; see Tahkokorpi et al., 2007). Relative coverages of each group
309	for each transect in 1976 and 2014 were calculated by summing up the taxon-specific relative
310	coverages.
311	
312	The fitted GAM models characterize the relative abundances of the above defined plant

313 groups along the altitudinal gradient during both sampling occasions. An additional

314 parametric term "year" tested the over-all change of relative abundance between 1976 and

315 2014. In the GAM models, betar family with logit link were used. The significance of terms

were obtained by using anova.gam function (Wood 2016). The function gam selects optimal smoothing based on generalized cross-validation. This procedure controls wiggliness and badness of fit to obtain optimal level smoothness and avoid overfitting (Wood 2016). The fitted GAM models were checked for residual distributions by using gam.check function of mgcv (Wood, 2016).

321

322 Moreover, we analyzed the taxon-specific changes with the lnRR method (Hedges et al.,

1999), where the natural logarithm of the ratio of coverage in 2014 to coverage in 1976 was

324 used as an index of abundance change of each taxon in each transect. To avoid dividing by

325 zero, we replaced the zero values with value obtained by dividing the smallest non-zero value

326 of the data by two. The statistical significances of the lnRR-values thus obtained were tested

327 for each taxon with pairwise t-tests, with transects as replicates, separately for open tundra

328 transects and for transects where trees were present. Based on lnRR-values, literature (Hämet-

329 Ahti et al., 1998; Hallingbäck, 2006; Hallingbäck et al., 2008; Steenroos et al., 2011; Hedenäs

330 & Hallingbäck, 2014), The Virtual flora by Naturhistoriska Riksmuseet

331 (http://linnaeus.nrm.se/flora/welcome.html), and field observations, we constructed Tables 1

and S2, to serve as indications of the underlying environmental causes, possibly responsible

333 for the observed community level changes.

334

335 The anticipated altitudinal shifts in occurrences of different taxa from 1976 to 2014 (see Pauli

et al., 2007; Gottfried et al., 2012) were primarily studied by comparing the altitudinal

337 centers of gravity of all identified taxa, which occurred in the material both in 1976 and in

338 2014. In our opinion, these values are maximally reliable indicators of the altitude where each

339 plant thrives best. Altitudinal centers of gravity were computed by first computing the

340 abundance of each taxon in a given transect as the sum of its coverages within individual

341	plots, using the class centers as abundance values, and thereafter computing weighted
342	averages of GPS based altitudes of each transect, using the coverage sums thus obtained as
343	weighting factors. To promote comparisons with other published studies, also minimum and
344	maximum altitudes of each identified taxon were computed (i.e. the GPS based lowest and
345	highest altitude at which the taxon was recorded), although these values are sensitive to
346	sampling errors and local vegetation processes. The statistical significance of the changes in
347	altitudinal centers of gravity and in the minimum and maximum altitudes of all identified taxa
348	and, separately, of vascular plants, lichens and bryophytes, was tested with pairwise t-test
349	with the taxa as replicates.
350	
351	Changes in species diversity were studied by computing Shannon-Wiener diversity indices for
352	each transect, pooling the plots belonging to the same transect and using taxon-specific
353	average coverages based on the class centers as input data. A pairwise t-test was used to test
354	the difference between 1976 and 2014.
355	
356	Statistical tests were carried out with SAS Enterprise guide, except for the ordination, which
357	was made with PC-ORD, and the tests based on GAM models, which were run using gam
358	function of the mgcv package of R software (Wood, 2011, 2016; R Core Team, 2016).
359	
360	Tree seeding experiment
361	
362	To study the invasion potential of the mountain birch, we performed a tree seeding
363	experiment within the northern part of the North Fennoscandian region of low arctic inland
364	climate, which also embraces Darju (Virtanen et al., 2016). Three sites were chosen along the
365	forest-tundra ecotone in close proximity to the Joatka fjellstue, Finnmark, Norway

366	(69°45'11"N, 24°00'00"E) in the context of the EU-project DART. The distances between the
367	sites in each location varied between 0.2 km and 1 km. Each site comprised an adjacent pair
368	of birch woodland and open tundra habitats. The vegetation consisted of lichen rich dwarf
369	shrub heath. For each treatment, three 8 m \times 8 m experimental plots were established in June
370	1999 in woodland and tundra habitats, respectively. These plots were randomly assigned to
371	one of the following treatments; control (no exclosure), reindeer exclosure, and a small mesh
372	exclosure, excluding all herbivorous mammals. Five hundred mountain birch seeds were
373	sown in each of the four disturbed and four undisturbed subplots in June in three consecutive
374	years (1999, 2000 and 2001). Seeds were collected locally in the area in the autumn of 1998.
375	In the laboratory these had a germinability of 18.2%. The emerging seedlings were counted in
376	August-September 1999, 2000, 2001, 2002 and 2007. In 2007, the heights of all seedlings
377	were measured to the nearest cm. The data were analyzed with a generalized mixed effect
378	model with quasipoisson errors, using the glmmPQL function within the MASS package in
379	the statistical software R.
380	
381	Results
382	
383	Changes in climate
384	
385	The trend towards a warmer and moister climate, strikingly visible in the long Karesuando
386	record (Fig. S2 and Fig. S3), had continued during the latest 50 years. The most significant
387	changes were observed in mean annual temperature ($p = 0.001$), in mean number of winter
388	days with melting temperatures (24 hrs mean $> 0^{\circ}$ C, p = 0.018), and in the sum of effective
389	temperatures (>+5°C, p=0.04). There had also been near-significant increase in mean
390	January-February temperatures (p=0.076).

391	
392	Mean annual temperature increased approximately by two degrees Celsius from 1964 to 2013
393	(CL \pm 95% 0.024), the sum of effective temperatures by 20 %, in absolute terms 120 dd (CL \pm
394	95% 2.4; Fig. 1a), and mean January-February temperature by three degrees Celsius (CL \pm
395	95% 0.068; Fig. 1b). Moreover, the winter climate pattern changed. Before the millennium
396	change, number of days with melting temperatures varied between 0 and 24, but intermediate
397	values prevailed. In the 2000's most winters had 20 or more days with melting temperatures
398	(Fig. 1c). Annual precipitation showed an increasing trend (Fig. 1d), albeit not statistically
399	significant, by 60 mm (p=0.13), whereas there were no clear change in the snow depth. (For
400	details and statistics, see Table S3.)
401	
402	Changes and constancy in vegetation patterns
403	
404	Both in 1976 and in 2014, the three lowermost transects were in woodlands, the fourth was in
405	the forest-tundra ecotone, and the rest were in open tundra. The distribution of wooded and
406	treeless areas had thus remained unchanged at the transect level. Also within tree line transect
407	(transect 4), wooded and open areas had the same distribution in 1976 and in 2014 (Fig. S6;
408	see also Fig. S1 and S7). There were no statistically significant increase in trunk wood
409	(p=0.10, t=-2.4, df = 3), although the estimates were higher in 2014 (from $3.3 \pm 1.2 \text{ m}^3$ /ha to
410	$7.6 \pm 2.0 \text{ m}^3/\text{ha.}$
411	
412	The cover of any of the four shrub species with a potential to reach height of over 0.5 m
413	showed no or only local change between 1976 and 2014. In 1976, shrub cover exceeding 1 %

- 414 was only encountered in the forest-tundra ecotone, with 6 % cover of shrubby mountain
- 415 birches. In 2014 shrub coverage was < 1 % in all transects. The mountain birch *Betula*

416 *pubescens* and the gray willow *Salix glauca* tended to have even lower cover in 2014 than in

417 1976 (Fig. S9). Common juniper showed no overall change along the elevation gradient, but

418 increased at the tree line transect (Fig. S8, see also S5-S7).

419

420 The field layer vegetation community had changed at all altitudes. In the ordination plane

421 defined by the two first PCoA axes, A strong shift towards more positive values along the

422 second axis (Fig. 2a; t = 11.28, p < 0.001) resulted in the non-overlapping ranges of transects

423 from 1976 and 2014 in the ordination space. Furthermore, transects had moved to more

424 positive values along the first axis of the PCoA (t = 2.29, p = 0.045). (Species data related to

425 this change is presented in Fig 2b, Table 1 and Table S2.) These changes in the vegetation

426 were accompanied by reduction in species diversity at the transect level. For the 1976 data,

427 the average Shannon-Wiener (H') was 2.67 and for the 2014 data 2.25 (t = -3.95, df = 10, p =

428 0.027).

429

There was a tendency for an upward shift in the altitudinal centers of gravity, minimum and
maximum of the occurrences, but it was often not statistically significant. For lichens the
change was statistically significant but quantitatively modest, whereas the centers of gravity
of vascular plants and bryophytes had not changed. (Table 2; for details, see Table S4). Upper

434 limits of the identified taxa had increased more profoundly, primarily in response to invasions

435 of several boreal vascular plants and bryophytes to the uppermost transect.

436

437 The investigation of abundance patterns on the group level revealed changes in the vegetation.

438 For most plant groups, these changes were most pronounced in the tundra. The collective

- 439 coverage of lichens had declined, especially at higher altitudes (Fig. 3). Evergreen dwarf
- 440 shrubs had increased and their peak moved from the woodland to the lower parts of the tundra

441 (Fig. 4). No over-all trends could be detected for forbs, graminoids or deciduous dwarf 442 shrubs, but subtle changes in altitudinal patterns were indicated by GAMs. The increase of 443 evergreens right above the treeline seems to coincide with a slight decline of graminoids (Fig. 444 5 and Fig. 4). No over-all change in deciduous dwarf shrubs was observed, but they tended to 445 decline at low altitudes and increase at the lower part of the tundra, expressing somewhat 446 similar shift to higher altitudes as evergreens.

447

448 The taxon-specific changes within each group showed large variation. For example, the 449 profound, collective reduction of the lichen cover reflected declines in three initially abundant 450 taxa – two reindeer lichens (Cladonia mitis, C. stellaris; Table 1, Fig. S11) and Flavocetraria 451 nivalis (Table S2, Fig. S11). Several lichen taxa had, however, stood their ground or increased 452 (Figs. S11–S13). The increasers include several fruticose species (e.g. *Cladonia subfurcata*, 453 Cetrariella delisei) and even a reindeer lichen, Cladonia arbuscula (Fig. S11, Tables 1 and 454 S2). The responses of evergreen and deciduous dwarf shrubs reflected the responses of the 455 northern crowberry (Fig. S8) and the dwarf birch (Fig. S9). The increased relative abundance 456 of the snow bed specialist Salix herbacea (form 0.004 to 0.018) contributed to the strong 457 increase of deciduous dwarf shrubs in the highest transect. Non-significant trends in moss 458 cover was primarily caused by an increase in three common boreal species, *Pleurozium* 459 schreberi, Dicranum scoparium and Polytrichum juniperinum, within woodland transects 460 (Fig. S10, see also Table S2). Also an increase of *Ptilidium ciliare*, at middle altitudes, and 461 increase of *Dicranum fuscescens/flexicaule* at high altitudes contributed to the over-all 462 pattern. 463

464 Changes in the highest transect deviated from the general pattern. Forbs had increased (Figs. 5 465 and S14) and eleven primarily boreal vascular plant and bryophyte taxa, which had not been

- 466 recorded on this transect in 1976 and had primarily occurred below the tree line, were now
- 467 present, most of them on several plots (Tables S5 and S6; for graminoids, see also Fig. S15).
- 468 This top transect differed also from others by showing a very strong decline in the coverage
- 469 sum of all plants from 127 % in 1976 to 27% in 2014.
- 470

471 Tree seeding experiment

472

473 In the absence of disturbance, 12 000 mountain birch seeds resulted in only 5 established 474 seedlings and only 2 that survived for 8 years. Introducing disturbance in the sowing event 475 increased the number of established seedlings to 67 and the number reaching the age of 8 476 years to 42, again out of 12 000 sown seeds. Combining disturbance with herbivory exclusion 477 increased significantly germination rate, but after 8 years, the difference between the numbers 478 of survived seedlings in exclosures (27) and open plots (15) was not statistically significant 479 (Table S8). Even when both competition from field layer plants and herbivory were removed, 480 tree seedling establishment was still very low (0.08%) and none of the seedlings reached a 481 height over 4 cm. (See details in Tables S7 and S8.) 482 483 Discussion 484 485 The long-term trend towards warmer and moister climate in the North Fennoscandian inland 486 (Gustavsson et al., 2011; Räisänen, 2016) has continued during the latest five decades. Due to 487 the ongoing climate change, summers have become warmer and winters milder, creating 488 conditions, which have elsewhere triggered large upward shifts in the altitudinal ranges of 489 plants (Pauli et al., 2007; Gottfried et al., 2012) and also caused a rapid advancement of trees 490 and tall shrubs to the tundra (Harsh et al., 2009; Hagedorn et al., 2014). In the Darju highland,

491	however, no signs of birch woodland or scrubland expansion were observed in any spatial
492	scale (Fig. S1, S6 and S7). The stability of the forest tundra ecotone of Darju is in contrast to
493	the tree line advance documented in many parts of northern Fennoscandia (Aune et al., 2011;
494	Mathisen et al., 2014; N.H.P. Sara, pers comm. 2015; but stable tree lines are also reported,
495	Callaghan et al., 2014). Moreover, the anticipated upwards shift in the altitudinal centers of
496	gravity of field layer plants was only observed for lichens, and it was modest even for them.
497	The altitudinal maxima had, on the other hand, increased more consistently, as several boreal
498	vascular plants and bryophytes, which were only detected at low altitudes in 1976, had
499	established altitudinal outposts in the highest transect (see Figs. S9, S10, S14 and S15, and
500	Table S5 and S6).
501	
502	The resistance of the tundra to the invasion of birches, willows and boreal forest floor plants
503	might be connected to the large changes in the vegetation community. Distribution patterns of
504	the taxa and the order of transects along the first PC1-axis (Fig. 2b, and Table S2) show that
505	this axis represents a gradient from arctic-alpine to boreal vegetation. Among species with
506	highest InRR-values, the ones with most negative ordination values along this axis are
507	primarily arctic, alpine or arctic-alpine species, and, conversely, the most positive loadings
508	are primarily obtained by boreal species (Supporting Table S2 and Table 1). The highest
509	values on the second axis are obtained by plants growing in moist sites and by plants
510	primarily found in bogs or in periodically wet depressions, while highest negative values are
511	obtained by plants adapted to dry sites (Fig. 2b, Supporting Table S2 and Table 1). In addition
512	to an overall shift in plant community composition between 1976 (lichen-rich tundra) and
513	2014 (ericoid-moss tundra), the second axis thus reflects also a gradient of increasing
514	moisture. In 1976, the dominating community type was a reindeer lichen heath with patches
515	of dwarf birch (Oksanen & Virtanen, 1995, see also Fig. S7a). This vegetation type, where the

516 dominating plants are either tolerant (dwarf birch) or indifferent (lichens) to frozen topsoil in 517 spring, is typical for the European low arctic tundra from the North Fennoscandian inland to 518 the Urals (Virtanen et al., 1999b, 2016). By 2014, the vegetation had changed towards a dwarf 519 shrub heath, with a bottom layer of shade tolerant mosses, as typical for the lower altitudes of 520 the Scandinavian mountain chain (Nordhagen, 1927; Oksanen & Virtanen, 1995; Virtanen et 521 al., 1999a, 2016) and Scandinavian mountain birch forests (Hämet-Ahti, 1963). The strong 522 expansion of the northern crowberry in the lower and middle parts of the tundra is especially 523 important in this context. The detritus produced by it is loaded with noxious chemicals, which 524 inhibit seedling establishment (Gallet et al., 1999; Nilsson et al., 2000; Aerts, 2010; Väisänen 525 et al., 2013; Mod et al., 2016) and could have contributed to the stability of the tree line on 526 Darju. The impact of ericoids might also be a plausible cause for the failure of boreal forest 527 plants like *Linnaea borealis* and *Trientalis europaea*, which managed to invade the highest transect, to increase correspondingly in the lower parts of the tundra. 528 529 530 The increasing abundance in the crowberry was associated with a warmer climate, which has 531 been observed to trigger a rapid increase in dwarf shrub biomass in the arctic (van der Wal &

532 Stien, 2014) and in the Scandinavian mountain chain (Vowles et al., 2017). The results of

533 PCoA indicate that changes in moisture conditions have been another important factor

favoring evergreen dwarf shrubs, probably primarily *via* milder winters and the consequent

relaxation of the drought stress due to frozen ground in spring. This stress can seriously

damage evergreen dwarf shrubs (Kullman, 1989; Tahkokorpi et al., 2007; Wheeler et al.,

537 2014) and is probably a major reason for the subordinate role of these plants in the European

538 low arctic tundra (Oksanen & Virtanen, 1995; Virtanen et al., 1999b, 2016).

539

540	Increasing competition by dwarf shrubs could be the reason for the reduced abundances of
541	lichens (Cornelissen et al., 2001; Fraser et al., 2014), which contribute to vegetation
542	composition of transects moving further away from the part of the ordination space with
543	mainly arctic species. However, responses were heterogeneous among lichen taxa, indicating
544	that also other factors were involved (Table 1, Fig. S11–S13, Table S2). Out of the four lichen
545	species with most prominent increases in abundance from 1976 to 2014 (Table 1), two
546	(Cladonia arbuscula, C. pyxidata) are primarily boreal, while the two others (Cladonia
547	subfurcata, Cetrariella delisei; Table 1) are widespread in the northern hemisphere and
548	tolerate freezing in solid ice (Dahl, 1957; Oksanen & Virtanen, 1995). So does the northern
549	crowberry (Preece & Phoenix, 2014). Our results thus indicate that, besides favoring boreal
550	species, the warming of the tundra may have been accompanied by the emergence of a new
551	kind of stress: a higher frequency of mild winter periods when the meltwater percolates
552	through the snowpack and freezes along the frozen ground, which is a serious stress for many
553	lichens (Dahl, 1957). In the 2000's, periodically mild winters have become the new climate
554	(see also Vikhamar-Schuler et al., 2016), thus having a persistent impact on the vegetation
555	(and becoming a hazard for reindeer husbandry, J. D. Labba and N.H.P. Sara, pers. comm.
556	2015).
557	

558 Periodically intense vertebrate herbivory belongs to the natural state of the tundra biome,

559 (Tihomirov, 1959; Batzli et al., 1981; Oksanen & Virtanen, 1998; Virtanen, 2000; Oksanen &

560 Olofsson, 2010; Olofsson et al., 2014; Saccone & Virtanen, 2016) and the impact of climate

561 change on the arctic vegetation is always modified by herbivore-plant interactions. Thus,

562 changing herbivore impacts have to be considered when interpreting the results. The shift to

563 more extensive reindeer husbandry and the consequent increase in the intensity of summer

564 grazing and trampling may have contributed to the decline of lichens (see Oksanen, 1978; den

565	Herder et al., 2004), but our results imply that this has not been the primary reason. The
566	shared character of lichens which increased from 1976 to 2014 was their primarily boreal
567	distribution, while species with primarily arctic-alpine distribution declined (Tables 1 and
568	S2). If the changes had been primarily driven by increasing intensity of summer grazing and
569	trampling, the crucial traits had been gross morphology and the brittleness of the thalli, and
570	the ability to disperse to sites with exposed soil (Oksanen, 1978; Olofsson et al., 2001;
571	Bråthen et al., 2007). The reindeer grazing might, however, have contributed to the stability
572	of the mountain birch tree line. The contrast between North Fennoscandian areas with and
573	without summer grazing (Aune et al., 2011) indicates that even the low rates of seedling
574	establishment indicated by our experiments suffice to trigger a gradual advancement of
575	mountain birch woodlands, if herbivores with high preference for mountain birch seedlings,
576	such as reindeer in early summer (Skjenneberg & Slagsvold, 1968), are absent. The
577	inhibition of mountain birch advancement on Darju thus appears to be the net result of several
578	interacting forces, including the direct and indirect impacts of evergreen ericoids and a
579	moderate intensity of summer grazing by reindeer.
580	
581	Although rodents have been fluctuating with regular intervals throughout the study period and
582	the time since the last outbreak was fairly similar between the two samplings (3-4 years), the
583	impact of rodents might have been stronger in 2014 as a result of the pronounced vole and
584	lemming outbreaks in 2007–2008 and 2010–2011 decimating the vegetation cover and plant
585	biomass (Olofsson et al., 2014; Ruffino et al., 2016; Hoset et al., 2017). Low absolute
586	coverages in 2014 indicate that the impact of the recent vole and lemming outbreak may have
587	been especially pronounced at the highest altitude (transect 11) with conditions maximally
588	favorable for Norwegian lemmings (see Moen et al., 1993; Virtanen, 2000; Olofsson et al.,

589 2012, 2014; Ruffino et al., 2016), although methodological issues may have contributed to

Page 25 of 51

Global Change Biology

590	them (see Methods). The resulting disturbance seems to have promoted the invasion of
591	sexually reproducing vascular plants (Table S5; Virtanen et al., 2010; Frost et al., 2013;
592	compare to Söyrinki, 1939) and bryophytes.
593	
594	Our results imply that the Fennoscandian low arctic tundra plant communities may develop
595	towards a novel state (Williams & Jackson, 2007), which combines features of the ericoid-
596	graminoid tundra, typical for Scandinavian mountains (Nordhagen, 1927; Dahl, 1957;
597	Oksanen & Virtanen, 1995; Virtanen et al., 2016), with features of north boreal forest floor
598	vegetation. This is only one of many directions vegetation change may take, but in areas with
599	at least moderate intensity of summer grazing by reindeer, this novel vegetation type might be
600	quite resistant to the invasion of trees and tall shrubs. Unfortunately, however, this novel
601	community appears to be characterized by intense plant-plant competition, resulting in
602	reduced species diversity (as predicted by Grime 1973, 1979) and conditions hostile for many
603	arctic species. Measures which prevent the invasion of trees and tall shrubs can thus preserve
604	the tundra as an open environment with high surface albedo (Cohen et al., 2013) but for the
605	arctic flora, the only dependable cure is to stop the global warming.
606	

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608

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886	Table 1. Taxon-specific changes in the tundra vegetation of the Darju highland from 1976 to
887	2014, for taxa with change significance of at least $p < 0.1$ (taxa ordered by lnRR). The lnRR
888	values are computed as means of natural logarithms of ratios of coverages in 2014 and 1976,
889	with transects as replicates. Cup lichens include all lichens with phyllodia along the ground
890	and an upright podetium. Abbreviations for plant characteristics: a = arctic+alpine, ar = arctic,
891	al = alpine, b=boreal or boreal+temperate, ab = widespread northern, $g+/g- =$ grazing favored
892	/ suffers from grazing, $d+/d-$ = favored by / suffers from physical disturbance, $i+/i-$ = resistant
893	/ sensitive to ground icing, w+/w- tolerates / is sensitive to wind exposure in late winter. As
894	the oceanic sectors of the arctic and alpine habitats have similar winter climate, plants have
895	been regarded as alpine if their arctic distribution is limited to areas facing ice-free oceans.
896	For symmetric reasons, plants have been regarded as arctic if their alpine ranges are restricted
897	to inland mountains

	lnRR	t	Р	Characteristics
Cladonia stellaris	-2.68	-9.98	< 0.0001	fruticose reindeer lichen, ab, g-, d-, i-, w-
Cladonia mitis	-2.22	-7.18	< 0.0001	fruticose reindeer lichen, a, g-, d-, i-, w-
<i>Lecidea</i> sp.	-1.89	-3.06	0.012	crustose lichens, ab, g+, d+, w+
Cetraria islandica	-1.54	-2.4	0.037	fruticose lichen, broad lobes, ab, d-, i-, w-
Cladonia macrophylla	-1.36	-2.61	0.026	cup lichen, a, g+, d+, w-
Solorina crocea	-0.91	-1.83	0.099	foliose lichen, ar, g+, d+, i-, w+
Carex brunnescens	+0.91	+1.89	0.088	graminoid, ab, g+, d+, i+, w-
Cladonia pyxidata	+0.97	+1.87	0.091	cup lichen, b, g+, d+, w-
Hieracium alpinum	+1.01	+2.27	0.047	mesomorphic forb, al, i-, w-
Cetrariella delisei	+1.05	+1.94	0.082	fruticose lichen, broad lobes, ab, d-, i+, w-
Trientalis europaea	+1.84	+2.21	0.052	mesomorphic forb, b, g-, d-, w-
Cladonia arbuscula	+1.95	+2.73	0.021	fruticose reindeer lichen ab, g-, d- , i-, w-

Cladonia subfurcata	+2.11	+3.13	0.011	branching needle lichen, ab, d-, i+, w-
Dicranum scoparium	+3.13	+4.20	0.002	small acrocarpic moss, b, d-, w-
Pohlia sp.	+3.30	+3.37	0.007	small acrocarpic moss, ab, g+, d+, w-
<i>Polytrichum juniperinum</i> s.1. ¹	+3.62	+3.26	0.009	robust acrocarpic moss, b, i+, w-

898 ¹includes *P. strictum*

899

901	Table 2. Changes in minimum, average and maximum altitudes in the occurrences of different
902	taxa and in their altitudinal centers of gravity (\pm 95% CL), with identified taxa as replicates.
903	Minimum and maximum altitudes have been computed from the lowest and highest altitude at
904	which the taxon was recorded, using the GPS based altitudes of each transect. When
905	computing altitudinal centers of gravity, each altitude where the taxon was encountered was
906	weighted by the abundance (coverage sum) of the taxon at this altitude. N = number of taxa
907	used in the analysis.

	Vascular plants	Lichens	Bryophytes	All taxa
	(N = 25)	(N = 34)	(N = 13)	(N = 72)
Minimum	+7 m ±11 m	+21 m ±21 m	+ 14 m ±18 m	+15 m ±11 m
Minimum	(p=0.21)	(p = 0.054)	(p = 0.11)	(p=0.009)
	+6 m ±19 m	+22 m ±21 m	-3 m ±21 m	+12 m ±20 m
Center of gravity	(p = 0.52)	(p = 0.046)	(p = 0.84)	(p = 0.076)
	+51 m ±57 m	+25 m ±20 m	+36 m ±28 m	+36 m ±21 m
Maximum	(p = 0.079)	(p = 0.016)	(p = 0.015)	(p = 0.002)

911 Supporting Information captions: Figures and Tables

- 912 Fig. S1. Map of the Darju highland.
- Fig. S2. Changes in annual mean temperatures at Karesuando during 1879–2008.
- Fig. S3. Changes in annual precipitation sum at Karesuando during 1879–2008.
- 915 Fig. S4. Number of overwintering reindeer in the reindeer herding district of Käsivarsi.
- 916 Fig. S5. Mountain birch woodland at the base of Darju (a) in 1976 and (b) in 2014
- 917 Fig. S6. The tree line area at transect 4 in 1976.
- Fig. S7. The general appearance of the forest tundra ecotone (a) in 1976 and (b) in 2014.
- Fig. S8. Relative proportions of evergreen dwarf shrubs in 1976 and 2014 along elevation
- 920 gradient
- Fig. S9. Relative proportions of deciduous dwarf shrubs in 1976 and 2014 along elevationgradient
- 923 Fig. S10. Relative proportions of bryophytes in 1976 and 2014 along elevation gradient
- Fig. S11. Relative proportions of fruticose lichens in 1976 and 2014 along elevation gradient
- 925 Fig. S12. Relative proportions of fruticose cup and needle form lichens in 1976 and 2014
- 926 along elevation gradient
- 927 Fig. S13. Relative proportions of *Lichenomphalia* and crustaceous lichens in 1976 and 2014
- 928 along elevation gradient
- 929 Fig. S14. Relative proportions of forbs in 1976 and 2014 along elevation gradient
- 930 Fig. S15. Relative proportions of graminoids in 1976 and 2014 along elevation gradient
- Table S1. Intended and real (GPS-based) altitudes of the highest points of each transect
- 932 Table S2. List of taxa of field layer plants with mean $|\ln RR| > 0.69$.
- 933 Table S3. Climate statistic and analyses.

- Table S4. Means and standard deviations for the highest and lowest altitudes and altitudinal
- 935 centers of gravity of occurrence for lichens, bryophytes, vascular plants, and for the whole set
- 936 of identified taxa, and statistical analyses for changes from 1976 to 2014.
- 937 Table S5. Vascular plant taxa which were encountered on transect 11 in more than trace
- amounts only in 1976 or only in 2014 and their occurrences on different plots.
- Table S6. Bryophyte taxa which had been absent in 1976 in transect 11 but were encountered
- 940 in more than trace amounts in 2014, and their occurrences on different plots.
- 941 Table S7. Numbers of live mountain birch seedlings in relation to disturbance and grazing
- 942 exclusion after 1 or 8 years.
- 943 Table S8. Statistical analysis results for mountain birch seedlings data based on a generalized
- 944 mixed effect model with quasipoisson errors.



Figure 1. Annual sums of effective temperatures (a), mean January-February temperatures (b), number of November-April days with 24 hrs average temperature exceeding 0oC (c) and annual precipitation sums (d) during 1964–2013 (dashed lines are linear trend lines for actual means; smoothed averages are averages over five years). Fig 1a 296x419mm (300 x 300 DPI)



Figure 1. Annual sums of effective temperatures (a), mean January-February temperatures (b), number of November-April days with 24 hrs average temperature exceeding 0oC (c) and annual precipitation sums (d) during 1964–2013 (dashed lines are linear trend lines for actual means; smoothed averages are averages over five years). Fig 1b 296x419mm (300 x 300 DPI)



Figure 1. Annual sums of effective temperatures (a), mean January-February temperatures (b), number of November-April days with 24 hrs average temperature exceeding 0oC (c) and annual precipitation sums (d) during 1964–2013 (dashed lines are linear trend lines for actual means; smoothed averages are averages over five years). Fig 1c 296x419mm (300 x 300 DPI)



Figure 1. Annual sums of effective temperatures (a), mean January-February temperatures (b), number of November-April days with 24 hrs average temperature exceeding 0oC (c) and annual precipitation sums (d) during 1964–2013 (dashed lines are linear trend lines for actual means; smoothed averages are averages over five years). Fig 1d 296x419mm (300 x 300 DPI)



Figure 2. (a) Distribution of data points from 1976 and 2014 in the ordination space in relation to the first and the second principal coordinate axis and (b) positions of some species important for interpretation (for abbreviations, see Table S2). Fig 2 296x419mm (300 x 300 DPI)



Figure 3. Relative coverages (shares out of total plant cover) of cryptogams in 1976 and 2014. Fitted lines based on generalized additive models. F-values and respective P-values based on gam.anova tests for the differences between the two years.

Fig 3 147x127mm (300 x 300 DPI)







Figure 5. Relative coverages (shares out of total plant cover) of forbs and graminoids in 1976 and 2014. Fitted lines based on generalized additive models. F-values and respective P-values based on gam.anova tests for the differences between the two years.

Fig 5 94x51mm (300 x 300 DPI)