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15 Recent changes in mountain birch forest structure and understory vegetation depend
16 on the seasonal timing of reindeer grazing

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32 **Key words:** *Betula pubescens* ssp. *czerepanovii*, reindeer, *Empetrum nigrum* ssp.

33 *hermaphroditum*, lichens, browsing, subarctic

Abstract

1. Subarctic forest-tundra ecotones dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii*) are an important habitat for semi-domestic reindeer (*Rangifer tarandus*). The seasonal timing of reindeer grazing may direct vegetation trajectories in these systems, because in the summer ranges, mountain birches are subjected to browsing, while in the winter ranges, reindeer feed on understorey vegetation and arboreal lichens but leave the mountain birches intact.
2. Based on earlier research, we predicted that (1) summer browsing dampens ongoing vegetation 'shrubification' in semi-dry and dry mountain birch forests and (2) 'shrubification' is accompanied by a decline in lichens. We tested these predictions through re-analysing forest structure and understorey vegetation after 12 years in areas where winter and summer ranges had been separated since the 1980's. We also tested how changes in lichen abundances align with changes in shrub abundances through correlation analyses.
3. The number of tall mountain birch seedlings had increased twice as fast in winter than summer ranges, while big mountain birches had increased in summer ranges. The dominant evergreen dwarf shrub mountain crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) had increased to a greater extent in winter ranges in a semidry habitat, and to a greater extent in summer ranges in a dry habitat. Deciduous dwarf shrub and graminoid biomass had increased similarly in summer and winter ranges.
4. We found no evidence to support that increasing shrub abundances had contributed to a decline in lichens; instead, the lichen cover increased with increasing number of mountain birch seedlings.
5. *Synthesis and application.* The vegetation trajectories of dry and semi-dry subarctic mountain birch forests depend greatly on whether the area is used as a winter or a summer range for the reindeer. The recent changes in vegetation are likely to lead to improved summer forage availability for the reindeer, while the opposite may be true for the winter forage availability.

63 Introduction

64 Subarctic mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests form the treeline ecotone in
65 many parts of the circumpolar sub-Arctic. In dry and semi-dry mountain birch habitats typical for
66 upland areas in northernmost Fennoscandia, mountain birches are usually polycormic (i.e., many-
67 stemmed; Kallio & Mäkinen 1978; Verwijst, 1988) and underlain by an understory vegetation
68 dominated by evergreen and deciduous dwarf shrubs, lichens and mosses (Oksanen & Virtanen,
69 1995). As a transitional zone between treeless tundra and boreal forest, this ecotone is subjected to
70 large-scale changes in response to climate warming (Tømmervik *et al.*, 2009; Biuw *et al.*, 2014;
71 Horstkotte *et al.*, 2017; Forbes *et al.*, 2020). Long-term vegetation inventories have revealed
72 increasing trends in the number of mountain birches and the proportion of graminoid- and
73 deciduous dwarf shrub –dominated habitats at the expense of lichen-dominated habitats
74 (Tømmervik *et al.*, 2004; 2009). These trends align with evidence from warming experiments
75 showing increasing dwarf shrub abundances and distributions both in treeless tundra (Buizer *et al.*,
76 2012; Elmendorf *et al.*, 2012; Kaarlejärvi *et al.*, 2012; Yläne *et al.*, 2015; Vowles & Björk, 2018)
77 and mountain birch forests (Kaarlejärvi *et al.*, 2012; Vowles *et al.*, 2017). By contrast, lichens
78 seem to decline under climate warming, possibly due to increasing competition with prostrate
79 vascular plants (Cornelissen *et al.*, 2001; Elmendorf *et al.*, 2012; Alatalo *et al.*, 2017; Løkken *et al.*,
80 2019).

81 Dry and semi-dry mountain birch forests form key foraging areas for the semi-domestic
82 reindeer (*Rangifer tarandus*) both during winter and summer. During the winter, reindeer favor
83 dry and semi-dry mountain birch forests due to a high abundance of ground (e.g. *Cladina* sp.) and
84 partly also epiphytic lichens (e.g., *Bryoria* spp.). During the summer, reindeer habitat selection
85 depends not only on forage availability but also insect avoidance, resulting in that the semi-dry
86 and dry mountain birch forests are used especially in early and late summer (Bezard *et al.*, 2015).
87 The importance of reindeer grazing and browsing for the vegetation in these systems is well
88 documented (Oksanen & Virtanen, 1995; Lempa *et al.*, 2005; Kumpula *et al.*, 2011; Sundqvist *et al.*,
89 2019). Browsing generally decreases the biomass of mountain birches (Oksanen *et al.*, 1995;
90 Helle, 2002; Den Herder & Niemelä, 2003; Kumpula *et al.*, 2011) whereas grazing on ground
91 vegetation may decrease the understory evergreen dwarf shrubs and lichens (Lempa *et al.*, 2005;
92 Bernes *et al.*, 2014; Sundqvist *et al.*, 2019, but see Vowles *et al.*, 2017) and increase the deciduous
93 dwarf shrubs (Sundqvist *et al.*, 2019). With respect to dwarf shrubs, the grazing impacts in

mountain birch forests seem to contrast those from treeless tundra. In these systems, large ungulates may dampen the increase in deciduous shrub abundance in response to experimental warming (Post & Pedersen, 2008; Cahoon *et al.*, 2012; Väisänen *et al.*, 2014) and along decadal vegetation trends (Vowles *et al.*, 2017; Yläne *et al.*, 2018) while having negligible effects on the climate-induced increase in evergreen dwarf shrubs (Bråthen *et al.*, 2017a; Vowles *et al.*, 2017).

To date, there is limited understanding how ongoing vegetation trends in mountain birch ecosystems depend on the seasonality of reindeer grazing. Whether reindeer use the area for foraging during the winter or the summer has a major importance, because the seasonal timing of habitat use determines which component of the ecosystem – mountain birches, understorey vascular plants, or arboreal and ground lichens – are consumed by the reindeer (Kumpula *et al.*, 2011). During summer, mountain birches constitute an important food resource for the reindeer, and in some areas in northernmost Finland, reindeer can remove as much as 90% of the foliage within their browsing height (Helle, 2002). During winter, when mountain birch foliage is not available, reindeer feed on arboreal and ground lichens as well as evergreen dwarf shrubs and herbaceous plants that they dig out from under the snow (Kojola *et al.*, 1995; Storeheier *et al.*, 2002; 2003). Secondly, the importance of trampling as a mechanism by which reindeer impact vegetation depends on season. During winter, a thick snow pack protects vegetation from trampling, whereas during summer, besides grazing trampling forms a major determinant for understorey vegetation that affects especially the lichens (Kumpula *et al.*, 2011).

Given the importance of the forest-tundra ecotone as a habitat for the reindeer, an improved foreseeing of the vegetation changes under warming climate could help adapting the herding of reindeer to the changing environment. Analyzing decadal vegetation trends under differing grazing regimes does not enable separating the individual effects of grazing and warming from each other, but reveals their cumulative effect giving insights into current vegetation changes. One major aspect in these trends is the availability of lichens, which is important for the winter body condition of reindeer as well as on the productivity of reindeer herds which affect the economic profitability of reindeer husbandry (Kumpula *et al.*, 2002; Pekkarinen *et al.*, 2017). Lichen availability is generally managed by regulating the reindeer numbers and in some reindeer co-operatives also by using pasture rotation, i.e., the protection of the main winter ranges from summer grazing and trampling, (Kumpula *et al.*, 2011; Pekkarinen *et al.*, 2015; 2017). However, as the increasing abundance of prostate vascular plants in response to climate warming may affect lichens negatively (Cornelissen *et al.*, 2001; Alatalo *et al.*, 2017), lichen abundances in the future

are dependent not only on the intensity and the seasonal timing of grazing, but also on plant competition with other species. The ongoing vegetation trends have therefore raised concerns on the quantity and quality of forage supply for the reindeer, as this will likely exert major socio-economic consequences (Turunen *et al.*, 2009; Kumpula *et al.*, 2019).

We hypothesized that the recent changes in the number of mountain birches and in the composition of understorey vegetation in dry and semi-dry mountain birch forests are highly divergent depending on the timing of reindeer grazing. To test this hypothesis, we re-analyzed 24 study sites after 12 years that had been subjected to only summer or only winter grazing by reindeer since the 1980s. Although seasonal pasture rotation between the summer and the winter ranges was originally designed to protect lichens from trampling, it has also affected the forest structure (Kumpula *et al.*, 2011). In the winter ranges, mountain birches have a ‘shrub-like’ polycormic growth form with a high number of twigs and seedlings at the ground level, whereas in the summer ranges, browsing leads to a more open woodland dominated by large and tall mountain birches with fewer stems and most of the foliage above the browsing height (Oksanen *et al.*, 1995; Helle, 2002; Den Herder & Niemelä, 2003; Kumpula *et al.*, 2011). Based on the observations of increased mountain birch abundance (Tømmervik *et al.*, 2009) and reindeer preference on mountain birch as summer forage (Kumpula *et al.*, 2011), we predicted mountain birch seedlings to increase at a slower rate in the summer ranges. In line with the finding that reindeer grazing decreases evergreen dwarf shrubs and increases deciduous dwarf shrubs in these types of mountain birch forests (Sundqvist *et al.*, 2019), we also predicted that the climate-induced increase in evergreen dwarf shrubs (*sensu* Kaarlejärvi *et al.*, 2012; Vowles *et al.*, 2017) is weaker in summer than winter ranges, whereas the climate-induced increase in deciduous dwarf shrubs (*sensu* Elmendorf *et al.*, 2012) is stronger in summer ranges. Because plant responses to environmental changes in sub-arctic ecosystems may be slow in dry habitats due to a nutrient-limitation of plant productivity (e.g. Ylänne *et al.*, 2015), we predicted that semi-dry habitats have changed to a greater extent than dry habitats. To test whether increasing shrub abundances is related to changes in lichens (*sensu* Cornelissen *et al.*, 2001; Elmendorf *et al.*, 2012; Alatalo *et al.*, 2017), we also examined correlations among the 12-year changes in lichens and vascular plants.

Materials and Methods

Study areas and field sites

The study was conducted in Inari and Utsjoki municipalities in Finland (Fig. 1a; latitude 68°54'–69°49', longitude 26°00'–27°47', altitude 165–410 m a.s.l.). The mean annual temperature in the area is 0.3 °C, mean annual precipitation 448 mm, and the mean maximum snow depth (during March) 73 cm (2010–2019, Finnish Meteorological Institute). The vegetation has more or less continuous areas of short-statured, shrub-like polycormic growth forms of mountain birch. Evergreen dwarf shrubs dominate the understorey vegetation (e.g. *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, hereafter *E. hermaphroditum*, *Vaccinium vitis-idaea* L. and *Linnaea borealis* L.). The deciduous dwarf shrub *V. myrtillus* L. is also common. The graminoid species *Deschampsia flexuosa* (L.) Trin is the most common graminoid species. The ground layer is dominated by the bryophytes *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum* Hedw. spp. and ground lichens *Cladina rangiferina*, *C. mitis* and *Cladonia* spp. Climate in this area has changed substantially during the past decades. Interpolated daily meteorological data (1981–2010) indicate that the annual degree day sum (DD) has increased by 62 per decade, which is not only related to warmer summers, but also to the lengthening of the growing season (Rasmus *et al.*, 2020). Heavy rains have become more frequent as there is also an increasing trend for the largest daily precipitation (3–6 mm per decade, 1 day per decade for the number of heavy precipitation days). Snow cover formation has delayed by 4–7 days per decade (Rasmus *et al.*, 2020).

The herding of semi-domesticated reindeer by the Sámi people has formed a major means of land-use in the study area for centuries (Kortesalmi, 2008). The livelihood originally adapted to long seasonal migrations between nutrient-rich coastal areas of the Arctic Ocean in Norway during summer and continental lichen-rich mountain areas in Finland and Norway during winter (Oksanen & Virtanen, 1995). In 1852, the seasonal migration of reindeer herders between Norway and Finland (at that time an autonomic district within Russia) was prevented by law (Kortesalmi, 2008). Since the 1880's, reindeer herding has been practiced within separate reindeer herding co-operatives. In most co-operatives, grazing has taken place in same areas throughout the year. In order to promote the regeneration of lichens, a pasture rotation system was introduced in some co-operatives during 1980's, implemented through seasonal pasture rotation fences that separate winter and summer ranges.

In 2003, we selected 24 study sites within Muddusjärvi (2 095 km², 10 sites Sallivaara (2 871 km², 12 sites) and Kaldoaivi (2 230 km², 2 sites) herding co-operatives, from which 12 sites represented winter ranges and 12 sites summer ranges (Fig. 1a, b; Stark *et al.*, 2007; Kumpula *et al.*, 2011). We selected pairs of field sites in mountain birch forest habitats, where vegetation type,

elevation, slope aspect and distance (300–6500 meters) from a rotation fence were as comparable as possible. We did not locate sites at the close vicinity of fences, because trampling is often heavily concentrated near the rotation fences. The two sites located in Kaldoaivi were assigned as winter range sites and used as a comparison to two summer range sites in Muddusjärvi. Kaldoaivi herding co-operative has not built a pasture rotation fence, but reindeer generally use the area of these sites only during winter (Kumpula *et al.*, 2011). Reindeer densities before the 2000's were close to 3 reindeer/km² whereas during the 2000's they have been approximately 2.5 reindeer/km² with no significant difference between summer and winter range (see Appendix S1 in Supporting Information). The study area has not been subjected to vast insect outbreaks, in contrast to large districts further north (e.g. Biuw *et al.*, 2014).

Vegetation and soil analyses

In each field site, vegetation analyses and soil sampling were conducted along a sinuous line with 90° angles (i.e., a zigzag transect), where the starting point of the transect was randomly chosen and the next measurement points defined by moving ten meters in 90° turns (N = 8). In each measurement point, two types of plots were established, one for assessing the number of mountain birches and the other for analyzing ground vegetation and soil properties. We counted the number of mountain birches within a circle of 50 m² (radius 3.99 m) classified into four size categories 1) big birches (trunk thickness from the height of 1.3 meter > 1.5 cm), 2) small birches (over 1.5 meter in height but the trunk thickness from the height of 1.3 meter < 1.5 cm thick), 3) tall seedlings (30–150 cm in height) and 4) small seedlings (< 30 cm in height). We analyzed understory vegetation by collecting the aboveground biomass of dwarf shrubs, graminoids and forbs from a 0.25 m² square (size 0.5 × 0.5 m) placed two meters at random from the center of measurement point. For *E. hermaphroditum* only those parts of the stem with attached leaves were collected and old and thick woody structures discarded. Once the vascular vegetation was removed, visual estimates of lichen and moss cover were done on 5% precision (1% precision for covers lower than 5%), and the height of the most abundant lichen and moss species was measured from five randomly selected points with a ruler. We also took composite soil samples (three cores, the entire organic layer) from the sampling points. The thickness of the humus layers was measured from each soil core.

In the laboratory, plant biomass samples were dried for 24 hours at 104 °C and weighed. Lichen biomass was calculated from lichen cover and height using the recorded correlation of

lichen biomass and volume in northern Finland ($LB_{d.m.} = (0.6134 \times LC \times LH) + (0.000038075 \times LC^2 \times LH^2)$), where $LB_{d.m.}$ is the dry matter biomass of reindeer lichens in a stand ($kg\ d.m.\ ha^{-1}$); LC is the average reindeer lichen cover (%); and LH is the average reindeer lichen height (mm) (Kumpula *et al.*, 2000). Soil samples were frozen ($-20\ ^\circ C$) until analysis and fresh soils homogenized by sieving (2-mm mesh) after thawing. Soils were then determined for moisture ($105^\circ C$, 12 h) and organic matter content (SOM%, loss on ignition at $475^\circ C$, 4 h). Soil sample volume and the total sample weight was used to calculate bulk density ($g\ dry\ soil\ dm^{-3}$) and SOM stock ($g\ SOM\ m^{-2}$).

Field inventories conducted in 2003 and 2015 differed in some ways. In 2003, only leaf biomass was collected for *Vaccinium vitis-idaea*, but in 2015, the whole plant biomass was collected, and thus cannot be fully compared. In 2003, we had analyzed ten sampling points per each site, and two vegetation squares for sampling point, whereas in 2015 we analyzed eight sampling points and one vegetation square for sampling point. In the data analyses, we standardized the number of replicates to be the same for both years, and therefore included only one vegetation square from the first eight sampling points from 2003 when comparing the years 2003 and 2015.

Statistical tests

To test the effect of grazing seasonality on vegetation change between the years 2003 and 2015, we used a linear mixed effects model with seasonal range, habitat and year as fixed factors and site as a random factor (Kumpula *et al.*, 2011). We used logarithmic transformations where necessary to meet the requirements of linear mixed effect model (i.e., normal distribution and equality of variances). Soil properties in 2015 were tested using a linear mixed effects model with seasonal range and habitat as fixed factors and site as a random factor.

To test for associations between the change in lichen cover and biomass and the change in mountain birch and dwarf shrub abundances, we first calculated the relative change between the years 2003–2015 for each plant group for each site. As *E. hermaphroditum* formed an overwhelming proportion of the total evergreen dwarf shrubs, we used the change in this species to represent the association between lichens and evergreen dwarf shrubs. Yet, as the dominant deciduous dwarf shrubs *V. myrtillus* ja *V. uliginosum* have rather similar functional characteristics, we used the sum of total deciduous dwarf shrubs as an explanatory variable. In addition, the changes in the numbers of different-sized mountain birches and the corresponding other

cryptogam coverage (i.e., lichen for mosses, mosses for lichens) were included as explanatory variables. Pearson's correlation was used to check possible autocorrelation among explanatory variables. We compared several linear mixed effect models where explanatory variables were added one at a time until the model, based on Akaike's Information Criteria (AIC), no longer improved with added variables (a forward-selection). The influence of explanatory variables was tested separately for the winter and summer range, as this excludes the role of grazing seasonality for lichen abundances and thus best identifies possible relationship between lichens and other plants. For investigating associations between vegetation and SOM stock, we also conducted linear mixed effects models for SOM stock in 2015 using the same explanatory variables. Analyses were conducted using SPSS 25 Statistical software.

261

262 Results

263 *The number of mountain birches*

264 The number of small mountain birch seedlings was higher in winter than summer ranges, and had
265 increased drastically during the past 12 years in both seasonal ranges (Fig. 2; main effects of
266 Habitat and Year; Table 1). The number of small mountain birch seedlings had increased to a
267 greater extent in dry than semi-dry habitats (Fig. 2; Habitat \times Year -interaction; Table 1). Tall
268 seedlings, which were more abundant in winter than summer ranges and in dry than semi-dry
269 habitats, had increased overall (Fig. 2, main effects of Range, Habitat and Year), but to a stronger
270 extent in winter than summer ranges (Range \times Year -interaction; Table 1) and in dry than semidry
271 habitats (Habitat \times Year -interaction; Table 1). There was no significant effect of seasonal range,
272 habitat or year on the number of small trees (Fig. 2, Table 1). The number of big trees had
273 increased overall, but this increase was the strongest in dry habitats in the summer ranges (Fig. 2;
274 main effect of Year, Range \times Habitat \times Year -interaction; Table 1).

275 *Understorey vegetation*

276 The average biomass of mountain crowberry, *E. hermaphroditum*, had increased by 50–150%
277 (Fig. 3; main effect of year; Table 1), but the change over time also depended on seasonal range
278 and habitat (Range \times Year, Habitat \times Year, and Range \times Habitat \times Year -interactions; Table 1). *E.*
279 *hermaphroditum* had increased to a stronger extent in summer than winter ranges in dry habitats,
280 but to a stronger extent in winter than in summer ranges in semi-dry habitats (Fig. 3). Deciduous

dwarf shrubs *Vaccinium myrtillus* had increased by 85% and the graminoid *Deschampsia flexuosa* by 136% irrespective of seasonal range or habitat (Table 1, main effects of Year; Fig. 3). For *V. uliginosum*, the change over time was stronger in dry (235%) than semidry (82%) habitats (Habitat \times Year -interaction; Table 1). The biomass of the evergreen dwarf shrub *Calluna vulgaris* had also increased and to a stronger extent in winter (217%) than summer (118%) ranges (main effect of Year, Range \times Year -interaction; Table 1).

The cover of *Cladonia* lichens was higher in winter than summer ranges and higher in dry than semidry habitats (Fig. 4, main effects of Seasonal range and Habitat), and had increased in dry habitats (Fig. 4, main effect of Year, Habitat \times Year -interaction; Table 1). Due to a decrease in *Cladonia* height across habitats and seasonal ranges, *Cladonia* biomass had remained unchanged in dry habitats, and decreased by 38% in semi-dry habitats (Fig. 4, Habitat \times Year -interaction; Table 1). In 2015, *Cladonia* biomass was 11.5 times higher in winter than summer ranges, when in 2003, *Cladonia* biomass had been 6.8 times higher in winter ranges. *Cladonia* lichens dominated the impact on the total lichen cover and we therefore do not present the results separately. The cover of mosses had increased by 178% (Fig. 4, main effect of Year; Table 1). The increase in moss cover was weaker in dry summer ranges than elsewhere (Range \times Year and Range \times Habitat \times Year -interactions; Table 1).

Correlations among the changes in plant groups between 2003-2015, and among vegetation and soil properties in 2015

Overall, summer and winter ranges showed similar correlations among the changes in plant groups. In the summer ranges, the best predictors for change in lichen cover between 2003 and 2015 were the number of mountain birch seedlings and the habitat (see Appendix S2). In the winter ranges, adding the change in deciduous dwarf shrub biomass to the changes in the number of mountain birch seedlings and habitat further improved the model (Appendix S2). Correlation plot showed a synchronized relationship (i.e. positive correlation) between the change in lichen cover and small mountain birch seedlings in both winter and summer ranges (Fig. 5a). For the change in moss cover, in both summer and winter ranges, the best predictors were the changes in the total deciduous dwarf shrub and *E. hermaphroditum* biomass together with the habitat (Appendix S2). Similar to the pattern observed in lichen cover and biomass, the relationship between the changes in the moss cover and deciduous dwarf shrubs was synchronized (Fig. 5b).

311 We found no statistically significant effects of seasonal range or habitat on soil
312 properties except for a higher bulk density in dry than semi-dry habitats (Table 2 and Appendix
313 S3). Further, linear mixed model showed no statistically significant associations between the soil
314 OM stock and any of the plant variables in the 2015 data.

315 Discussion

316 Our resampling of the mountain birch forests in northern Finland revealed that the number of
317 mountain birches and the biomass of evergreen dwarf shrubs had increased substantially in the
318 study sites during the past 12 years in line with earlier results on change in mountain birches
319 (Tømmervik *et al.*, 2009) and evergreen dwarf shrubs (Maliniemi *et al.*, 2017; Vuorinen *et al.*,
320 2017). Yet, the increase in these plant groups varied with seasonal range and habitat, revealing that
321 the seasonal use of reindeer ranges was a major driver for the ongoing forest-tundra ecotone
322 change. Graminoids, deciduous dwarf shrubs and mosses had become more abundant, which also
323 agrees with previous findings on current vegetation trends (Tømmervik *et al.*, 2009) and from
324 climate warming manipulations (Ylänne *et al.*, 2015). For these plant groups, however, the change
325 was more or less similar in both summer and winter ranges.

326 *Season range effects on the mountain birch forest structure*

327 The number of mountain birches had increased in both summer and winter range, but the changes
328 varied among the different-sized mountain birches. Following our prediction that browsing on
329 mountain birches may dampen their increase, tall mountain birch seedling numbers had increased
330 more in winter than summer ranges. However, small seedlings had increased similarly in both
331 winter and summer ranges although still remaining more abundant in the winter ranges, and the
332 number of small trees had stayed unchanged. By contrast, the number of big mountain birch trees
333 had increased in summer ranges, which could reflect a higher growth allocation of the mountain
334 birch to the main trunk under browsing. These size-dependent effects of browsing on mountain
335 birches support earlier results near altitudinal treeline, where sheep browsing reduced the growth
336 of smaller mountain birches, while tall birches were more resistant to browsing even when still
337 within the browsing height (Speed *et al.*, 2011). Our results also align with findings from riparian
338 areas showing that high reindeer densities may keep small *Salix* willows in a ‘browse trap’ where
339 they remain low, whereas shrub growth into a certain height provides a ‘browse escape’ (Bråthen
340 *et al.*, 2017b). Browsing-induced trends in the mountain birch forest structure thus seem linked

341 with the morphological responses of mountain birch to browsing. Overall, our data indicate that
342 although summer browsing clearly inhibits the climate-driven ‘shrubification’ of mountain birch
343 forests, the current browsing intensity does not seem to entirely prevent seedlings from increasing
344 in numbers. This agrees with vegetation inventories from northern Norwegian reindeer ranges
345 (Tømmervik *et al.*, 2009) and with local observations (Horstkotte *et al.*, 2017; Forbes *et al.*, 2020)
346 indicating that these systems are becoming increasingly forested.

347 The patterns detected in our study indicate that – if seedling numbers continue to
348 increase more rapidly in winter ranges whereas big trees continue to increase in summer ranges –
349 the differentiation of the mountain birch forest structure between seasonal ranges (as described in
350 Helle, 2002; Den Herder & Niemelä, 2003; Kumpula *et al.*, 2011) will amplify in time. Yet, given
351 the strong increase in small mountain birch seedlings in both seasonal ranges, reductions in the
352 browsing pressure would likely rapidly promote mountain birch ‘shrubification’ also in the
353 summer ranges. Browsing on mountain birches may have a particularly high importance in
354 Finland, because supplementary winter time feeding supports the present reindeer numbers and
355 partly shifts the food limitation of reindeer from winter to summer nutrition (Kumpula *et al.*,
356 2002). This may also have led to a situation where reindeer continuously graze in the same areas
357 when in the past summer range areas were changed every couple of years (Kumpula *et al.*, 2011).
358 It has been suggested that the current browsing intensity on mountain birches in Finland may be
359 strong enough to prevent the renewal of these woodlands and result in a gradual transformation of
360 these areas into open tundra (Oksanen *et al.*, 1995). During the timeframe of our study, we did not
361 detect any evidence towards this, in line with the results by Vuorinen *et al.* (2017). However, the
362 cumulative effect of browsing in combination with other disturbances – such as major insect
363 outbreaks – could contribute to keeping these areas open and cause mountain birch forests to
364 transform into treeless tundra (Jepsen *et al.*, 2008; Biuw *et al.*, 2014).

365 *Habitat-specific grazing impact on the increase of evergreen shrubs*

366 The biomass of evergreen shrubs that mostly consisted of *E. hermaphroditum*, had increased to a
367 considerable extent, agreeing with earlier studies (e.g. Maliniemi *et al.*, 2017; Vuorinen *et al.*,
368 2017; Vowles *et al.*, 2017). The rapid rate of increase in *E. hermaphroditum* biomass is
369 noteworthy, because it could in time drive tundra communities towards slower process rates and
370 lower biodiversity (Bråthen *et al.*, 2017; Vowles & Björk, 2018). *E. hermaphroditum* is known for
371 its capacity to gain dominance through suppressing other plant species through dense clonal

372 growth, by allelopathic phenolic compounds, and by producing decomposition-resistant litter that
373 decelerates soil nutrient cycling (Gallet *et al.*, 1999; Bråthen *et al.*, 2010). In our study sites, we
374 found no difference in SOM stocks between the seasonal ranges and no correlations between *E.*
375 *hermaphroditum* biomass and soil properties. The ecosystem effects of *E. hermaphroditum* could
376 thus be slower than could be detected within the timeframe of the study.

377 Earlier studies have indicated that reindeer grazing decreases evergreen shrub
378 abundance in mountain birch forests (Sundqvist *et al.*, 2019) but may not suppress climate-
379 induced increase in them (Bråthen *et al.*, 2017; Vowles *et al.*, 2017). In our study, the change in *E.*
380 *hermaphroditum* biomass over time interacted with habitat and seasonal range type. We suggest
381 that this phenomenon derives from the food selection of reindeer under current vegetation regimes
382 together with the disturbance sensitivity of this species. *E. hermaphroditum* is unpalatable to most
383 herbivores and relatively sensitive to disturbance (Tybirk *et al.*, 2000). For example, clipping
384 experiments have demonstrated its recovery to be much weaker compared with other species
385 (Manninen *et al.*, 2011), and that, when combined with fertilization, *E. hermaphroditum* could
386 recover and out-compete other plant species after a 50% biomass loss, but not after a complete
387 biomass removal (Aerts, 2010). *E. hermaphroditum* may also decrease in abundance after winter
388 conditions promoting pathogenic outbreaks (Olofsson *et al.*, 2011), due to intense winter
389 disturbance by rodents (Tuomi *et al.*, 2019), and after moth outbreaks (Biuw *et al.*, 2014). Overall,
390 the different studies demonstrate that only a very high disturbance levels seem to break up the
391 dominance of crowberry (Olofsson *et al.*, 2005; Väisänen *et al.*, 2013), which likely explains why
392 *E. hermaphroditum* biomass had increased in both summer and winter ranges (*sensu* Bråthen *et*
393 *al.*, 2017a; Vowles *et al.*, 2017).

394 Yet, despite the unpalatability of evergreen dwarf shrubs such as *E. hermaphroditum* to
395 most herbivores, low lichen abundances in northernmost Finland have caused a shift in the
396 reindeer winter nutrition towards consuming evergreen dwarf shrubs as part of winter diet (Kojola
397 *et al.*, 1995; Ophof *et al.*, 2013). We suggest that this might largely explain why, in dry habitats
398 that constitute the most common winter foraging sites for the reindeer, the increase in *E.*
399 *hermaphroditum* was weaker in winter than summer range. *E. hermaphroditum* is also consumed
400 by the reindeer during summer particularly when leaves are young and contain low concentrations
401 of allelochemicals (Iversen *et al.*, 2014) and is sensitive to trampling-induced damage (Tybirk *et*
402 *al.*, 2000). This might largely explain why, in semi-dry habitats that constitute more common
403 summer foraging sites for the reindeer, the increase in *E. hermaphroditum* was weaker in summer

404 than winter range. The strength at which the reindeer suppress the increase in *E. hermaphroditum*
405 could thus be driven by the reindeer foraging behavior during different seasons. This interpretation
406 agrees with earlier studies showing the effects of reindeer grazing on vegetation and soil processes
407 to be highly dependent on the spatial patterns of habitat use (Moen *et al.*, 2009; Stark *et al.*, 2015).

408 *Increases of graminoid and deciduous dwarf shrub abundance irrespective of seasonal grazing*

409 Deciduous dwarf shrubs *V. myrtillus* and *V. uliginosum* together with the graminoid *D. flexuosa*
410 had increased similarly in both summer and winter ranges, which contrasted our prediction that
411 grazing could even intensify the increase in these species (Sundqvist *et al.*, 2019). This result
412 aligns with observations from northern Norwegian reindeer ranges showing increased area of
413 graminoid- and deciduous dwarf shrub –dominated habitats at the expense of shrub- and lichen-
414 dominated mountain birch habitats (Tømmervik *et al.*, 2004; 2009). The increase in deciduous
415 dwarf shrubs could be mainly driven by climate warming, or alternatively, grazers may influence
416 these plant groups through several mechanisms that counteract each other's effects. Deciduous
417 *Vaccinium* species and graminoids are favoured in the reindeer summer diet (Kumpula *et al.*,
418 2011), but they also are resilient to disturbance and benefit from nutrient enrichment (Manninen *et*
419 *al.*, 2011). As soil nitrogen availability in mountain birch forests is sometimes higher in the
420 summer ranges (Stark *et al.*, 2007), different mechanisms could lead to no net effect of grazing on
421 how deciduous dwarf shrub and graminoid abundances change through time.

422 *Synchronized relationship between vegetation 'shrubification' and cryptogam abundances*

423 The changes in lichen abundances were largely attributed to the change in *Cladonia* lichens.
424 During the past 12 years, in dry habitats, the cover of *Cladonia* lichens had increased while its
425 biomass had remained unchanged. In semi-dry habitats, by contrast, the cover of *Cladonia* lichens
426 showed no change, yet the biomass had decreased. Interestingly, similar results of increasing cover
427 and decreasing biomass have been reported for some co-operatives in the Finnish reindeer range
428 inventories (Kumpula *et al.*, 2019). Trampling is well known to reduce the height of the mat-
429 forming ground lichens (Ahti, 1977; Suominen & Olofsson, 2000), but it also induces physical
430 fragmentation of the lichens. As lichens regenerate from fragments in the ground, it is possible
431 that some trampling levels may simultaneously causes a lower lichen height and biomass but a
432 higher lichen cover.

433 As climate warming may reduce lichens through increased competition from vascular
434 plants (Cornelissen *et al.*, 2001; Alatalo *et al.*, 2017), it is important to assess whether increasing
435 mountain birch seedlings and dwarf shrubs indirectly decrease lichen abundances for practical
436 reindeer management. If – as indicated in our findings – protecting winter ranges from summer
437 grazing and browsing simultaneously promotes ‘shrubification’ of mountain birch forests, pasture
438 rotation could indirectly intensify plant competition between lichens and vascular plants.
439 Consequently, seasonal pasture rotation might be less efficient in restoring the lichen grounds in a
440 future warmer climate. Yet, we found no evidence to support that increasing shrub abundance had
441 contributed to a decline in lichens. Instead, the changes in lichen cover and biomass showed a
442 positive relationship with small mountain birch seedling change. This synchronized association
443 between lichens and mountain birch seedlings rather suggests that the importance of plant
444 consumption and trampling outweighed that of plant competition. The reasons for our findings
445 may derive from facts that reindeer graze on lichens in dry habitats to some extent also during
446 summer (Bezard *et al.*, 2015). Further, the vulnerability of lichens to increasing plant competition
447 may vary among the lichen species (Martin & Mallik, 2007) and be lower in dry and semi-dry
448 habitats that usually have less developed plant cover compared with habitats with more prostrate
449 plants (Cornelissen *et al.*, 2001; Yläne *et al.*, 2015). Interestingly, this result also contrasts
450 findings from northern Norway with higher lichen abundances that by removing ‘the barrier
451 effect’ of a thick lichen coverage, reindeer grazing promotes birch seed germination and sprouting,
452 and lead to an establishment of tree clusters (Tømmervik *et al.*, 2004; 2009).

453 We also detected a substantial increase in moss cover in the ground layer (as in
454 Tømmervik *et al.*, 2009), which showed a positive relationship with increasing in dwarf shrubs
455 and demonstrated another positive association between vascular plants and cryptogams. This
456 suggests that mosses in these relatively dry systems could indirectly benefit from a thicker dwarf
457 shrub layer providing a more stable and humid microclimate.

458 *Implications for reindeer forage availability*

459 Our findings indicated that the northern Finnish mountain birch ecosystems are currently
460 undergoing a remarkable change both in forest structure and understorey vegetation. In our study
461 areas, increasing mountain birch seedling numbers, dwarf shrub biomass and moss coverage
462 emerged as general trends, but the strength of these changes varied among seasonal ranges and
463 habitats. Contrasting with the prediction that vegetation changes at a faster rate in semi-dry than

464 dry habitats, trends in deciduous dwarf shrubs and graminoids were similar for both habitats, small
465 mountain birch seedlings had increased more in dry habitats, and the habitat-specific trends in
466 evergreen dwarf shrubs interacted with seasonal grazing. Put together, the seasonal foraging
467 patterns of reindeer shaped vegetation trajectories differently depending on habitat, and
468 consequently, a mosaic of differing vegetation trajectories was formed depending on both the
469 seasonality of grazing and habitat.

470 Our results indicated that the current summer browsing pressure is not enough to halt
471 the ‘shrubification’ of summer range, which increases important summer forage plants for the
472 reindeer, such as mountain birch foliage and the deciduous dwarf shrubs *V. myrtillus* and *V.*
473 *uliginosum* (Kumpula *et al.*, 2011). If the current vegetation trends continue, the quality of
474 summer ranges for the reindeer could thus improve in the future. Yet, the question remains what
475 are the main trends and drivers for vegetation change in terms of the winter forage. Notably, lichen
476 biomass had stayed unchanged in dry habitats and declined in semi-dry habitats during the past 12
477 years despite lower reindeer numbers prior to 2015 than prior to 2003. The higher lichen biomass
478 in winter than summer ranges supports that pasture rotation promotes lichen abundances
479 (Pekkarinen *et al.*, 2017), but yet, combined pasture rotation and reduced reindeer numbers had
480 not enabled the lichen biomass to increase in time. It is possible that climate warming affects
481 lichens through yet unidentified interactions. One potential mechanism could be delayed snowfall
482 (Forbes *et al.*, 2020; Rasmus *et al.*, 2020) leading the reindeer to enter the winter range territories
483 before a formation of a thick snow layer protecting lichens from trampling. It is also known that
484 other means of land-use, such as forestry, contract the realized available range area for the
485 reindeer, leading to a higher number of reindeer in the remaining ranges (Jaakkola *et al.*, 2013;
486 Kumpula *et al.*, 2014; Sandström *et al.*, 2016). Although we studied mountain birch sites, the
487 majority of the total winter range area in the studied reindeer co-operatives constitute of pine
488 (*Pinus sylvestris* L.) forests subjected to forestry (Kumpula *et al.*, 2019). According to current
489 models, lichen biomass would increase only under considerable reductions in reindeer numbers
490 (Pekkarinen *et al.*, 2015), but still, the reduction of reindeer number should be added by other
491 measures, such as ageing of the forest structure in winter ranges (Kumpula *et al.*, 2019). This
492 ongoing trend in reindeer ranges could possibly lead to an increase in the proportion of other
493 plants in the winter diet of reindeer (Kojola *et al.*, 1995; Ophof *et al.*, 2013).

494

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498

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505

506 **Data availability statement**

507 Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.4qrfj6q91> (Stark,
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509

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Table 1. The effect of seasonal range (summer or winter range), habitat (semi-dry or dry), year (2003 and 2015), and their interactions on the number of mountain birches and the biomass of understorey dwarf shrubs, graminoids, lichens and mosses. F- and P-values are obtained by Linear Mixed Effects with seasonal range, habitat and year as fixed factors and site as a random factor.

	Seasonal range		Habitat		Year		Seasonal range × Habitat		Seasonal range × Year		Habitat × Year		Seasonal range × Habitat × Year	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
<i>Betula pubescens</i>														
ssp. <i>czerepanovii</i>														
small seedlings	3.0	0.098	10.7	0.004	69.3	0.000	0.4	0.556	2.2	0.135	24.7	0.000	0.1	0.962
tall seedlings	31.0	0.000	18.7	0.000	43.7	0.000	1.6	0.225	18.2	0.000	16.5	0.000	1.2	0.282
small trees	0.4	0.541	0.1	0.979	2.2	0.143	2.7	0.116	2.1	0.151	0.9	0.343	3.1	0.080
big trees	3.2	0.088	1.0	0.332	8.5	0.004	1.2	0.288	2.1	0.146	1.5	0.220	4.1	0.043
<i>Empetrum nigrum</i>	1.7	0.208	1.5	0.237	75.6	0.000	4.3	0.052	6.1	0.014	6.3	0.012	15.2	0.000
<i>Vaccinium myrtillus</i>	0.3	0.575	0.5	0.497	7.4	0.007	0.1	0.982	0.1	0.709	1.0	0.308	0.1	0.825
<i>Vaccinium vitis-idaea</i>	0.7	0.422	0.6	0.464	0.1	0.769	0.1	0.779	0.1	0.788	0.7	0.419	0.1	0.873
<i>Vaccinium uliginosum</i>	0.1	0.721	3.8	0.067	29.8	0.000	0.4	0.541	0.1	0.776	7.3	0.007	0.8	0.364

<i>Calluna vulgaris</i>	3.0	0.100	1.1	0.303	10.6	0.001	1.9	0.187	8.4	0.004	1.9	0.172	8.8	0.003
<i>Deschampsia flexuosa</i>	0.2	0.666	1.2	0.291	6.6	0.010	0.1	0.848	0.1	0.862	2.4	0.121	0.1	0.733
<i>Cladonia</i> biomass	9.5	0.006	1.1	0.307	1.2	0.278	0.7	0.408	1.3	0.265	8.4	0.004	5.3	0.022
<i>Cladonia</i> sp. (%)	17.6	<0.001	8.0	0.010	18.8	<0.001	2.4	0.137	3.0	0.137	21.2	<0.001	2.8	0.098
Mosses (%)	0.2	0.649	5.0	0.036	66.5	<0.001	0.0	0.845	4.8	0.029	2.2	0.143	5.3	0.022

Table 2. Soil properties in the summer and the winter ranges of a dry and semidry habitat in northern Finnish reindeer management districts. Values are mean + S.E. in parentheses, N = 24 sites, 8 replicates within site.

Variable	Dry habitat		Semidry habitat	
	Summer range	Winter range	Summer range	Winter range
Moisture (%)	47.3 (5.0)	34.2 (3.1)	36.3 (1.9)	39.6 (2.0)
SOM (%)	45.9 (4.4)	67.5 (3.2)	70.2 (2.1)	67.9 (2.0)
Bulk density (kg dry soil dm ⁻³)	0.37 (0.06)	0.26 (0.03)	0.20 (0.03)	0.21 (0.02)
Humus thickness (cm)	1.4 (0.14)	2.1 (0.14)	2.2 (0.09)	2.1 (0.12)
SOM stock (kg m ⁻²)	2.0 (0.2)	3.1 (0.2)	2.6 (0.2)	2.3 (0.1)

Figure legends:

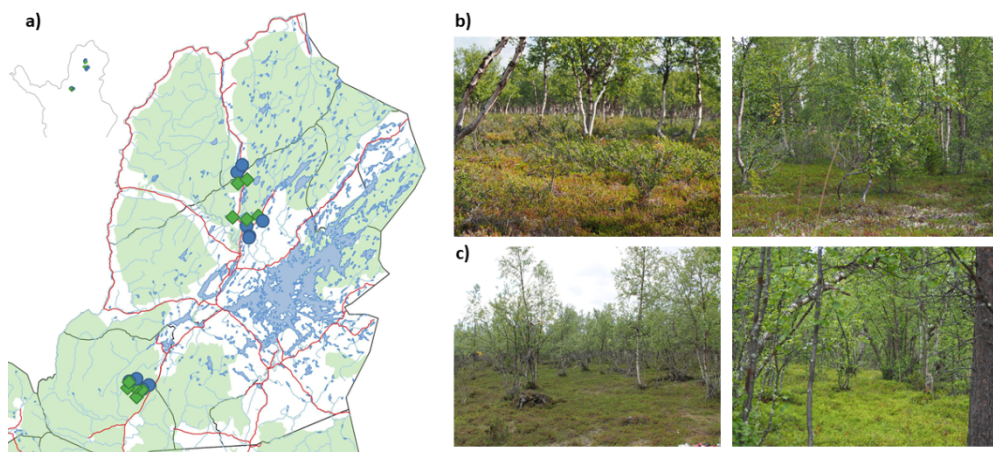
Figure 1. a) The study sites in summer and winter ranges in Muddusjärvi, Sallivaara and Kaldoaivi herding co-operatives in northern Finland. Green area indicates a nature conservation area, green dots summer range sites and blue dots winter range sites. b) Summer and winter range site in a dry habitat. c) Summer and winter range site in a semi-dry habitat.

Figure 2. The number of different-sized mountain birches in summer and winter ranges of the reindeer in dry and semi-dry habitats (mean + S.E., N = 24 sites, 8 replicates within site).

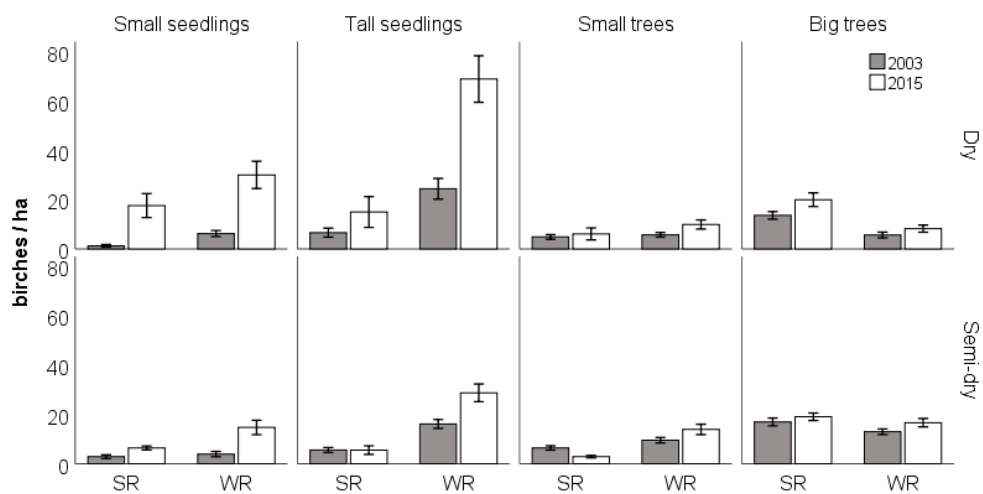
Figure 3. The biomass of understorey dwarf shrubs in summer ranges (SR) and winter ranges (WR) of the reindeer in dry and semi-dry habitats (mean + S.E., N = 24 sites, 8 replicates within site).

Figure 4. The cover of *Cladonia* lichens and mosses, and the height and biomass of *Cladonia* lichens in summer ranges (SR) and winter ranges (WR) of the reindeer in dry and semi-dry habitats (mean + S.E., N = 24 sites, 8 replicates within site).

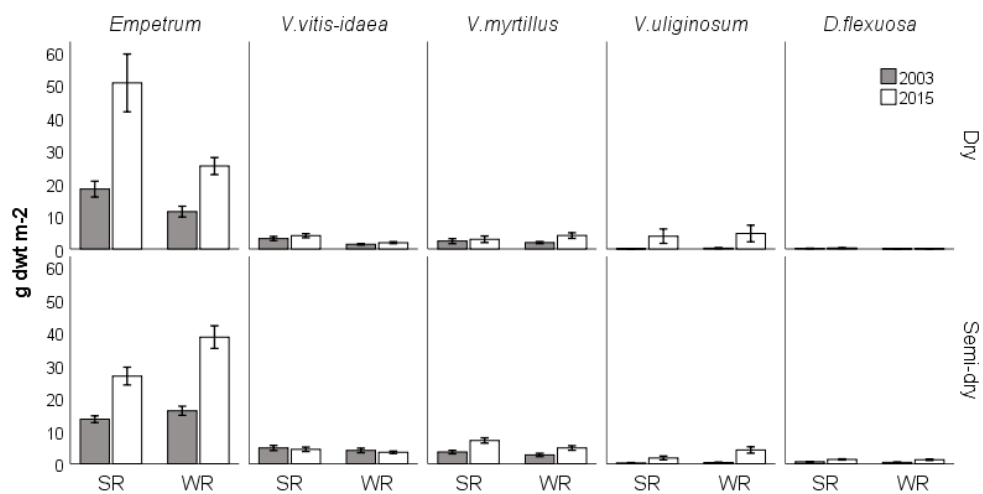
Figure 5. Correlations between the 12-year changes in *Cladonia* lichen cover and mountain birch seedling numbers, and between the changes in moss cover and deciduous dwarf shrub biomass in winter and summer ranges.



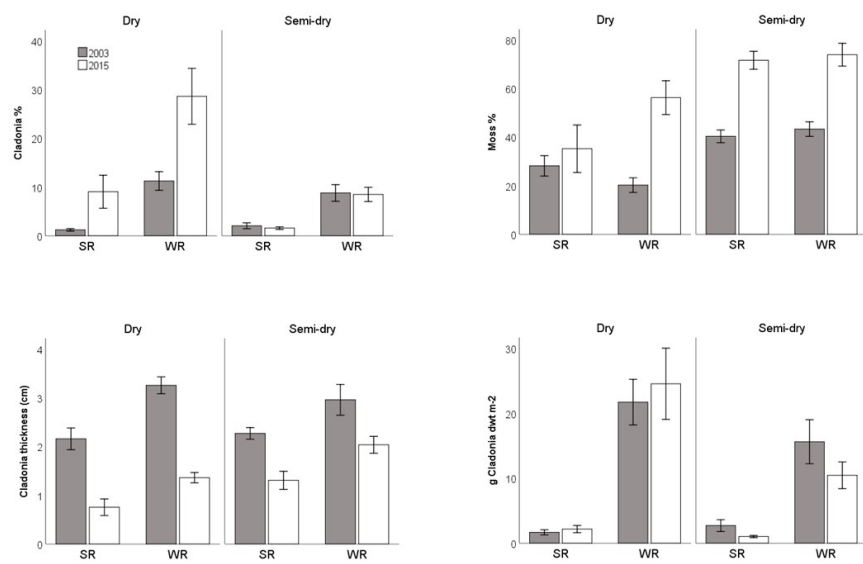
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