High resistance to climatic variability in a dominant tundra shrub species

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Climate change is modifying temperature and precipitation regimes across all seasons in northern ecosystems. Summer temperatures are higher, growing seasons extend into spring and fall and snow cover conditions are more variable during winter. The resistance of dominant tundra species to these season-specific changes, with each season potentially having contrasting effects on their growth and survival, can determine the future of tundra plant communities under climate change. In our study, we evaluated the effects of several spring/summer and winter climatic variables (i.e. summer temperature, growing season length, growing degree days, and number of winter freezing days) on the resistance of the dwarf shrub *Empetrum nigrum*. We measured over six years the ability of *E.nigrum* to keep a stable shoot growth, berry production, and vegetative cover in five *E. nigrum* dominated tundra heathlands, in a total of 144 plots covering a 200-km gradient from oceanic to continental climate. Overall, *E. nigrum* displayed high resistance to climatic variation along the gradient, with positive growth and reproductive output during all years and sites. Climatic conditions varied sharply among sites, especially during the winter months, finding that exposure to freezing temperatures during winter was correlated with reduced shoot length and berry production. These negative effects however, could be compensated if the following growing season was warm and long.Our study demonstrates that *E. nigrum* is a species resistant to fluctuating climatic conditions during the growing season and winter months in both oceanic and continental areas. Overall, *E. nigrum* appeared frost hardy and its resistance was determined by interactions among different season-specific climatic conditions with contrasting effects.

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10   ABSTRACT

11   Climate change is modifying temperature and precipitation regimes across all seasons in northern

12   ecosystems. Summer temperatures are higher, growing seasons extend into spring and fall and

13   snow cover conditions are more variable during winter. The resistance of dominant tundra

14   species to these season-specific changes, with each season potentially having contrasting effects

15   on their growth and survival, can determine the future of tundra plant communities under climate

16   change.

17   In our study, we evaluated the effects of several spring/summer and winter climatic variables

18   (i.e. summer temperature, growing season length, growing degree days, and number of winter

19   freezing days) on the resistance of the dwarf shrub *Empetrum nigrum*. We measured over six

20   years the ability of *E. nigrum* to keep a stable shoot growth, berry production, and vegetative

21   cover in five *E. nigrum* dominated tundra heathlands, in a total of 144 plots covering a 200-km

22   gradient from oceanic to continental climate.

23   Overall, *E. nigrum* displayed high resistance to climatic variation along the gradient, with

24   positive growth and reproductive output during all years and sites. Climatic conditions varied

25   sharply among sites, especially during the winter months, finding that exposure to freezing

26   temperatures during winter was correlated with reduced shoot length and berry production.

27   These negative effects however, could be compensated if the following growing season was

28   warm and long.

29   Our study demonstrates that *E. nigrum* is a species resistant to fluctuating climatic conditions

30   during the growing season and winter months in both oceanic and continental areas. Overall, *E.*

31   *nigrum* appeared frost hardy and its resistance was determined by interactions among different

32   season-specific climatic conditions with contrasting effects.

33   INTRODUCTION

34   Climate change is taking place across all seasons. In tundra ecosystems in particular, there is

35   evidence of a long term warming trend during winter, spring and summer (Epstein, Bhatt et al.

36   2017) resulting in longer growing seasons and varying snow cover conditions (Xu, Myneni et al.

37   2013). An increase in extreme winter warming events, where snow melts in midwinter and

38   exposes tundra vegetation to subsequent frost damage, has also been reported (Bjerke, Treharne

39   et al. 2017). Studying how dominant tundra species respond to this season-specific climatic

40   variability, can help predict the potential resilience of tundra communities under climate change.

41   Species with traits providing reduced sensitivity to environmental variability, such as long-life

42   span and seed bank accumulation (i.e. storage effects) (Chesson 2000), or with plastic growth

43   rates (Jump and Penuelas 2005), are expected to have high overall resistance to climate change

44   (Oliver, Heard et al. 2015). Here we define resistance as the capacity of a species to remain

45   stable in the face of environmental perturbations through persistence (i.e. positive growth and

46   reproduction) (Oliver, Heard et al. 2015, Ingrisch and Bahn 2018). Thus, under the predicted

47   climate warming scenario, a resistant species should grow and reproduce at a similar or higher

48   rate under warmer conditions. For example, shrubs, which account for much of the biomass in

49   tundra ecosystems (Walker, Raynolds et al. 2005), appear resistant to increasing summer

50   temperatures, responding with increased biomass and flowering (Myers-Smith, Forbes et al.

51   2011, Buizer, Weijers et al. 2012). However, some shrubs display poor resistance signs, such as

52   shoot death and low productivity, in response to changing winter conditions, e.g., extreme winter

53   warming events (Bjerke, Karlsen et al. 2014). Hence, the overall resistance of tundra shrubs to

54   climatic variability appears to be season-dependent and is currently not well understood.

55   A common approach for studying the impact of climate change on plant resistance is through

56   manipulation experiments during the growing season (e.g. Elmendorf et al. 2012). However,

57   experimental studies have been found to under predict the effects of climate change (Wolkovich,

58   Cook et al. 2012). Further, there are calls for the integration of summer and winter conditions in

59   climate studies, especially in seasonally snow-covered ecosystems (Sanders-DeMott and

60   Templer 2017). Thus, observational studies encompassing a range of ongoing yet differing

61   climate change developments during all seasons, can provide insight in to the long-term adaptive

62   potential of species and help predict their resistance to climate change.

63   *Empetrum nigrum* is an evergreen dwarf shrub that creates vast areas of monospecific vegetation

64   in tundra ecosystems across the northern hemisphere (Tybirk, Nilsson et al. 2000). *E. nigrum* is a

65   niche constructing species and its ecosystem modifying properties are well documented (Wardle,

66   Nilsson et al. 1998, Tybirk, Nilsson et al. 2000). For example, *E. nigrum* has been linked to a

67   reduction in species richness in tundra plant communities (Mod, Heikkinen et al. 2016, Bråthen,

68   Gonzalez et al. 2018), and has been found to slow down the recovery of tundra heathland after

69   simulated winter warming damage mainly due to its allelopathic properties (Aerts 2010). Further,

70   *E. nigrum* has responded to warmer growing seasons with an increase in biomass, flowering, and

71   fruiting in both manipulation experiments (Buizer, Weijers et al. 2012) and observational studies

72   (Bråthen, Gonzalez et al. 2018). However, there are also reports of decreasing reproductive and

73   vegetative output caused by winter extreme events (Bokhorst, Bjerke et al. 2010, Bokhorst,

74   Bjerke et al. 2011) and outbreaks of the pathogenic fungus *Arwidssonia empetri* under increased

75   snow cover (Olofsson, Ericson et al. 2011). Nevertheless, *E. nigrum* thrives in a wide range of

76   habitats, from exposed ridges to more sheltered depressions and appears to have high

77   morphological plasticity to cope with varying snow cover conditions (Bienau, Hattermann et al.

78   2014), in addition to being resistant to ice encapsulation (Preece, Callaghan et al. 2012). Hence,

79   the future abundance and distribution of *E. nigrum* in tundra ecosystems under climate change is

80   currently not well understood. Since *E. nigrum* has a strong influence on plant community

81   structure and diversity, hence reducing plant community resilience (Oliver, Heard et al. 2015),

82   understanding its response to climate change is imperative for making predictions of the vast

83   areas where it is present.

84   The goal of our study was to investigate the resistance of *E. nigrum* to fluctuations of

85   temperature and precipitation over multiple winter and summer seasons along a steep climatic

86   gradient. To achieve this, we measured over six years shoot growth, berry production, and

87   vegetative cover in five *E. nigrum* dominated tundra heathlands, in a total of 144 plots covering a

88   200-km gradient from oceanic to continental climate. Using soil-surface temperature loggers, we

89   registered how often the vegetation was exposed to freezing temperatures (i.e. number of

90   freezing days) in addition to fluctuations in growing season length, summer temperature and

91   growing degree days. We expect *E. nigrum* to be a species capable of persisting under varying

92   environmental conditions because it has a broad ecological niche occurring along a gradient of

93   temperature, moisture and bedrock types (NBIC 2005, Bråthen, Gonzalez et al. 2018), it is able

94   to dominate heathlands under a range of climates (Büntgen, Hellmann et al. 2015), and is a slow

95   growing, long lived species (Bell and Tallis 1973). However, we still expect *E. nigrum* fitness to

96   be defined by climatic conditions across all seasons and hypothesize that shoot length and berry

97   production will be dependent on an interaction of growing season and winter conditions. Further,

98   we aim to confirm a) that higher summer temperatures and longer growing seasons can give

99   longer shoots and more berries (e.g. Büizer et al 2012) and, b) that freezing exposure (e.g.

100   Bokhorst et al. 2009) or shallow snow cover (Bienau, Hattermann et al. 2014) can give shorter

101   shoots or decrease *E. nigrum* biomass and cover.

102   MATERIAL AND METHODS

103   Study sites

104   The study took place between 2010 and 2016 in five *E. nigrum* dominated tundra heathlands in

105   northern Norway between 69.17-70.02°N and 18.75-20.9° E (Figure 1). The study sites were

106   located at the *Betula pubescens* tree line ecotone along a 200-km climatic gradient, ranging from

107   oceanic to continental conditions. The sites were chosen due to their contrasting climatic

108   conditions, that is, coastal sites are normally characterized by cool summers, mild winters and

109   varying snow cover conditions, while continental sites have warm summers and extremely cold

110   winters which allow for a stable and deep snow cover. Snow cover at the study sites usually

111   remains until mid-June and bedrock is mainly gabbro (Table 1). Besides *E. nigrum*, other less

112   abundant species across all sites were *Betula nana*, *Vaccinium uliginosum*, *Vaccinium myrtillus*

113   and *Vaccinium vitis-idaea* (PanarcticFlora 2017).

114   Study design and sampling

115   In June 2011, ten blocks were established in each of the sites (Fig.1). Blocks had at least 90% *E.*

116   *nigrum* cover, a maximum slope of 5 degrees and were placed a minimum of five meters apart to

117   avoid including the same *E. nigrum* individual in different blocks, since long-lived, clonally

118   reproducing species can have multiple modular units (Miller 2012). Each block consisted of

119   three 50 cm x 50 cm permanently marked plots placed beside each other with a 40-cm

120   separation. Two blocks were unfortunately dropped during the study due to diverse issues (one in

121   Skibotn and one in Gukhesjávri, Fig.1), hence we had a total of 48 blocks and 144 plots for

122   vegetation analyses.

123   Each year, all sites were sampled within one or two days from each other at the end of the

124   growing season in late August. *E. nigrum* cover and berry production were measured with the

125   use of a wooden frame (50 cm x 50 cm) divided in 16 subplots (0.0125 m^2 each) by registering

126   presence/absence of live *E. nigrum* biomass and *E. nigrum* berries in the 16 subplots. Shoot

127   length was measured by selecting five different annual shoots each year (i.e. shoots grown during

128   that summer) in each plot (total of 15 shoots per block). In 2017, *E. nigrum* biomass per plot was

129   measured using the point intercept method with 20 pins per plot (Bråthen and Hagberg 2004) and

130   converting the total number of hits using established calibration functions (Ravolainen, Yoccoz

131   et al. 2010).

132   Climatic variables

133   Temperature and precipitation based climatic variables were used in this study (Table 2). Three

134   temperature loggers (Thermochron iButtons**®**) were placed at ground level at each site (i.e. one

135   at the top, middle and bottom of study site) to measure soil surface temperature every 3 hours all

136   year round (during 2010-2016) and were used to calculate all temperature variables. Mean daily

137   temperatures per site were calculated as the average of the three temperature loggers. Number of

138   freezing days and annual climatic variables were calculated from sampling date to sampling date

139   (i.e. from late August to late August next year) since *E. nigrum* flower and vegetative buds are

140   fully formed at the end of the growing season and are therefore subjected to any climatic

141   variability during the previous autumn/winter (Bell and Tallis 1973). Hence, the number of

142   freezing days for each sampling year belongs to the previous winter season. We calculated three

143   growing degree day variables by summing all daily mean temperatures above 1°C (GDD+1),

144 2°C (GDD+2) and 5°C (GDD+5) starting from the date when the average daily logger

145 temperature was above 1°C, 2°C or 5°C respectively, for three or more consecutive days until the

146 sampling date. Although the common threshold in northern climates to determine both growing

147 season and growing degree days is set to >5°C (GDD+5) (Körner 1999), *E. nigrum* is known to

148 both flower and start growing straight after snow melt (i.e. GDD+1 or GDD+2), and we were

149 interested in testing this assumption. We further calculated the number of winter warming

150 extreme events (EE) during December-March, by summing the periods of more than two days

151 when air temperatures were above +2 °C (Bokhorst, Phoenix et al. 2012) and soil surface

152 temperatures were above +1°C (suggesting absence of snow). Precipitation variables were

153 gathered from publicly available maps and online databases (seNorge 2017). The Continentality

154 Index for each study site was calculated according to Rivas-Martinez et al 2011(37), showing a

155 range of 21.8 to 31 indicating a gradient from oceanic/maritime to continental climate.

156 Statistical analyses

157 All data were sampled at plot level, averaged to block level and analyzed using the statistical

158 environment R (R Development Core Team 2016). An exploratory analyses of the data was done

159 using non-metric multidimensional scaling (NMDS) set to two dimensions with a Bray-Curtis

160 dissimilarity test in the "vegan" package in R (Oksanen, Blanchet et al. 2018). NDMS allowed us

161 to visualize and interpret the relationship between the climatic variables and our response

162 variables with the use of rank orders. The exploratory variables used in the NMDS included all

163 climatic variables (Tab. 2) except the extreme event variable (EE), because we recorded no

164 extreme events except three episodes on the island of Rebbenes. We also included biomass

165 measured in 2017 in the NMDS analyses and we assumed that, since *E. nigrum* is a slow

166 growing species, the biomass measured in 2017 was a good overall representative measure for

167 each site.

168 Further, linear mixed effect models (Pinheiro, Bates et al. 2017) were used with block as the

169 random factor and mean shoot length or mean berry frequency as response variables. The choice

170 of predictor variables was based on the exploratory NMDS results and Pearson correlation values

171 between variables. We used Akaike Information Criterion (AIC) to rank the models and chose

172 the final model with the lowest AIC value (Johnson and Omland 2004).

173 RESULTS

174 Variability along the climatic gradient of biotic and abiotic variables

175 Both biotic and climatic variables varied between years and along the climatic gradient (Figure 2

176 and 3). Mean shoot length varied among sites and was between 0.65 and 3.2 cm (mean of 1.3 cm

177 across sites), with shorter shoots found in continental sites (Figure 2a). Shoot length varied little

178 between years (Figure 2b). Mean berry frequency, in contrast, had a larger variation between

179 years and among sites (Figure 2c-d). The cover of *E. nigrum* during the six years was constant in

180 all plots showing 16 out of 16 subplots with *E. nigrum* live biomass (supplemental raw data). We

181 did not register any large-scale mortality or browning during the study in any of our study plots

182 (V.T. González, personal observation). *E. nigrum* biomass registered in 2017 increased with

183 continentality index, finding more biomass in continental areas, whereas mean shoot length was

184 on average shorter in continental areas (Figure 4).

185 There was a sharp contrast in temperature between study sites along the climatic gradient during

186 the winter months (Fig. S1), finding a fluctuating snow cover (i.e. soil surface temperature

187 loggers registered below freezing temperatures) mainly at the two most continental sites (Fig.

188 S1). Among the climatic variables, the number of freezing days (FD), non-growing season

189   precipitation (NGSP) and growing season length (GSL) were contrasting between sites rather

190   than between years, finding three times fewer freezing days and twice the precipitation at the

191   coast (Fig. 3 a, k, g). The two most continental sites had many freezing days each year,

192   registering on average seven months a year with freezing temperatures (Fig S1), though FD were

193   registered along the entire climatic gradient and in all years (Fig. S1). Mean summer temperature

194   (ST) varied less among sites and more between years (Fig. 3f), while growing degree days

195   (GDD) and growing season precipitation (GSP) varied between both sites and years (Fig.3 c, d, i,

196   j). No extreme winter warming episodes (EE) were registered except for the island of Rebbenes

197   where three episodes occurred between 8-10 February 2012, between 4-5 December 2014, and

198   finally between 15-18 of March in 2015.

199   Exploratory analyses

200   The nonmetric multidimensional scaling (NMDS) exploratory analyses had a stress value of 0.09

201   indicating a good fit of the data with the number of selected dimensions (i.e. two). Mean shoot

202   length was mainly related to NMDS axis 1 and partly to axis 2, whereas berry frequency was

203   largely related to axis 2. Further, the response variables differed in their correlation with the

204   ordination space (R^2) finding that berry frequency had a low correlation value ($R^2 = 0.01$) while

205   mean shoot length was better correlated with the ordination space ($R^2 = 0.43$). The climatic

206   variables varied also in the relation with the NMDS axes. The first axis was strongly related with

207   FD, followed by GSP and NGSP (Figure 5). The second axis was related with all other variables,

208   that is, growing season length (GSL), summer temperature (ST), all three growing degree day

209   variables (GDD+1, GDD+2, GDD+3) and biomass (Fig. 5). Overall, from the first NMDS axis,

210   FD was the best correlated variable with the ordination space (Fig. 5) while from the second

211   NMDS axis, although biomass appeared as the strongest variable, the effect of all variables was

212   small and similar (Fig. 5). Further, all sampling years appeared to be climatically similar (Fig

213   S2a) and there was a climatic overlapping among sites, except for the two most continental sites

214   (continentality index (CI) of 30.1 and 31) and the mid-continental site (CI of 24.2) (Fig S2b).

215   The Pearson correlation tests among the predictor variables selected by the NMDS, showed that

216   several variables were correlated to each other (Table S1). A main finding was that FD was

217   correlated with all other variables except GDD (all three). Further, GDD (all three) were strongly

218   positively correlated with ST and GSL (Tab. S1). Thus, to test the main hypothesis of our study

219   (i.e. understanding the effect of climatic fluctuations during all seasons on *E. nigrum* resistance),

220   the NMDS results and Pearson correlation values suggested the best climatic variables were the

221   number of freezing days (FD) and the growing degree variables (GDD+1, GDD+2, GDD+5),

222   which represented winter and spring/summer seasons respectively.

223   *E. nigrum* resistance under climatic variability

224   We selected through the Akaike information criterion (AIC) GDD+1C, out of all three growing

225   degree day variables, in interaction with FD as the optimal predictor-variable combination since

226   it had the lowest AIC. We used this combination for both mean shoot length and mean berry

227   frequency as response variables.

228   Results from the linear mixed effects models showed a significant interaction between FD and

229   GDD+1 on both mean shoot length and mean berry production (Table S2). Thus, during colder

230   growing seasons there was a negative effect of an increase of FD on mean shoot length and

231   milder negative effect on berry production, while under warmer growing seasons this negative

232   effect was less apparent in shoot length and turned positive in the case of berry production

233   (Figure 6).

234   DISCUSSION

235   Our study illustrates how the common evergreen dwarf shrub *E. nigrum* is resistant to fluctuating

236   climatic conditions during the growing season and winter months by showing positive vegetative

237   growth and reproductive output in all sites and in all years. Exposure to freezing temperatures

238   during winter was correlated with shorter shoot growth and reduced berry production the

239   following season, however, if the following season was warm and long it appeared to

240   compensate for these negative effects. Thus, *E. nigrum* fitness was affected by climatic

241   conditions during both winter and spring/summer.

242   Exposure to extreme low temperatures can damage vegetation either directly through freezing or

243   winter desiccation, or indirectly through ice encasement after rain-on-snow episodes and

244   refreezing of melted snow (Blume-Werry, Kreyling et al. 2016, Bjerke, Treharne et al. 2017).

245   Under varying snow cover conditions, evergreen dwarf shrub foliage is likely subjected to

246   freezing temperatures, as their branches might protrude from the snowpack. In our study, *E.*

247   *nigrum* appeared to be regularly exposed to freezing temperatures during large parts of the winter

248   months but was nevertheless able to grow and reproduce even during colder growing seasons,

249   which suggests that this species is generally frost hardy and, as experimental studies have shown,

250   possibly resistant to ice encapsulation (Preece, Callaghan et al. 2012, Preece and Phoenix 2014).

251   In contrast to studies showing large mortality of *E. nigrum* in tundra heathlands after extreme

252   winter warming events (Bokhorst, Bjerke et al. 2009, Bjerke, Karlsen et al. 2014), we did not

253   find indications of browning episodes during the course of the study in spite of the low

254   temperatures registered at most sites during the winter months. One possible explanation is that

255   in contrast to winter warming episodes, we did not register above zero temperatures during the

256   winter months (except for the three short episodes at the coastal site of Rebbenes) indicating

257   spring-like development was not initiated and the plant remained dormant. *E. nigrum*

258   experiences deep dormancy during the winter months and has been found able to remain

259   undamaged by temperatures down to -40 C (Körner 1999). Nevertheless, we did not see any

260   indications of browning of the vegetation in our plots at the coastal site of Rebbenes the years it

261   did experience winter warming episodes.

262   The mean shoot lengths registered during our study were similar to those registered in other *E.*

263   *nigrum* studies (Wipf, Rixen et al. 2006, de Witte and Stöcklin 2011, Bienau, Hattermann et al.

264   2014). The small variation in shoot length between years confirms that *E. nigrum* is a slow

265   growing species with a conservative growth strategy. Thus, our assumption that the biomass

266   measured in 2017 was an appropriate overall representation of biomass amounts of each site was

267   supported by this finding. It is worth noting that *E. nigrum* biomass was higher at continental

268   sites, but the shoot length was the shortest. In shallow or varying snow cover conditions, *E.*

269   *nigrum* has been found to have short internodes and to form low mats close to the ground as to

270   avoid having apical growth stems constantly exposed to the freezing temperatures (Bienau,

271   Hattermann et al. 2014). This in turn could be a selective force on growth during summer, that is,

272   sites with low snow cover might have densely structured dwarf shrubs with a larger number of

273   shoots, as indicated by biomass amounts, but shorter as to be less exposed during winter months.

274   Thus, winter conditions could affect *E. nigrum* structure and hence modify the growth pattern

275   during the summer months, reflecting the complex interactions between all seasons on this

276   common tundra species.

277   We found a negative effect of increasing freezing days on mean shoot length, however, warmer

278   growing season conditions appeared to compensate for this effect, confirming our hypothesis that

279   the overall resistance of this species is defined by both spring/summer and winter conditions.

280   The evergreen dwarf shrub *Cassiope tetragona*, has recently been found to respond to damage by

281   experimental winter freezing conditions with enhanced shoot growth (Milner, Varpe et al. 2016).

282   Though we did not monitor yearly shoot mortality or damage, our study suggests that *E. nigrum*

283   might respond in a similar manner to winter freezing exposure, by showing a plastic growth rate

284   dependent also on spring and summer climatic conditions. Nevertheless, *E. nigrum* showed

285   positive shoot growth in all sites during all years indicating the resistance of this species to

286   climatic variability.

287   Berry production was also found dependent on spring/summer and winter conditions and

288   appeared to be specially promoted by warmer and longer summers, which could indicate that *E.*

289   *nigrum* berry production could increase under climate warming. However, we did also find a

290   slight increase of berry frequency with continentality that also could be due to an increase in

291   biomass, as berry frequency was mostly related with NMDS axis 2 which corresponded with

292   biomass amounts. This would confirm, in line with previous studies, increasing amounts of

293   biomass to be associated with higher flowering and fruiting (Buizer, Weijers et al. 2012,

294   Kaarlejarvi, Baxter et al. 2012, Bråthen, Gonzalez et al. 2018). Thus, the increase in berry

295   production associated with increasing freezing days and warmer summers could be a direct result

296   of an increase in biomass due to compensatory shoot growth stimulated by freezing during the

297   colder seasons. *E. nigrum* flowering buds are formed during the previous autumn and both

298   flower and berry production have been found unaffected by experimental winter warming

299   treatments and icing episodes (Preece, Callaghan et al. 2012). Thus, a higher reproductive output

300   might be expected if the growing season conditions are optimal (long and warm growing seasons

301   as showed in this study) despite the colder winter conditions. Nevertheless, freezing or icing-

302   induced enhancement of vegetative or reproductive output has important implications for climate

303   change studies and as to avoid biased conclusions both winter and growing season conditions

304   should be considered.

305   It is worth noting that growing season length starting with +1 degrees Celsius explained most

306   variation in both shoot length and berry productivity. Some evergreen species are known to

307   break winter dormancy even before snow melt, as soon as light penetrates a shallow snow cover

308   (Körner 1999). It appears *E. nigrum* is able to start growth and reproduction very early during the

309   growing season, which could be advantageous in light of the predicted earlier spring snowmelt

310   following climate change (Wipf 2010, Krab, Roennefarth et al. 2018). Hence, the predicted

311   increase in growing season length with climate change could promote *E. nigrum* encroachment

312   in areas where it is dominant. Recent studies have particularly showed an encroachment of *E.*

313   *nigrum* in tundra areas (Vowles, Gunnarsson et al. 2017, Vuorinen, Oksanen et al. 2017,

314   Maliniemi, Kapfer et al. 2018) which might be explained by its ability to respond to varying

315   climatic conditions as shown here, and its niche construction ability (Bråthen, Gonzalez et al.

316   2018).

317   CONCLUSIONS

318   Overall, our study highlights the synergistic effect of all seasons on the growth and reproduction

319   of the common evergreen dwarf shrub *E. nigrum*. The findings presented here, suggest that *E.*

320   *nigrum* is frost hardy and able to persist under varying winter temperature conditions by

321   showing increased reproductive and vegetative output under warmer growing season conditions,

322   thus further perpetuating the positive feedback surrounding shrub expansion in the tundra in

323   connection with climate change (Myers-Smith, Forbes et al. 2011). Our study further supports

324   the importance of better understanding the linkages between all seasons on the impact of climate

325   change on dominant tundra species.

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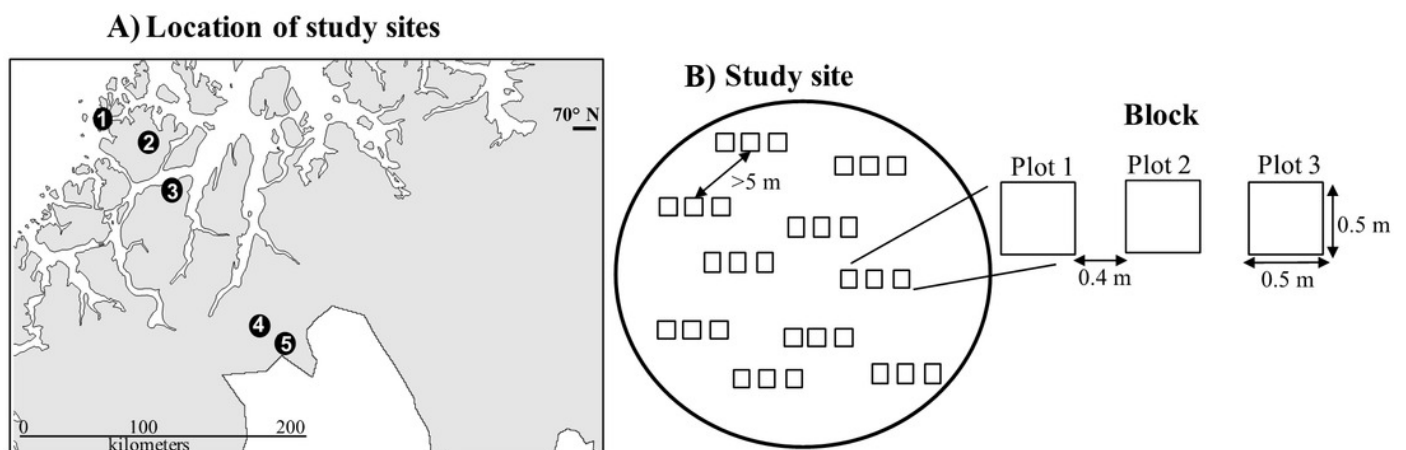
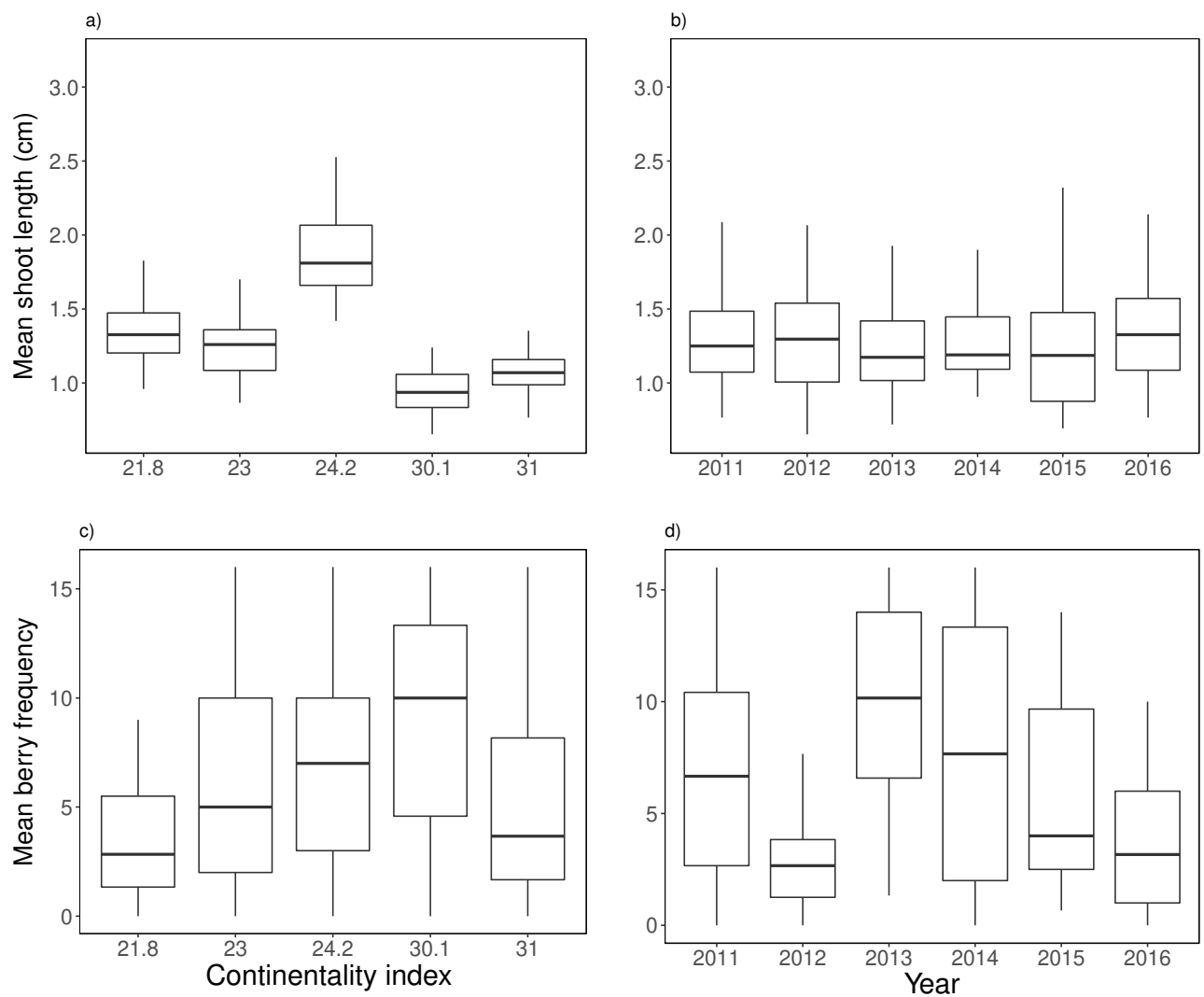
489

490

Figure 1

Study sites

a) Location of study sites. The names and Continentality Index of the sites from coast to inland were: 1) Rebbenes (21.8), 2) Skogsfjord (23), 3) Snarby (24.2), 3) Skibotn (30.1), and 4) Gukhesjávri (31); and b) Study design

Biotic variable variation between years and along the climatic gradient

Mean shoot length (a-b) and mean berry frequency (c-d). Boxplots are presented with median and non-overlapping boxes are indicative of statistical significance.

Variation between years (i.e. 2011-2016) and along the climatic gradient (i.e. Continentality Index) of abiotic variables.

Freezing days (FD) (a-b), growing degree days (GDD+1) (c-d), summer temperature (ST) (e-f), growing season length (GSL) (g-h), growing season precipitation (GSP) (i-j) and non-growing season precipitation (NGSP) (k-l). Boxplots are presented with median and non-overlapping boxes are indicative of statistical significance.

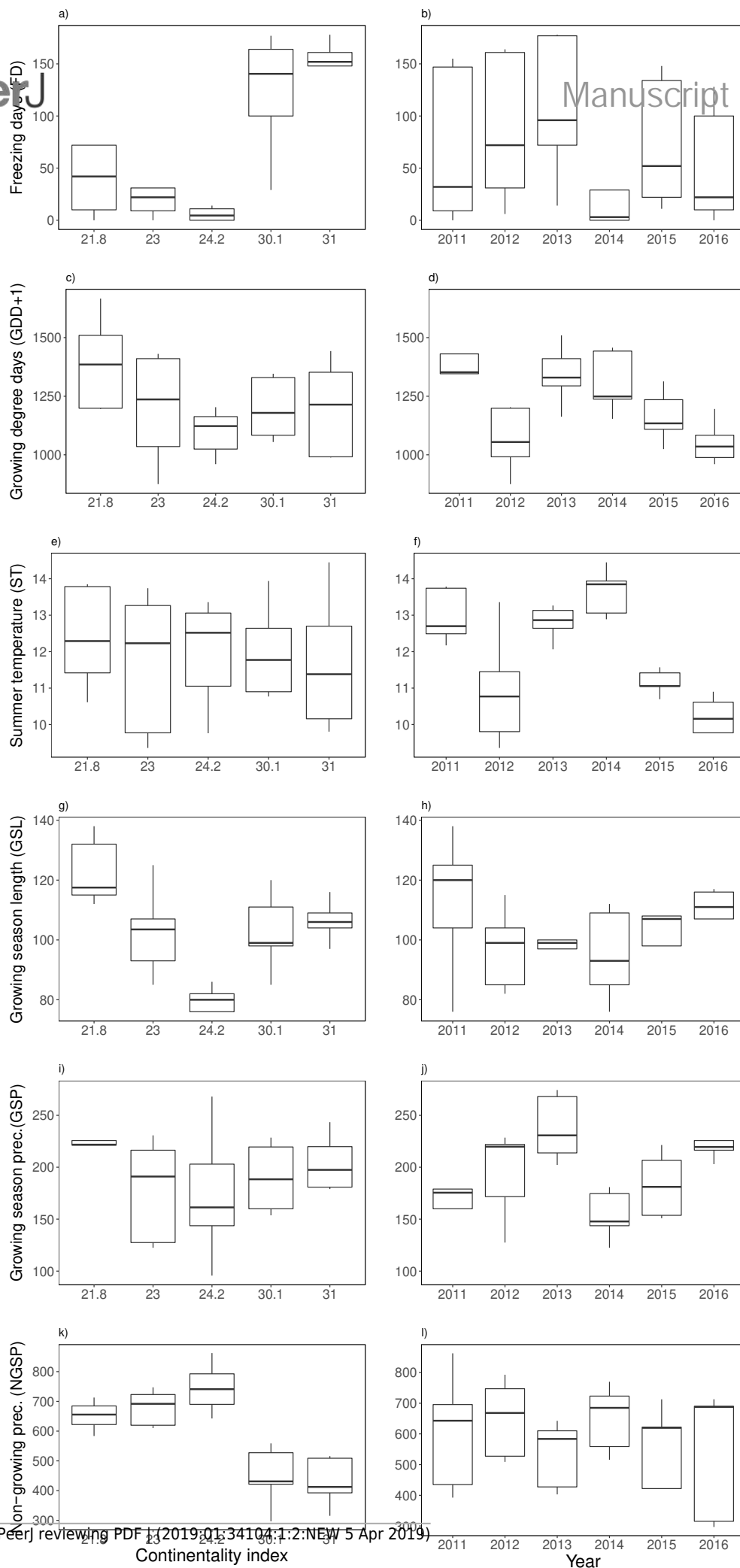
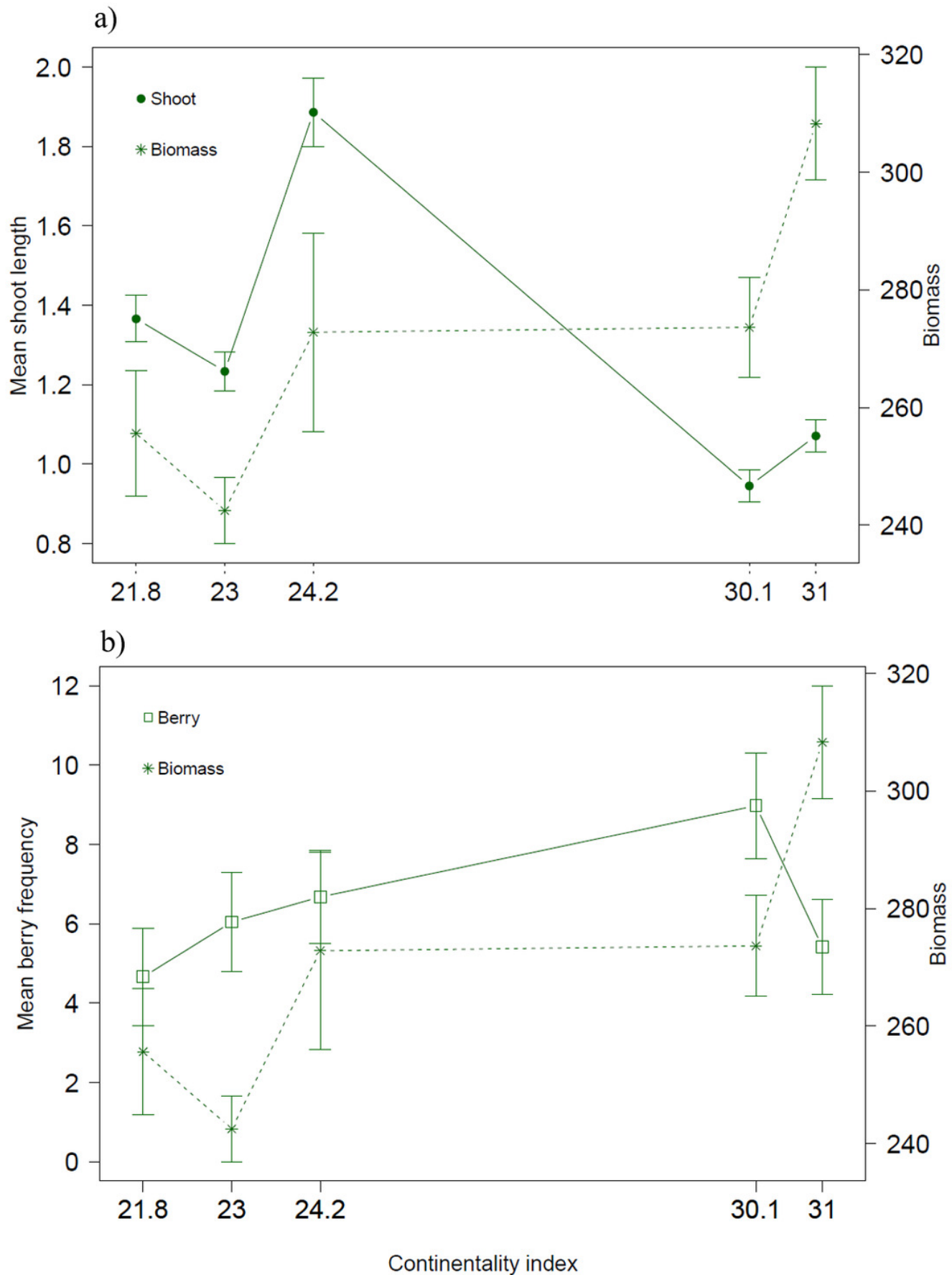



Figure 4

Biotic variables along the climatic gradient.

Biomass (g/m ^{2}) together with a) mean shoot length (cm) and b) mean berry frequency

a)

b)

NMDS plot from exploratory analyses

The plot illustrates the relationship between response variables (green arrows): mean shoot length (Shoot) and mean berry frequency (Berry) and predictor variables (in blue) with the ordination space: freezing days (FD), growing degree days (GDD), summer temperature (ST), growing season length (GSL), growing season precipitation (GSP) and non-growing season precipitation (NGSP).

NMDS plot

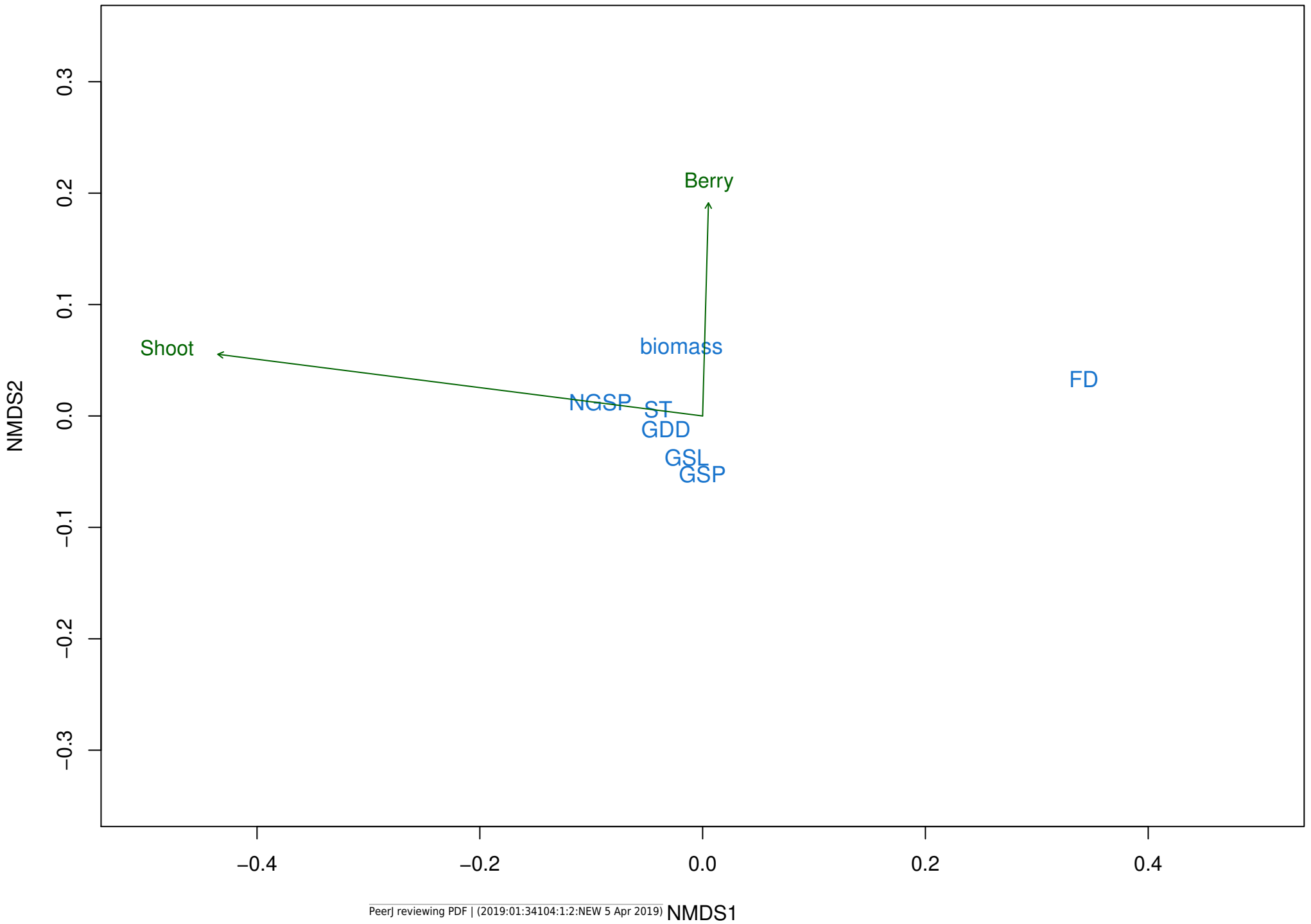
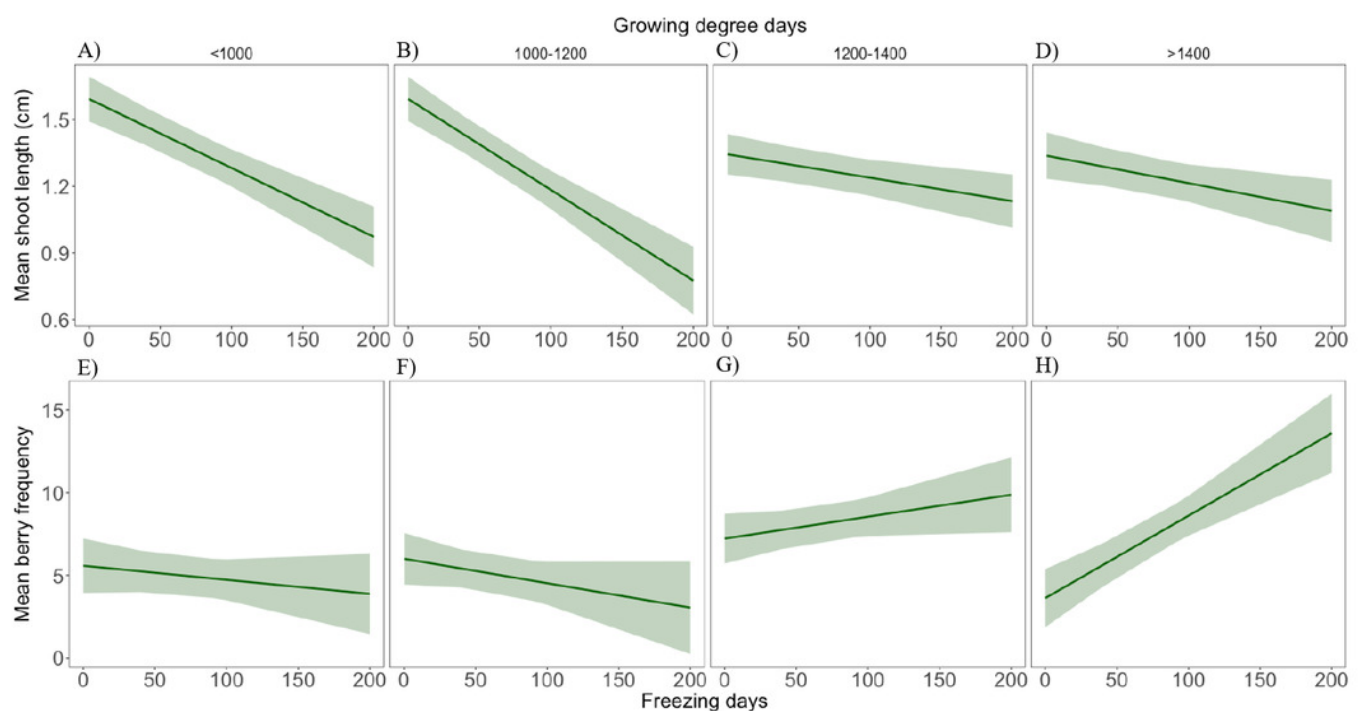



Figure 6

Interactive effect of number of freezing days and growing degree days on response variables.

Mean shoot length (a-d) and mean berry frequency (e-h). The mean is presented with 95% confidence intervals

Study site characteristics

Environmental variables were registered on site (i.e. elevation, soil pH and soil organic horizon), and climatic temperature variables were calculated using on-site temperature loggers placed at soil surface level during all six study years. Precipitation data, snow depth and bedrock were gathered from publicly available databases (i.e. www.senorge.no).

	Rebbenes	Skogsfjord	Snarby	Skibotn	Guhkesjávri
Latitude/Longitude	70° 10'; 18°45'	69° 57'; 19° 15'	69° 45'; 19° 30'	69° 14'; 20° 33'	69° 10'; 20° 42'
Continentality index	21.8	23	24.2	30.1	31
Mean annual temp. (°C)	2.2	0.5	0.6	-2	-1.9
Mean summer temp. (°C)	12.37	11.77	12.04	11.96	11.64
Elevation (m a.s.l.)	10	264	266	580	510
Continentality index	21.8	23	24.2	30.1	31
Soil pH	4	4	4.5	3.5	4
Soil organic horizon depth (cm)	5-10	3-10	2-5	3-10	5-10
Mean annual prec. (mm)	871.18	860.49	917.19	634.16	628.2
Mean summer prec. (mm)	218.75	179.86	172.16	189.75	202.98
Snow depth (cm/year)	2.41	12.9	25.2	39.2	39.9
Bedrock	Amphibolite	Basalt	Mica gneiss, schist and metasandstone	Metasandstone and schist	Gneiss and migmatite

Definition of environmental variables used in this study

All temperature variables were calculated from on-site temperature loggers. Precipitation was gathered from the publicly available database www.senorge.no

Variable	Definition
Freezing days (FD)	Sum of days between sampling dates where the mean daily temperature was below -1°C. Hence, the number of freezing days for each sampling year belongs to the previous winter season.
Summer temperature (ST)	Mean daily temperature of June, July and August (until sampling date).
Growing season length (GSL)	Sum of days from the date where the average daily logger temperature was above 5°C for three or more consecutive days until sampling date.
Growing degree days (GDD+1, GDD+2, GDD+5)	Sum of all daily mean temperatures above 1°C (GDD+1), 2°C (GDD+2) and 5°C (GDD+5) starting from the date when the average daily logger temperature was above 1°C, 2°C or 5°C respectively, for three or more consecutive days until the sampling date.
Growing season precipitation (GSP)	Mean daily precipitation from start of the growing season until sampling date (i.e. same days as GSL).
Non-growing season precipitation (NGSP)	Mean daily precipitation from sampling date until start of the next growing season (i.e. until start of GDD+1).
Extreme events (EE)	Sum of periods of more than two days when air temperatures were above +2 °C, and surface temperatures were above +1°C (suggesting absence of snow).