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## Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models

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**Abstract** Dense ungulate populations in forest accompanied by high grazing intensities have potential to affect plant population dynamics, and such herbivory effects on populations are hypothesised to differ along environmental gradients. We investigated red deer grazing and resource interaction effects on the performance and dynamics of the functionally important boreal shrub *Vaccinium myrtillus* using integral projection models (IPMs). We sampled data from 900 *V. myrtillus* ramets in 30 plots in two subsequent years across the boreo-nemoral pine forest on the island Svanøy, western Norway. The plots spanned two environmental gradients; a red deer grazing intensity gradient (assessed by *Cervus elaphus* pellets) and a relative resource gradient (DCA-ordination of species composition). The use of IPMs enabled projections of population growth rate ( $\lambda$ ) using continuous plant size instead of forcing stage division upon the demographic data. We used the environmental gradients as continuous variables to explain the dynamics of *V. myrtillus* populations and found that both increasing grazing intensity and resource levels negatively affected  $\lambda$  of the *V. myrtillus* populations. Interestingly, these factors interacted: the negative effects of grazing were strongest in the resource rich vegetation, and higher resource levels reduced  $\lambda$  more strongly than at low resource levels when grazing intensities became higher. Populations with  $\lambda > 1$  were projected if the grazing intensity was  $\leq$  to the mean grazing intensity at the island and indicated that *V. myrtillus* is relatively tolerant of grazing. Variance decomposing showed that the decrease of  $\lambda$  along the grazing gradient, both at low and high resource levels, was largely caused by reductions in plant growth. The use of IPMs together with important environmental gradients offered novel possibilities to study the synthesised effect of different factors on plant population dynamics. Here we show that the population response of an abundant boreal shrub to ungulate grazing depends on resource level.

**Keywords** *Cervus elaphus*, environmental gradient, IPM, LTRE, population dynamics

### Introduction

The structure and composition of the boreal forest is influenced by multiple biotic and abiotic variables, of which plant-animal interactions such as herbivory are amongst the most important biotic factors (Pastor et al. 1988; Proulx and Mazumder 1998). During the last three decades, several native ungulate species have expanded their range and population sizes in the forests of Northern Europe, causing amplified grazing intensities (Fuller and Gill 2001; Milner et al. 2006; Mysterud et al. 2002). In Norway, *Cervus elaphus* L (red deer) is one of

51 the wild ungulates that for centuries played a minor role as landscape structuring agent. Today  
52 the current number of *C. elaphus* in Norway is a historical high and has increased fourfold  
53 since the early 1980's as indexed by culling numbers (Statistics Norway 2008).

54 The population dynamics of plant species are influenced by environmental factors, of  
55 which herbivory and resource availability are among the most influential (Ehrlén 2002;  
56 Hawkes and Sullivan 2001; Maron and Crone 2006). Plants in the boreal forest may suffer  
57 reduced biomass and size as a direct result of grazing (McInnes et al. 1992; Rydgren et al.  
58 2001; Väre et al. 1996). Moreover, reproduction may be affected as a consequence of this size  
59 reduction, if resources need to be allocated to other structures or if the grazing results in direct  
60 removal of reproductive units (Bastrenta 1991; Ehrlén 1995a; García and Ehrlén 2002). These  
61 consequences of grazing on the performance of a plant species can cause subsequent effects  
62 on demography and population dynamics (Bastrenta 1991; Ehrlén 1995b; Rydgren et al.  
63 2001). Examinations of plant-animal interactions, such as herbivory, are therefore essential  
64 for understanding plant life histories (Ehrlén 2002). Plant species have mechanisms that  
65 enable them to compensate for negative effects of herbivory, and some species may even  
66 benefit from certain levels of grazing by means of increasing individual growth potentially  
67 affecting population growth rates (Augustine and McNaughton 1998). It has been  
68 hypothesised that plants growing in high resource conditions can recover better after  
69 herbivory (Bryant et al. 1983). A meta-analysis, however, showed that existing evidence did  
70 not support this hypothesis for plants in general; woody plants appeared to compensate best  
71 after herbivory in low resource conditions, for example, low nutrient levels (Hawkes and  
72 Sullivan 2001). Spatial variation in plant population-level effects of herbivory are very  
73 common but still little investigated along environmental gradients (Maron and Crone 2006).  
74 Plant population studies rarely take into account that the performance of the species varies  
75 along environmental gradients, and plant population studies could thus benefit from using a  
76 framework of vegetation-environmental relationships (Rydgren 1997). The paucity of such  
77 studies prevents precise conclusions about the importance of variation in both herbivory and  
78 resource levels, and the interaction between them, on the demography and population  
79 dynamics of plants.

80 To understand the impact of dense populations of ungulates on the function and structure  
81 of ecosystems, it is important to know how functionally important plant species respond to  
82 different grazing intensities by dominant grazers. The dwarf clonal shrub *Vaccinium myrtillus*  
83 L. (bilberry) is a widespread and dominant species in large parts of the boreal forest (Økland  
84 1996). Through its early flowers in spring, deciduous leaves in summer, extensive berry  
85 production in autumn and evergreen stems in winter, *V. myrtillus* also plays an important  
86 ecological role as food source for many animal species (Faber and Lavsund 1999; Hjältén et  
87 al. 2004; Wegge et al. 2005; Welch et al. 1997). *V. myrtillus* is considered relatively grazing-  
88 tolerant (Dahlgren et al. 2007) although it has been shown that its size and reproduction are  
89 negatively affected by increasing grazing intensities of one of the main large herbivores, *C.*  
90 *elaphus*, that feeds and depends on it (Hegland et al. 2005). It is still unknown whether the  
91 population dynamics of *V. myrtillus* are significantly affected by ungulate grazing, partly  
92 because *V. myrtillus* has considerable compensation abilities due to its clonality (Dahlgren et  
93 al. 2007; Tolvanen 1994; Tolvanen et al. 1994). In general, there are few population studies  
94 on mammal herbivory effects on perennial shrub dynamics compared to studies on herbs  
95 (Maron and Crone 2006).

96 In a landscape-scale study we investigated the performance of *V. myrtillus* populations  
97 along a red deer grazing intensity gradient (*Cervus elaphus* pellet counts) and how the  
98 population dynamics were modified by a resource gradient (as revealed by DCA-ordination of  
99 the forest-floor vegetation). We analysed the effects of changes in the survival, growth,  
100 flowering and clonal propagation on the dynamics of *V. myrtillus* along the grazing and

101 resource gradients by means of integral projection models (IPMs; Easterling et al. 2000).  
102 IPMs have the advantage that state variables like plant size are modeled in a continuous  
103 fashion rather than in artificial discrete steps. Furthermore, IPMs are particularly useful when  
104 the aim is (like in our study) to project the consequences of the responses of individuals to  
105 environmental gradients for the dynamics of a population: continuous, empirical functions of  
106 these responses are better included in IPMs than in matrix models with discrete classes. We  
107 hypothesise that increasing ungulate grazing will affect the dynamics of *V. myrtillus* by  
108 decreasing survival, flowering and population growth rate. As *V. myrtillus* is a woody plant  
109 we expect that the effects of grazing will be most unfavourable for the population growth rate  
110 when the resource levels are relatively high.

111

## 112 **Material and methods**

113

### 114 Study area and species

115

116 The study was carried out in 2002 and 2003 on Svanøy, an 11 km<sup>2</sup> island on the western coast  
117 of Norway (61°30N, 5°05E) in the county Sogn og Fjordane. Svanøy is situated in the boreo-  
118 nemoral zone and forest vegetation dominated by *Pinus sylvestris* (pine) covers most of the  
119 island, which has an oceanic climate (Skogen and Lunde 1997). Twelve study sites were  
120 located in relatively open pine-forest, with a forest floor dominated by *Vaccinium myrtillus*  
121 plants. The population of *Cervus elaphus* on Svanøy has been large and expanding ever since  
122 around 1990 and the density on the island is representative for west Norway (*personal*  
123 *communication* J.T. Solheim).

124 *V. myrtillus* is a deciduous clonal dwarf shrub with evergreen stems that mainly occurs in  
125 the Eurasian boreal zone and regularly constitutes 40% of the ground cover (Kuusipalo  
126 1988). Clonal propagation is substantial, in particular after severe disturbance such as forest  
127 fires (Schimmel and Granström 1996). The number of seeds per fruit in boreal areas is  
128 typically around 25, but seedling recruitment in dense forest floor vegetation is rare (e.g.  
129 Eriksson and Fröberg 1996). Seedling germination and emergence from the soil seed bank are  
130 both restricted to gaps exposing the soil surface (Eriksson and Fröberg 1996; Jauhainen  
131 1998). There are various reports on the status of the *V. myrtillus* soil seed bank; many studies  
132 report a transient seed bank, but viable seeds appears to occur deep into the soil (Granström  
133 1982; Hill and Vander Kloet 2005; Rydgren and Hestmark 1997).

134

### 135 Experimental design and sampling procedures

136

137 The 12 study sites were selected within mature bilberry-pine forest, according to a vegetation  
138 map (by Skogen and Lunde 1997), and spread across the island. Study sites had been little  
139 influenced by forestry the last 50 years (see also Fig. 1 in Hegland et al. 2005). During the  
140 winter of 2000 we established a grazing enclosure and an ungulate grazed control area of 10 ×  
141 10 m at each site. The sites were restricted to flat areas less than 200 metres above sea level  
142 dominated by *V. myrtillus* to reduce variation due to altitude and aspect. Ten of the sites were  
143 situated in forest with wild-living *C. elaphus* as the main grazer and these sites represented a  
144 natural grazing regime. The other two sites were located at the deer farm of the Norwegian  
145 Red Deer Centre and represented an area with high grazing intensities by *C. elaphus*. Grazing  
146 intensities have been high ever since deer farming started in 1993 (*personal communication*  
147 J.T. Solheim). We estimated the variation in grazing intensities per site within the grazed  
148 control areas by recording the presence of pellet groups in 100 1m<sup>2</sup> square plots randomly  
149 distributed within a radius of 100 m around the grazed control areas. Thereby we obtained an  
150 index of grazing intensity per site and plot ranging from 0 to 100. We sampled pellet groups

151 in June and August 2001, and used the mean frequency from these two sampling events which  
152 in grazed areas was observed to range from 4 to 47.5. To control for the possible interannual  
153 variability in grazing intensities we resampled all sites five years later and found a high  
154 correlation ( $r = 0.81$ ,  $n = 12$ ,  $P < 0.0005$ ) indicating stable grazing intensities in time across  
155 sites. Pellet group count is reckoned to be an efficient method for measuring the relative  
156 density and habitat use of ungulates (Härkönen and Heikkilä 1999), and appear to be  
157 significantly correlated with an index of herbivore damage recorded directly on *V. myrtillus*  
158 (Hegland *et al.* 2005). In this study the grazing gradient spans the full grazing intensity from  
159 no grazing, via low and intermediate to very high levels of grazing; the latter comparable to  
160 areas with high winter-densities in west-Norway (S.J. Hegland, pers. obs). Sheep were also  
161 grazing on Svanøy, but as revealed by pellet counts they were of less importance in the study  
162 sites. From the plant perspective both red deer and sheep can be expected to have a similar  
163 impact on vegetation as both belong to the intermediate grazer-browser group (cf. Bodmer  
164 1990). However, one should be aware of that sheep, even at relative low densities, can affect  
165 vegetation significantly due to aggregation behaviour (Albon *et al.* 2007).

166 Within all 12 sites, both in fenced exclosures and grazed control areas, we randomly  
167 placed seven plots of  $1 \times 1$  m, which were at least 0.5 m from the closest tree. Each plot was  
168 divided into 100 subplots of  $10 \times 10$  cm. In June 2001 the abundance of vascular plants and  
169 bryophytes in each plot was recorded as frequency out of 100 subplots. To summarise species  
170 variation along main vegetation gradients we performed DCA ordination (Detrended  
171 correspondence analysis; Hill 1979 ) using CANOCO, version 4.5 with standard options  
172 including detrending by segments and no downweighting of rare species (ter Braak and  
173 Šmilauer 2002). Prior to ordination we changed the range of the abundance scale from 100 to  
174 16 by use of a power function according to (Rydgren 1993), thereby achieving a  
175 recommended intermediate weighting of species (Rydgren 1993, Økland 1990). We used the  
176 Ellenberg indicator value system to calculate surrogate variables for each plot for four  
177 environmental variables: nitrogen, reaction, moisture and light. The taxa occurring in a plot  
178 and for which Ellenberg *et al.* (2001) provided an indicator value was used. Our data set  
179 consisted of 67 taxa, and we had Ellenberg values for 33 (nitrogen), 42 (reaction), 43  
180 (moisture) and 48 (light). All four variables were significantly correlated ( $P < 0.001$ ) with  
181 DCA axis 1 (sample plot ordination). The variables with the strongest correlation were light  
182 ( $r_s = -0.687$ ) and nitrogen ( $r_s = 0.665$ ), followed by reaction ( $r_s = 0.599$ ), and moisture ( $r_s =$   
183  $0.392$ ). All four variables were also significantly correlated except reaction and moisture; the  
184 strongest correlation was between light and nitrogen ( $r_s = -0.864$ ). Thus, we interpreted the  
185 first DCA axis, the main vegetation gradient, to represent a complex-gradient in nutrients and  
186 light which we named the 'resource gradient'.

187 To examine variation in demography of *V. myrtillus* along the main vegetation gradient,  
188 interpreted as a resource gradient, we divided DCA-axis 1 (axis length was 1.98 S.D. units)  
189 into three equal sized segments. Within each segment we randomly selected four grazed and  
190 four ungrazed plots within the ten regular forest sites (i.e. 12 plots within each grazing  
191 condition). This random plot selection resulted in an uneven number of plots per site, for  
192 example some sites only including grazed or ungrazed plots and others containing both types.  
193 In the two forest sites within the deer farm we sampled all the randomly selected 14 grazed  
194 plots because we previously observed that the high grazing intensities could lead to loss of  
195 tagging and thus loss of data. Consequently, the subsequent year (2003) we could only use  
196 data of ramets within six of these grazed farm-plots. None of the ungrazed plots within the  
197 two farm blocks were included in our field measurements because we assumed that ramets  
198 that had experienced such extreme grazing could bias the results strongly. Altogether, we  
199 sampled demography data on *V. myrtillus* along the two environmental gradients from 30  
200 plots across 12 different sites.

201 We sampled *Vaccinium myrtillus* ramets in all the 30 demographic plots in August 2002  
202 and 2003. In 2002, we tagged and mapped a minimum of 25 ramets, i.e. above ground main  
203 stems derived from the underground rhizome network (sensu Flower-Ellis 1971; Appendix 1),  
204 within each demographic plot to allow relocation the next year. Tagging, using a loose plastic  
205 strip around the stem base in combination with a coloured ring on the strip, followed a  
206 standardised procedure: we divided each demographic plot (1m<sup>2</sup>; see above) into 16 square  
207 subplots and started tagging ramets in one of the four centre subplots and continued until at  
208 least 25 ramets were marked, always including all ramets within a subplot. In 2003 new  
209 emerging ramets were only censused if they were found in the same subplots censused in  
210 2002. At both censuses we measured the following variables on every tagged ramet  
211 (Appendix 1 for details): 1) the height of the ramet from ground level to highest point (H,  
212 cm); 2) the number of annual shoots (green stems with leaves) on the ramet (AS); 3) the  
213 diameter of the stem (DS, mm) measured at the base by ground level with a slide calliper);  
214 and 4) the number of berries.

215 In August 2002 we also collected another data set consisting of 150 ramets sampled  
216 across the island. These ramets were measured (variables 1-3, see above), and dried to  
217 constant weight at 70 °C in a drying cabinet. We then constructed a multiple regression model  
218 (sensu Økland 1995) from the data on dry mass (DM, in g), ramet height, the number of  
219 annual shoots on a ramet, and the diameter of the stem. The following model for dry mass  
220 estimation of *V. myrtillus* explained most of the variation, (R<sup>2</sup>=0.944; p< 0.001):  
221  $\log_2(\text{DM}) = 1.41700 \times \log_2(\text{DS}) + 0.97104 \times \log_2(\text{H}) + 0.44153 \times \log_2(\text{AS}+1) - 7.52070$ . We  
222 used the right side of this function as our non-destructive estimate of plant size, *z* (see below).

223

#### 224 Primary data analysis

225

226 To investigate the impact of the inferred grazing and the resource gradient on the performance  
227 and dynamics of *Vaccinium myrtillus*, we analysed the changes in all important life cycle  
228 components: the survival and flowering probabilities of ramets, the annual growth rate of  
229 surviving ramets, the berry and clonal offspring production and the size distributions of clonal  
230 offspring, along these two gradients. In regression analyses we started with a full model that  
231 included the explanatory continuous variables ramet size at the beginning of a transition (i.e.  
232 dry mass:  $\log_2 \text{DM}$ ;  $z_1$ ), grazing intensity index (i.e. pellet counts: *g*), sample plot scores along  
233 DCA axis 1 (i.e. proxy for resource levels: *v*; see above), sample plot scores along DCA axis  
234 2, and all their interactions. Two plant density variables were also included per plot: *V.*  
235 *myrtillus* plant density (on a 1 to 100 scale) and total plant density (1-100 scores added over  
236 all present species). Density scores were obtained from the vegetation analyses in 2001 (see  
237 ‘Experimental design and sampling procedures’). Site and plot within site were included as  
238 random factors to represent our nested sampling design in these generalized linear mixed  
239 models (lme- and lmer- functions in nlme- and lme4-packages in the statistical software R; R  
240 Development Core Team 2009). These full models were reduced by repeated backward  
241 elimination of non-significant (p<0.05) interactions and main factors, until only significant  
242 fixed effects and interactions remained (Crawley 2007; Zuur et al. 2009). The DCA axis 2 and  
243 both plant density variables were eliminated in all cases and were therefore not included in the  
244 final models presented in the results (see Table 1) nor in the population models (see below).

245 The annual survival probability ( $p_s$ ) and the probability that a ramet was flowering at the  
246 time of census ( $p_f$ ) were analysed with general linear regression models (glm) in binomial  
247 error-distribution. The data of both censuses (2002, 2003) were combined in the analysis of  
248 the flowering probability. The number of berries ( $n_b$ ) produced by the flowering ramets was  
249 modelled with a glm with Poisson error-distribution. The growth of the surviving ramets was  
250 studied by analysing the ramet size distribution after a year ( $z_2$ ). The number of clonal



251 offspring per ramet ( $m_c$ ) was calculated by using the ratio of the number of new clonal  
252 offspring in a plot in 2003 and the number of ramets in that plot in 2002.  $m_c$  was analysed  
253 with a glm with quasi-Poisson error-distribution.  $m_c$  and the size distribution of clonal  
254 offspring were modelled as a function of the plot-level parameters  $g$  and  $v$ , but not of  $z_1$   
255 because it was not possible to determine which old ramet had produced which new clonal  
256 offspring due to invisibility of the buried rhizomes (see also Jongejans et al. 2008).

257 The remaining life cycle components involved seeds and seedlings. These demographic  
258 rates were not analysed over the grazing and resource gradients because they were very rare.  
259 Precise measurements of these life cycle components are difficult to obtain and calculations of  
260 probabilities, for the use in projection modelling, were therefore set at values that are  
261 plausible given the literature available on this species (see 'Study area and species' for  
262 references): 1) the probability of seedling establishment ( $p_e$ ) was set at 0.015, since seedling  
263 establishment in forest vegetation appears very low; 2) the probability of seeds entering the  
264 seed bank ( $p_d$ ) was set at 0.25 because studies have shown that a seed bank sometimes is  
265 present; 3) the probability of seeds staying in the seed bank ( $p_b$ ) was set at 0.5 because  
266 although seed bank often is transient, viable seeds appear even deep in the soil; 4) the  
267 probability of seedling establishment from the seed bank was set at 0.015 because  
268 establishment from seed bank in closed forest floor vegetation is rare; 5) the mean and  
269 variance of a normal distribution of seedling sizes ( $N(\mu, \sigma^2)$ ) were set at -9 and 0.5 (log<sub>2</sub>-  
270 scale), respectively, which resulted in smaller seedlings than any surviving or clonal ramet  
271 recorded by us because we recorded only one seedling; and 6) the number of seeds per berry  
272 ( $m_s$ ) was set at 25. To check how robust our model outcomes were we performed a sensitivity  
273 analysis in the light of the uncertainty of the estimations of these latter demographic rates.  
274 The results confirmed that the rates that involved seeds and seedlings were of little  
275 importance themselves for the dynamic in the studied populations (Appendix 2). The seedling  
276 establishment rate also affects the importance of the flowering rate, but neither the patterns  
277 nor the ranking of the flowering LTRE contribution (see below) relative to the contributions  
278 by other vital rates changed when seedling establishment was even halved or doubled  
279 (Appendix 2).

280  
281 Analysis of effects on population dynamics

282 We used Integral Projection Models (IPM's; Easterling et al. 2000; Ellner and Rees 2006),  
283 to integrate all these life cycle changes into estimated changes in the projected population  
284 growth rate ( $\lambda$ ) over the range of environmental conditions outlined by the grazing and  
285 resource gradients. Since all data were gathered and all analyses done at the organisational  
286 level of a single ramet we used ramets as the unit in our population models. We necessarily  
287 made the assumption that ramets behave independently because the rhizome network they  
288 might still be attached to is buried deep (> 10 cm) below-ground. Any genet-network related  
289 effects are therefore masked in this study. This independency assumption must often be made  
290 in demographic studies of plant species (e.g. Jongejans et al. 2008).

291 In normal matrix models individuals are categorised into discrete classes based on, for  
292 example, age or size. For *V. myrtilus* we found that ramet size (log<sub>2</sub> DM) significantly  
293 explained the variation in important demographic rates (see analyses below), but found no  
294 obvious discrete size classes. Therefore we chose to use IPMs in which state variables like  
295 ramet size can be included in a continuous fashion. We constructed a projection model that  
296 combined the continuous state variable ramet size with a single discrete class for seeds in the  
297 soil seed bank (Ellner and Rees 2006). In our IPMs the number of seeds and the number of  
298 ramets of various sizes in a population in a year ( $n_{t+1}$ ) depended on the population size and  
299 constitution in the previous year ( $n_t$ ) and on the annual transition rate between the different  
300 types of individuals:

301 
$$n_{t+1} = \begin{pmatrix} p_b & p_f m_b m_s p_d \\ p_e N_f(\mu, \sigma^2) & p_s N_z(\mu, \sigma^2) + m_c N_c(\mu, \sigma^2) + p_f m_b m_s p_e N_f(\mu, \sigma^2) \end{pmatrix} n_t \quad (1)$$

302 in which the first column gives the contributions to  $n_{t+1}$  by seeds in the seed bank at time  $t$ ,  
 303 and the second column the contributions of ramets of various sizes. The vital rates  $p_s$ ,  $p_f$ ,  $m_c$ ,  
 304  $m_b$  as well as the normal distributions of the sizes of surviving ramets ( $N_z(\mu, \sigma^2)$ ) and clonal  
 305 offspring ( $N_c(\mu, \sigma^2)$ ) at time  $t+1$  were functions of grazing, resources and ramet size at time  $t$ ,  
 306 as presented in Table 1 and the Results section. The functions resulting from the statistical  
 307 analyses above were therefore directly included in the IPMs.

308 Integral projection models have the same analytical tools as matrix projection models.  
 309 Here we calculated the elasticity ( $e$ ) of  $\lambda$  to changes in the annual demographic transition rates  
 310 to see whether survival and growth, sexual reproduction or clonal propagation contributes  
 311 most to  $\lambda$  (de Kroon et al. 2000; Easterling et al. 2000):

312 
$$e_{\tau_{z_t, g, v}^k} = \frac{\tau_{z_t, g, v}^k}{\lambda} \frac{\partial \lambda}{\partial \tau_{z_t, g, v}^k} \quad (2)$$

313 In which the  $k^{\text{th}}$  demographic rate ( $\tau$ ) can be a function of ramet size ( $z_t$ ), grazing intensity ( $g$ )  
 314 and a resource gradient ( $v$ ). To unravel any changes in  $\lambda$  along the grazing and resource  
 315 gradients, we applied the variance decomposition technique LTRE (life table response  
 316 experiment; Horvitz et al. 1997, Jongejans and de Kroon 2005) to our integral projection  
 317 models (see also Williams and Crone 2006). We used the LTRE to investigate which changes  
 318 in the demographic rates cause the changes in  $\lambda$  along the grazing intensity gradient (both at  
 319 the lowest and at the highest level of the resource gradient) and along the resource gradient  
 320 (both with high grazing intensity and without grazing). As reference points we used the  
 321 halfway points among these combinations. In the LTRE the difference between the projected  
 322 population rate in a focal situation ( $\lambda^F$ ) with that in a reference situation ( $\lambda^C$ ) was  
 323 approximated by the variable  $\alpha$ :

324 
$$\lambda^F \cong \lambda^C + \alpha \quad (3)$$

325 This  $\lambda$ -difference approximation  $\alpha$  was calculated by taking the sum (over all  $k$  demographic  
 326 rates  $\tau$ ) of the products of the differences in the demographic rates ( $\tau_F - \tau_C$ ) and the sensitivity  
 327 ( $s$ ) values of those demographic rates:

328 
$$\tilde{\alpha} = \sum_k (\tau_{z_t, g_F, v_F}^k - \tau_{z_t, g_C, v_C}^k) s_{\tau_{z_t, g, v}^k} \left| \frac{1}{2} (A_{g_F, v_F} + A_{g_C, v_C}) \right. \quad (4)$$

329 in which  $A_{G, V}$  is the integral projection model at a certain position on the grazing and resource  
 330 axes. The sensitivity values were calculated for an IPM built with demographic rates halfway  
 331 the focal and reference situations. All statistical and modelling analyses were done in R (R  
 332 Development Core Team 2009).

## 334 Results

### 335 Growth and survival of ramets

336 The survival and growth of ramets in 2003 (year  $t+1$ ) were both significantly positively  
 337 explained by size in 2002 (year  $t$ ; Fig. 1a-b, Table 1). Flowering at the time of each of the two  
 338 censuses was also significantly explained by plant size in those years (Fig. 1c). Both the  
 339 grazing intensity gradient (i.e. the number of pellet group counts) and the resource gradient  
 340 (based on DCA-axis 1, see Appendix 1) affected these demographic processes (Table 1 and  
 341  
 342



343 2). Increasing grazing intensity reduced the survival and growth of ramets as well as the  
344 flowering probability, whereas an increasing resource level affected the survival and  
345 flowering probabilities negatively but growth positively. Significant interactions of size and  
346 both grazing intensity and resource levels in the model for growth emphasises that grazing  
347 and resources affected small and large plants differently. The size of clonal offspring (Fig. 1d)  
348 was positively affected by both increasing grazing intensities and increasing resource levels,  
349 and the significant interaction between them indicated that the effect of the variables were not  
350 independent of each other (Table 1 and 2). On average 1 out of 10 shoots produced a new  
351 clonal shoot ( $m_c = 0.100$ ,  $n = 30$ ). The number of berries per flowering shoot ( $m_b$ ) was 1.95 ( $n$   
352 = 66).

353 We also performed pairwise comparisons between grazed and ungrazed plots to be certain  
354 that the effects of grazing intensity above was not a artefact of some other underlying factor.  
355 Results of these analyses were in agreement with those presented above: survival (90.4% vs  
356 80.7%,  $p = 0.004$  and flowering (7.9% vs. 1.3%,  $p = 0.001$ ) was higher in ungrazed plots,  
357 whereas the size of clonal offspring was highest in grazed plots ( $p = 0.015$ ).

358

### 359 Population growth rate

360

361 The variation in the projected population growth rate ( $\lambda$ ) showed the synthesised effect of the  
362 variation in grazing intensities and resource levels on all demographic rates (Fig. 2). The  
363 negative effects of grazing appeared to be strongest in the more resource-rich vegetation, and  
364 higher resource levels reduced  $\lambda$  more strongly when grazing intensities became higher. The  
365 lowest  $\lambda$ 's (down to 0.65; upper right corner of Fig. 2) were therefore projected to occur in  
366 relatively resource-rich, heavily grazed forest. The highest  $\lambda$ 's (up to 1.10; bottom left corner  
367 of Fig. 2) were projected in the relatively resource-poor forest inside the exclosures where  
368 grazing was zero. However, populations with a positive growth rate ( $\lambda > 1$ ), or  $\lambda$  close to 1,  
369 were found as long as the grazing intensity stayed at  $ca < 0.20$ . Populations with a negative  $\lambda$   
370 dominated when grazing became more intense, and  $\lambda$  generally decreased most profoundly in  
371 forest with higher levels of resources.

372

### 373 The relative importance of demographic processes for population growth rate

374

375 Elasticity analysis for a stable population ( $\lambda \approx 1$ , reference point C in Fig. 2) showed that  
376 survival and growth together contributed 91.9% to  $\lambda$  (Fig. 3a), whereas sexual reproduction  
377 contributed 0.3% (Fig. 3b) and clonal propagation 7.5% (Fig. 3c). These elasticity values  
378 added up to 99.59% (Fig. 3d), whereas the missing 0.41 % comes from other transitions (see  
379 also Appendix 2 for a sensitivity analysis of our estimates of the seed bank parameters).

380 Life Table Response Experiments (LTRE) analyses were performed along the four edges  
381 of the grazing-resource 'landscape' plotted in Fig. 2. Along a gradient of grazing intensity at  
382 low resource levels (Fig. 4a), as well as along the grazing gradient at high resource levels  
383 (Fig. 4b), growth reductions were most important for the decrease in  $\lambda$  (i.e. consistently  
384 decreasing lines). Reduced flowering also affected  $\lambda$  along the grazing gradient, but only  
385 when both grazing and resources were low (Fig. 4a). Without grazing, an increase along the  
386 resource gradient reduced the flowering probability. This had a large impact on  $\lambda$ , although  
387 positive contributions of increased growth partly buffered this negative impact (Fig. 4c).  
388 Reductions in survival, growth and clonality (but not in flowering probability) lead to a  
389 decline in  $\lambda$  along the resource gradient when grazing intensity was high (Fig. 4d).

390

391

392

## 393 Discussion

394 The population dynamics of the clonal shrub *Vaccinium myrtillus* was clearly affected by  
395 variation in grazing intensity of *Cervus elaphus* and the effect was modified by the resource  
396 levels in the pine forest at Svanøy. The interplay of the two studied gradients led to several  
397 interesting findings. Indeed, the effects of grazing were different for population growth rate  
398 (Fig. 2) and vital rates (Fig. 4) at low and high resource levels for this dominant and  
399 functionally important species. Population growth rate of *V. myrtillus* was projected to  
400 increase with decreasing intensity of grazing. The highest population growth rate ( $\lambda$ ),  
401 however, occurred where the forest was poor in resources. There was a steady decrease in  
402 population growth rate with grazing intensity and the decline was strongest in the most  
403 resource-rich vegetation. Such modification of grazing-effects by resource levels is not  
404 generally expected, but it appears that the growth and reproduction of woody plants often  
405 respond in such interacting way (Hawkes and Sullivan 2001). We found a large variation in  
406 the population growth rate, ranging from 0.65 to 1.10, along the two environmental gradients.  
407 Although we only possess data from two censuses we believe that the pattern in  $\lambda$  along the  
408 gradients probably would not change considerably if we used data from a longer timeframe. It  
409 is known that long-lived species like *V. myrtillus* are expected to show a much more stable  
410 population dynamic than short-lived species (García et al. 2008). For example, Ehrlén (1995b)  
411 studying herbivory impacts on population dynamics of *Lathyrus vernus*, found little between-  
412 year variation in  $\lambda$ , but far more variation between sites and populations (see also Colling and  
413 Matthies 2006). Moreover, as the environmental gradients span a relatively large range, and  
414 show surprisingly little variation across years (i.e. grazing intensity, see Methods), the  
415 relationship between the environmental gradients and  $\lambda$  may also be relative consistent over  
416 time.

417 Why does herbivory affect the population growth rate of *V. myrtillus* most profoundly in  
418 the relatively resource rich forest? Potentially, the food-preferences of herbivores could  
419 explain some of the negative effect that resource levels have on plant performance. Studies  
420 have shown that rodent herbivores graze preferentially on *V. myrtillus* shoots that were  
421 damaged and had received supplemental nitrogen (Dahlgren et al. 2007; Grellmann 2002;  
422 Strengbom et al. 2003), perhaps because fertilised shoots may have lower concentrations of  
423 phenolic compounds (Strengbom et al. 2003). However, as *C. elaphus* graze at similar  
424 intensity in both resource rich and –poor sites on Svanøy (i.e. points with similar positions  
425 along x-axis in Fig. 2; and lack of correlation,  $r=0.05$ , between average DCA-score per site  
426 and grazing intensities per site) herbivore preferences cannot directly explain the response of  
427 the population growth rate. *V. myrtillus* may also possess competitive advantage through a  
428 relative higher tolerance to ungulate grazing than the surrounding plant species. The species  
429 has an efficient clonal propagation after major environmental disturbances (Schimmel and  
430 Granström 1996), and this may be one character that provide *V. myrtillus* with such  
431 advantage. Competitive advantages generally explain why some species dominate certain  
432 grazing influenced systems (e.g. Fornara and Du Toit 2007). Another plausible explanation  
433 can be related to the concept of a species' niche that is, at least partly, determined by  
434 environmental variables (Austin 2007). In our data set (Appendix 1) *V. myrtillus* shows an  
435 optimum in the more resource poor part along the inferred gradient. The niche concept may  
436 explain the better performance and tolerance to grazing here. Further support for the niche  
437 explanation can be found through the higher abundance of *V. myrtillus* in the intermediate to  
438 resource-poor parts of the boreal forest (Rydgren 1993; Rydgren 1996; Økland 1996). The  
439 latter explanation justifies the investigations of plant population dynamics along major  
440 environmental gradients.

441 The projected population growth rate of *V. myrtillus* populations stays  $> 1.0$  until a certain  
442 level of grazing intensity. We cannot relate our measure of grazing intensity to a distinct level

443 of *C. elaphus* density (see Methods for some approximations), but as long as the grazing  
444 intensity did not exceed the mean grazing intensity on the island, ca 0.2 on the relative scale  
445 excluding zero-grazing areas (Fig. 2), the population growth rate was  $> 1.0$  or close to 1.0.  
446 Such grazing intensity is equal to a grazing pressure of ca. 5-10% of the annual shoots on *V.*  
447 *myrtillus* ramets (Hegland *et al. unpublished results*). Rodent grazing has also shown to  
448 increase the production of new ramets in *V. myrtillus* although it generally reduced biomass  
449 and number of ramets in boreal forest populations (Dahlgren *et al.* 2007; Grellmann 2002).  
450 The populations of *V. myrtillus* at Svanøy have a population growth rate largely determined  
451 by survival and growth of ramets. The dynamic element was the emergence of clonal  
452 offspring, whereas the contribution of reproduction to the population growth rate was low and  
453 corroborates earlier findings that new plants do not emerge from seeds within closed  
454 vegetation (Eriksson and Fröberg 1996). Species with life history characteristics such as high  
455 longevity, a relatively persistent seed bank and forest dwelling, as largely the case for *V.*  
456 *myrtillus* are often buffered against large reductions in population growth rate after herbivory  
457 (Maron and Crone 2006).

458 Integral projection models proved to be useful in this study as the clonal shrub *V.*  
459 *myrtillus* cannot easily be divided into distinct size classes. A forcing of such class-division  
460 on the individuals of the studied populations could have given a different result (Easterling *et al.*  
461 *et al.* 2000, Zuidema *et al.* 2010). Our approach were novel in the sense that we not only treated  
462 plant size as a continuous state variable, but also analysed population dynamics along  
463 continuous gradients of important environmental factors: grazing intensity and resource  
464 levels. This allowed us to examine the gradual interaction effects of resources and grazing on  
465 population dynamics. Furthermore we applied a continuous scale type of the Life Table  
466 Response Experiment, enabling us to pinpoint how the different demographic processes  
467 contribute to the rate of change in population growth rate within the resource-grazing  
468 landscape. The approach to study population dynamics of plant species along major  
469 environmental gradients takes into account that the performance of species varies along such  
470 gradients (Austin 2007; Rydgren 1997). As the population study was integrated with a  
471 vegetation-dynamical study (Hegland *et al. unpublished results*) we could study the  
472 performance of *V. myrtillus* populations along major vegetation gradients. Demographic  
473 studies are often useful when investigating species response to changes in environmental and  
474 nature management related processes (Auestad *et al.* 2010; Hegland *et al.* 2001; Jongejans and  
475 de Kroon 2005; Oostermeijer *et al.* 1996). The approach presented here may contribute to a  
476 further knowledge on how species respond to changes in factors that affect their habitat.

477 The advantage of using an indirect gradient measure for measuring resource levels is its  
478 compound nature (i.e. the species composition) that reflects the resource availability at a  
479 temporal scale exceeding the given value at the specific time of a soil sample (*sensu* Økland  
480 1990). The grazing intensity gradient was also based on an indirect measure, i.e. the pellet  
481 group counts. Levels of grazing are inherently difficult to estimate. However, as our relative  
482 measure of grazing intensity correlated quite strongly with a grazing index obtained  
483 independently on plants in each block ( $r=0.79$ ; see Hegland *et al.* 2005) we believe that the  
484 variation in this environmental gradient also is sufficiently reflected by the variable used.

485 We did not aim at estimating the full lifetime dynamical response of *V. myrtillus* in this  
486 study as this would require  $>10$  years of sampling for a species with such high longevity.  
487 Instead we used the data from 900 ramets, spread across the island Svanøy, sampled in two-  
488 subsequent years to infer how *C. elaphus* grazing affected the population growth rate of the  
489 ecological important species *V. myrtillus*. *V. myrtillus* is a preferred food species for *C.*  
490 *elaphus*, in particular during the part of the year when nutritious material from grasses and  
491 herbs are less available (Latham *et al.* 1999). However, the grazing of *C. elaphus* on the plant  
492 species has to exceed the average grazing intensity of Svanøy to lead to serious declines in *V.*

493 *myrtilus* populations. Given the high elasticity value of ramet survival it is probable that the  
494 genet level of *V. myrtilus* is quite resistant to the current average grazing intensity on Svanøy.  
495 The highest population growth rate were found at the lower end of the resource gradient, and  
496 therefore we conclude that *V. myrtilus* populations are most vulnerable to declines due to of  
497 grazing when resource levels in the forest are high.

498  
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507

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- 669
- 670 **Online appendices**
- 671 **Appendix 1** Illustration of *Vaccinium myrtillus* with indication of measurements performed as  
 672 basis for the modelling approach
- 673 **Appendix 2** Sensitivity analyses of seed and seedling parameters
- 674

Table 1 Mixed-effect models (lme) fitted to the plant size data of surviving ( $N_z$ ) and new clonal offspring ( $N_c$ ) of *Vaccinium myrtillus* ramets

Fixed Effects	Estimate	S.E.	d.f.	t-value	P-value
<i>Size at t+1 of surviving ramets</i> ( $z_{t+1}$ , variance about the growth curve, $\sigma^2 = 0.755 \exp(-0.042z_{t+1})$ , $n = 689$ , $P < 0.001$ )					
intercept	-0.015	0.163	656	-0.091	0.928
size at start ( $z_t$ )	0.803	0.045	656	17.741	<0.001
grazing intensity ( $g$ )	-4.662	0.650	16	-7.176	<0.001
resources, dca1 ( $v$ )	0.182	0.153	16	1.191	0.251
size*grazing ( $z_1g$ )	-0.725	0.155	656	-4.674	<0.001
size*resource ( $z_1v$ )	0.083	0.042	656	2.004	0.046
<i>Size at t+1 of clonal offspring</i> ( $z_{t+1}$ , variance about the clonal offspring size curve, $\sigma^2 = 2.60 \exp(.062z_{t+1})$ , $n = 81$ , $P < 0.001$ )					
intercept	-5.347	0.362	50	-14.788	<0.001
grazing intensity ( $g$ )	0.752	1.869	50	0.403	0.689
resources, dca1 ( $v$ )	1.137	0.383	16	2.972	0.009
grazing*resources ( $gv$ )	-5.374	2.145	50	-2.505	0.016

Notes:  $z$  = size,  $z_t$  = size in year  $t$ ,  $z_{t+1}$  = size in year  $t+1$ ,  $g$  = grazing intensity,  $v$  = resource level (i.e. DCA axis 1, see methods for details).

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Table 2 Mixed-effects models (lmer) fitted to the survival and flowering data of *Vaccinium myrtillus* ramets

Fixed Effects	Estimate	S.E.	z-value	P-value
<i>Survival probability</i> (Logit ( $p_s$ ), $n = 813$ , $P < 0.001$ )				
intercept	3.779	0.374	10.092	<0.001
size at start ( $z_t$ )	0.339	0.062	5.487	<0.001
grazing intensity ( $g$ )	-1.655	0.758	-2.184	0.029
resource dca1 ( $v$ )	-0.573	0.252	-2.271	0.023
<i>Flowering probability</i> (Logit ( $p_f$ ), $n = 1583$ , $P < 0.001$ )				
intercept	-0.100	0.471	-0.212	0.832
size at start ( $z_t$ )	1.249	0.138	9.032	<0.001
grazing intensity ( $g$ )	-9.568	4.248	-2.253	0.024
resource dca1 ( $v$ )	-1.740	0.521	-3.341	<0.001

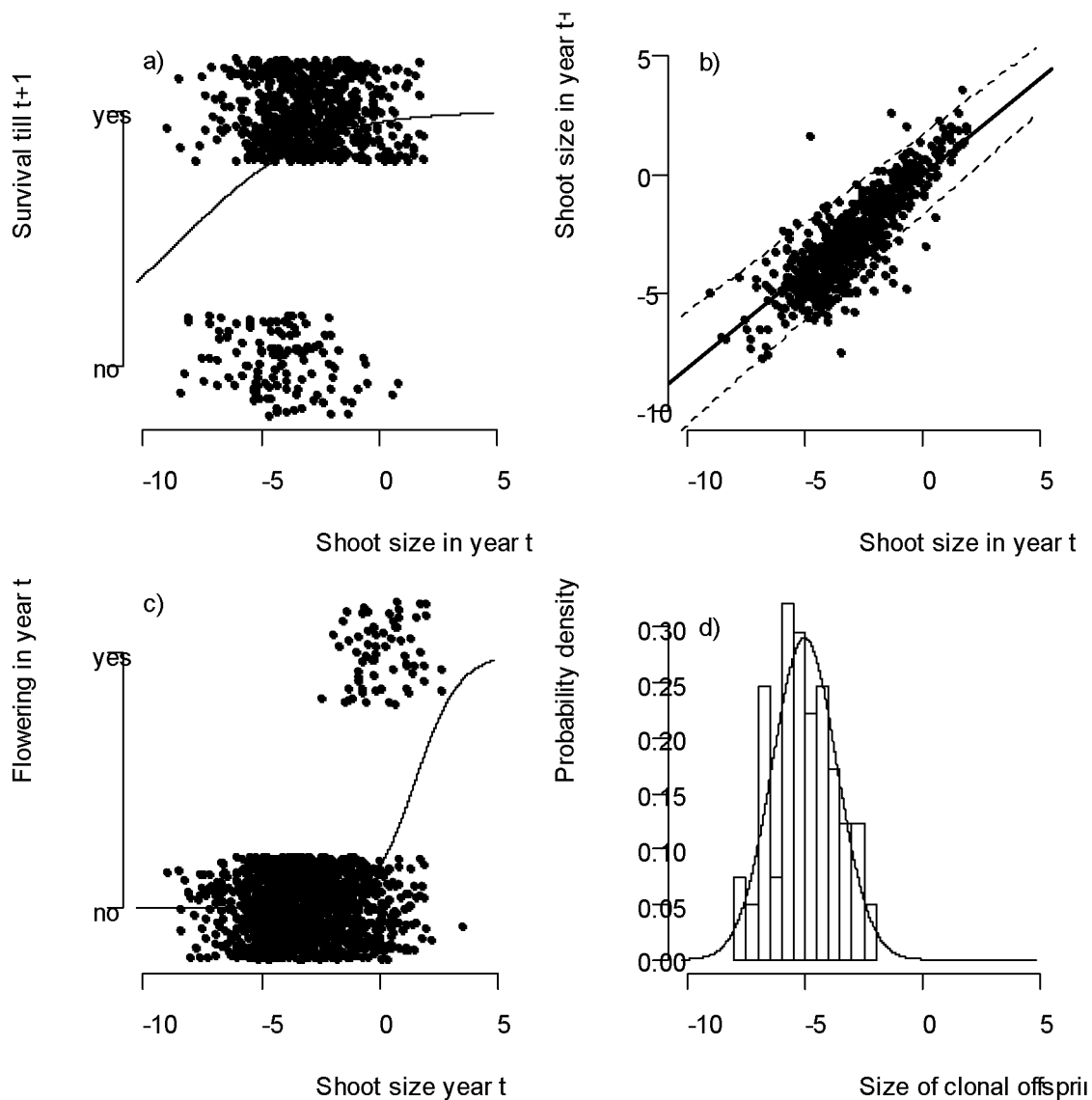
Notes:  $z$  = size,  $z_t$  = size in year  $t$ ,  $z_{t+1}$  = size in year  $t+1$ ,  $g$  = grazing intensity,  $v$  = resource level (i.e. DCA axis 1, see methods for details).

679

680 **Figure legends**  
681

Fig.1

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685 Fig. 1. Survival (a; from 2002 till 2003), growth (b; from 2002 till 2003), flowering (c; at the

686 time of the census, combining 2002 and 2003 data) and clonal offspring size (d; in 2003) of

687 *Vaccinium myrtillus* from all plots in the population at the island Svanøy in western Norway.

688 The regression lines were fitted to the plotted data and are therefore not the same as the

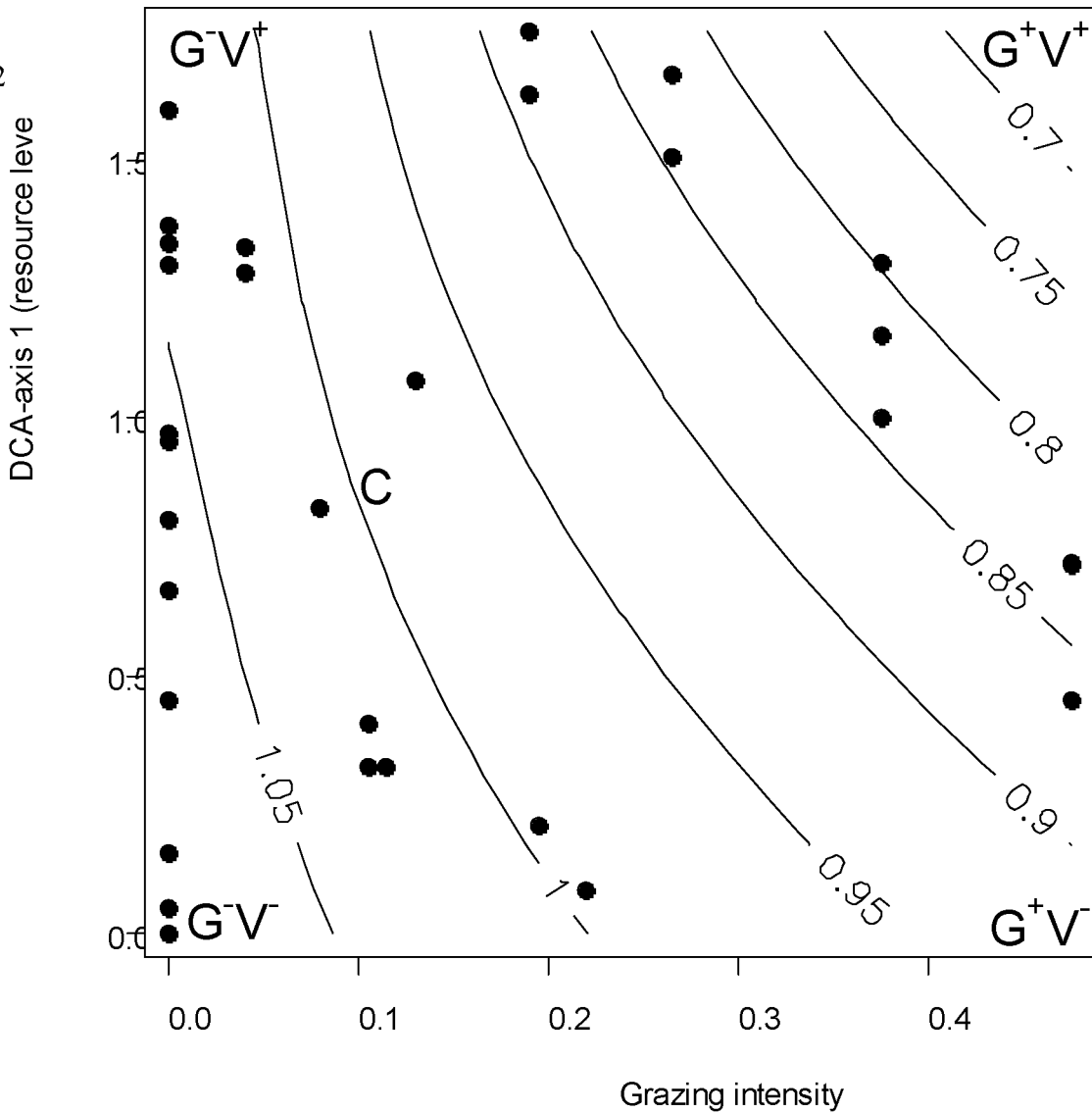
689 analyses that included grazing and resource parameters (Table 1) used in the population

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models. Size is dry mass expressed as  $\log_2$ .

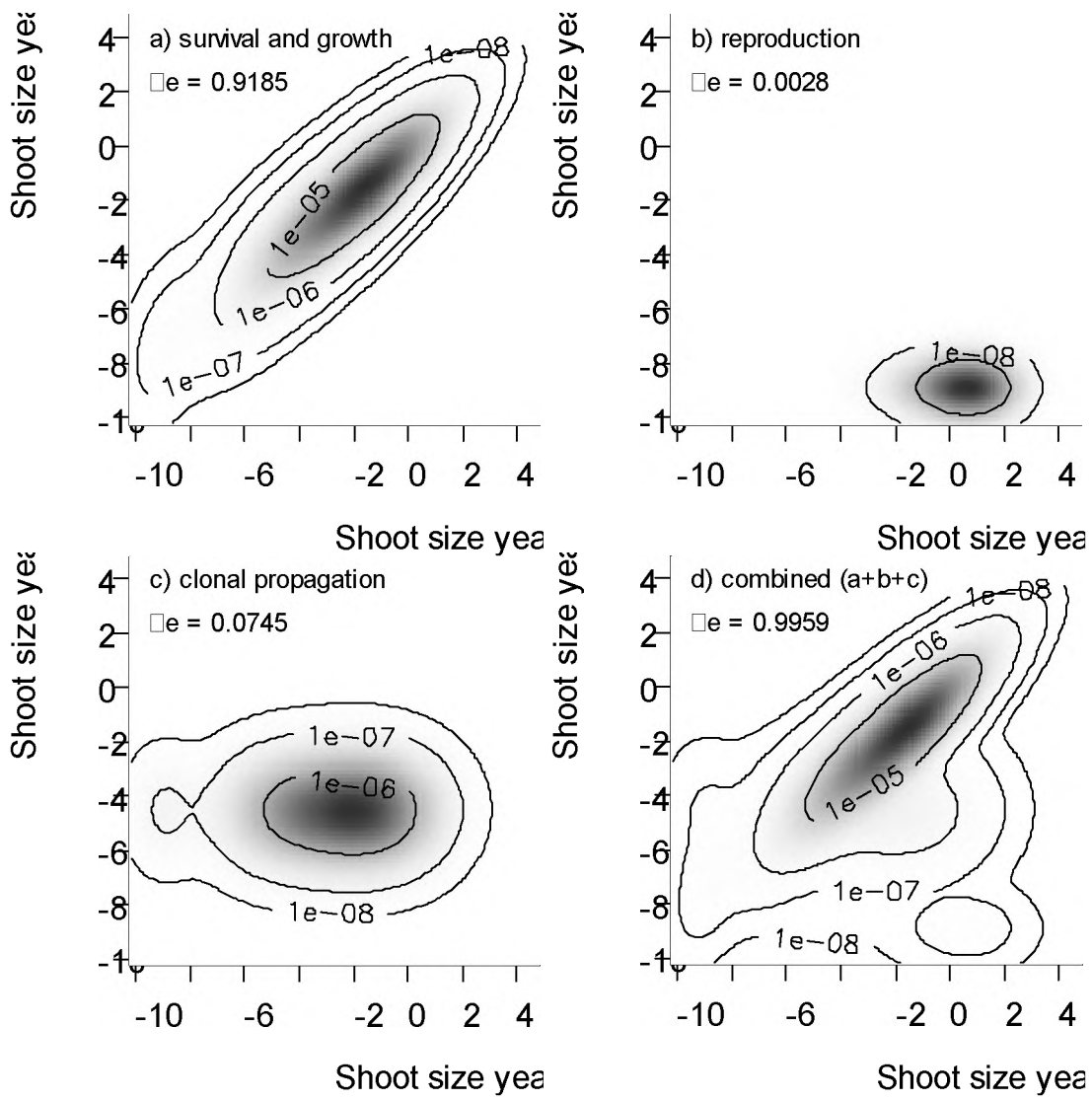
Fig.2



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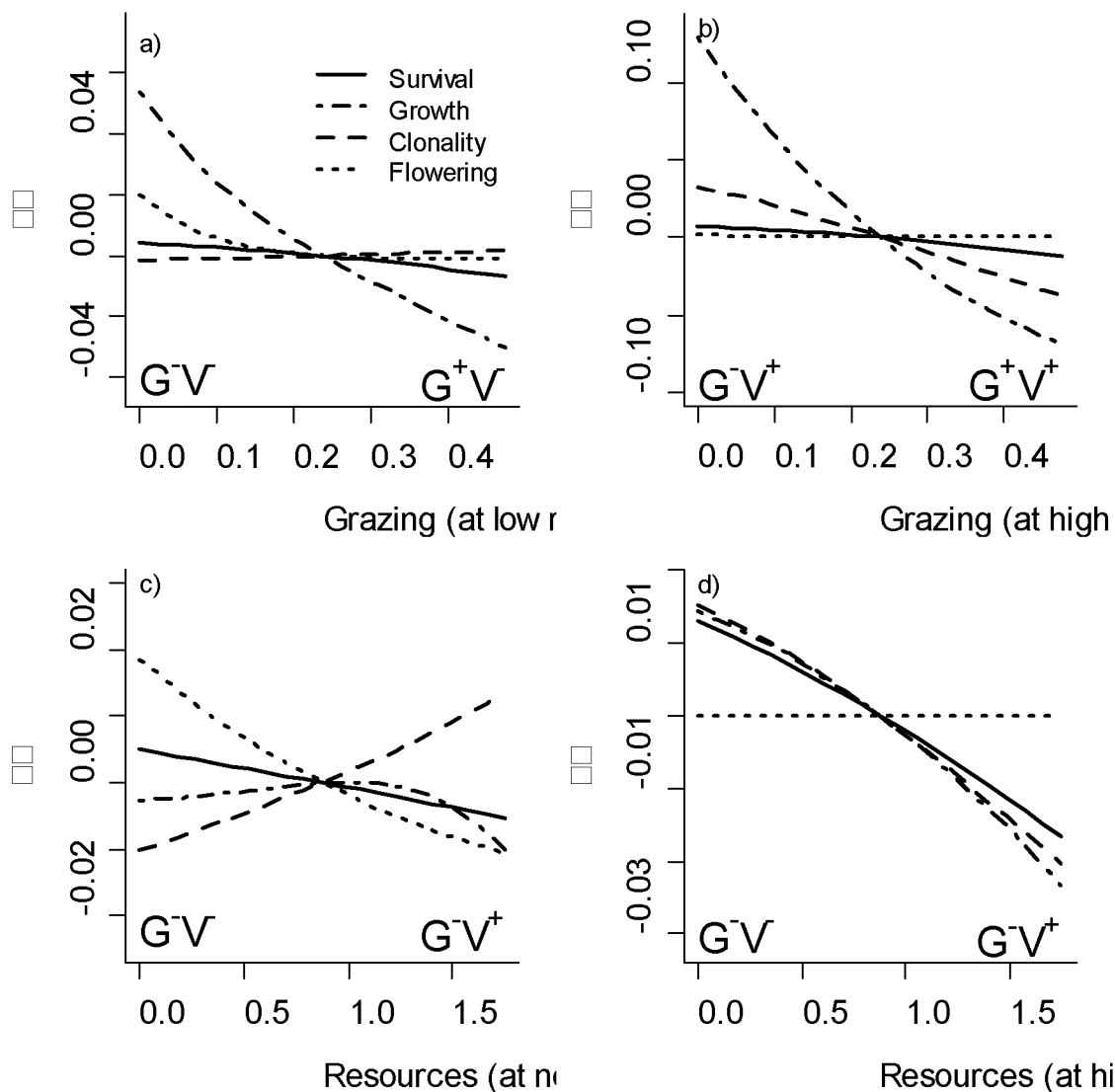
Fig. 2. The population growth rate ( $\lambda$ ) of *Vaccinium myrtillus* as projected with the integral projection models, which included the responses to the gradients of grazing intensity and resource levels (DCA-axis 1, proxy for resource levels), within the pine forest on the island of Svanøy. The black dots indicate the relative positions of the 30 plots along the grazing and vegetation (i.e. resource level) gradients. The capital letters indicate 5 scenarios that were used in the elasticity analysis (Fig. 3) and LTRE analyses (Fig. 4).

Fig.3



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703  
 704 Fig. 4. LTRE effects, with the midpoint of the four scenarios as the reference point. The  
 705 gradients in the four figures correspond to the four sides of the lambda ( $\lambda$ )-contour plot (hence  
 706 the letters near the x-axes; Fig 2): the effect of grazing intensity at a) low resource- and b)  
 707 high resource levels, and the effect of resource availability (i.e. DCA-axis 1) at c) no grazing  
 708 and d) high grazing intensity). The four lines should add up to the difference in  $\lambda$  between the  
 709 points on the four gradients and the  $\lambda$  at the midpoint. The steepness of the different lines  
 710 indicates their importance along the gradients.

711  
 712 Fig. 3. Contour plots of the lambda ( $\lambda$ )-elasticity values at the stable population dynamics at  
 713 point C in Fig. 2. The integrated elasticity values of sexual reproduction (b) and clonal  
 714 propagation (c) are much lower than of the survival and growth of shoots (a), which therefore  
 715 dominated the combined elasticity plot (d). The missing 0.0041 is the combined elasticity  
 716 value of the transition involving the seed bank. Size is dry mass expressed as  $\log_2$ . The  
 717 contour lines indicate isoclines of different orders of  $\lambda$ -elasticity densities.  
 718