PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

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 the 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 consecutive 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* faecal pellets), and a relative resource gradient (DCA-ordination of species composition). The use of IPMs enabled projections of population growth rate (λ) 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 λ 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 λ more strongly than at low resource levels when grazing intensities became higher. Populations with $\lambda > 1$ were projected if the grazing intensity was less than or equal to the mean grazing intensity on the island, and indicated that *V. myrtillus* is relatively tolerant of grazing. Variance decomposing showed that the decrease of λ 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

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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. 2000, 2002).

In Norway, *Cervus elaphus* L. (red deer) is one of the wild ungulates that for centuries played a minor role as landscape-structuring agent. Today, the current number of *C. elaphus* in Norway is at a historical high and has increased fourfold since the early 1980s as indexed by culling numbers (Statistics Norway 2008).

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

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

In a landscape-scale study, we investigated the performance of *V. myrtillus* populations along a red deer grazing intensity gradient (*Cervus elaphus* faecal pellet counts) and how the population dynamics were modified by a resource gradient (as revealed by DCA-ordination of the forest-floor vegetation). We analysed the effects of changes in the survival, growth, flowering and clonal propagation on the dynamics of *V. myrtillus* along the grazing and resource gradients by means of integral projection models (IPMs; Easterling et al. 2000). IPMs have the advantage that state variables like plant size are modelled in a continuous fashion rather than in artificial discrete steps. Furthermore, IPMs are particularly useful when the aim is (like in our study) to project the consequences of the responses of individuals to environmental gradients for the dynamics of a population: continuous, empirical functions of these responses are better included in IPMs than in matrix models with discrete classes. We hypothesise that increasing ungulate grazing will affect the dynamics of *V. myrtillus* by decreasing survival, flowering and population growth rate. As *V. myrtillus* is a woody plant, we expect that the effects of grazing will be most unfavourable for the population growth rate when the resource levels are relatively high.

Materials and methods

Study area and species

The study was carried out in 2002 and 2003 on Svanøy, an 11-km^2 island on the western coast of Norway (61°30′N, 5°05′E) in the county Sogn og Fjordane. Svanøy is situated in the boreo-nemoral zone, and forest vegetation dominated by *Pinus sylvestris* (pine) covers most of the island, which

has an oceanic climate (Skogen and Lunde 1997). Twelve study sites were located in relatively open pine-forest, with a forest floor dominated by *Vaccinium myrtillus* plants. The population of *Cervus elaphus* on Svanøy has been large and expanding ever since around 1990, and the density on the island is representative for west Norway (J.T. Solheim, personal communication).

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

Experimental design and sampling procedures

The 12 study sites were selected within mature bilberry–pine forest, according to a vegetation map (by Skogen and Lunde 1997), and spread across the island. Study sites had been little influenced by forestry the last 50 years (see also Hegland et al. 2005: Fig. 1). During the winter of 2000, we established a grazing exclosure and an ungulate grazed control area of 10×10 m at each site. The sites were restricted to flat areas less than 200 m above sea level dominated by *V. myrtillus* to reduce variation due to altitude and aspect. Ten of the sites were situated in forest with wild-living *C. elaphus* as the main grazer, and these sites represented a natural grazing regime. The other two sites were located at the deer farm of the Norwegian Red Deer Centre and represented an area with high grazing intensities by *C. elaphus*. Grazing intensities have been high ever since deer farming started in 1993 (J.T. Solheim, personal communication). We estimated the variation in grazing intensities per site within the grazed control areas by recording the presence of faecal pellet groups in one hundred 1-m^2 plots randomly distributed within a radius of 100 m around the grazed control areas. In this way, we obtained an index of grazing intensity per site and plot ranging from 0 to 100. We sampled pellet groups in June and August 2001, and used the mean frequency from these two sampling events which in grazed areas was observed to range from 4 to 47.5. To control for the possible interannual variability in grazing intensities, we resampled all

sites 5 years later and found a high correlation ($r = 0.81$, $n = 12$, $P < 0.0005$) indicating stable grazing intensities in time across sites. Pellet group counts are reckoned to be an efficient method for measuring the relative density and habitat use of ungulates (Härkönen and Heikkilä 1999), and appear to be significantly correlated with an index of herbivore damage recorded directly on *V. myrtillus* (Hegland et al. 2005). In this study, the grazing gradient spans the full grazing intensity from no grazing, via low and intermediate to very high levels of grazing; the latter comparable to areas with high winter-densities in west-Norway (S.J. Hegland, personal observation). Sheep were also grazing on Svanøy, but as revealed by pellet counts they were of less importance in the study sites. From the plant perspective, both red deer and sheep can be expected to have a similar impact on vegetation as both belong to the intermediate grazer-browser group (cf. Bodmer 1990). However, one should be aware of that sheep, even at relative low densities, can affect vegetation significantly due to aggregation behaviour (Albon et al. 2007).

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

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

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

In August 2002, we also collected another dataset consisting of 150 ramets sampled across the island. These ramets were measured (variables 1–3, see above), and dried to constant weight at 70°C in a drying cabinet. We then constructed a multiple regression model (sensu Økland [1995]) from the data on dry mass (DM, in g), ramet height, the number of annual shoots on a ramet, and the diameter of the stem. The following model for dry mass estimation of *V. myrtillus* explained most of the variation, ($R^2 = 0.944$;

$P < 0.001$): $\log_2(DM) = 1.41700 \times \log_2(DS) + 0.97104 \times \log_2(H) + 0.44153 \times \log_2(AS + 1) - 7.52070$. We used the right side of this function as our non-destructive estimate of plant size, z (see below).

Primary data analysis

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

The annual survival probability (p_s) and the probability that a ramet was flowering at the time of census (p_f) were analysed with general linear regression models (glm) in binomial error-distribution. The data of both censuses (2002, 2003) were combined in the analysis of the flowering probability. The number of berries (n_b) produced by the flowering ramets was modelled with a glm with Poisson error-distribution. The growth of the surviving ramets was studied by analysing the ramet size distribution after a year (z_2). The number of clonal offspring per ramet (m_c) was calculated by using the ratio of the number of new clonal offspring in a plot in 2003 and the number of ramets in that plot in 2002. m_c was analysed with a glm with quasi-Poisson error-distribution. m_c and the size distribution of clonal offspring were modelled as a function of the

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	SE	df	t value	P value
Size at $t + 1$ of surviving ramets[a]					
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 ($z_t g$)	−0.725	0.155	656	−4.674	<0.001
Size × resource ($z_t v$)	0.083	0.042	656	2.004	0.046
Size at $t + 1$ of clonal offspring[b]					
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

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 "Materials and methods" for details)

[a] z_{t+1}, variance about the growth curve, $\sigma^2 = 0.755 \exp(−0.042 z_{t+1})$, $n = 689$, $P < 0.001$

[b] z_{t+1}, variance about the clonal offspring size curve, $\sigma^2 = 2.60 \exp(0.062 z_{t+1})$, $n = 81$, $P < 0.001$

plot-level parameters g and v, but not of z_1 because it was not possible to determine which old ramet had produced which new clonal offspring due to invisibility of the buried rhizomes (see also Jongejans et al. 2008).

The remaining life cycle components involved seeds and seedlings. These demographic rates were not analysed over the grazing and resource gradients because they were very rare. Precise measurements of these life cycle components are difficult to obtain, and calculations of probabilities, for the use in projection modelling, were therefore set at values that are plausible given the literature available on this species (see "Study area and species" for references): (1) the probability of seedling establishment (p_e) was set at 0.015, since seedling establishment in forest vegetation appears very low; (2) the probability of seeds entering the seed bank (p_d) was set at 0.25 because studies have shown that a seed bank is sometimes present; (3) the probability of seeds staying in the seed bank (p_b) was set at 0.5 because although seed bank often is transient, viable seeds appear even deep in the soil; (4) the probability of seedling establishment from the seed bank was set at 0.015 because establishment from seed bank in closed forest floor vegetation is rare; (5) the mean and variance of a normal distribution of seedling sizes ($N_1(\mu, \sigma^2)$) were set at −9 and 0.5 ($\log_2$-scale), respectively, which resulted in smaller seedlings than any surviving or clonal ramet recorded by us because we recorded only one seedling; and (6) the number of seeds per berry (m_s) was set at 25. To check how robust our model outcomes were, we performed a sensitivity analysis in the light of the uncertainty of the estimations of these latter demographic rates. The results confirmed that the rates that involved seeds and seedlings were of little importance themselves for the dynamic in the studied populations (ESM, Appendix 2). The seedling establishment rate also affects the importance of the flowering rate, but neither the patterns nor the ranking of the flowering LTRE contribution (see below) relative to the contributions by other vital rates changed when seedling establishment was even halved or doubled (ESM, Appendix 2).

Analysis of effects on population dynamics

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

In normal matrix models, individuals are categorised into discrete classes based on, for example, age or size. For *V. myrtillus*, we found that ramet size ($\log_2$ DM) significantly explained the variation in important demographic rates (see analyses below), but found no obvious discrete size classes. Therefore, we chose to use IPMs in which state variables like ramet size can be included in a continuous fashion. We constructed a projection model that combined the continuous state variable ramet size with a single discrete class for seeds in the soil seed bank

(Ellner and Rees 2006). In our IPMs, the number of seeds and the number of ramets of various sizes in a population in a year (n_{t+1}) depended on the population size and constitution in the previous year (n_t) and on the annual transition rate between the different types of individuals:

$$n_{t+1} = \begin{pmatrix} p_b & p_f m_b m_s p_d \\ p_e N_1(\mu, \sigma^2) & p_s N_z(\mu, \sigma^2) + m_c N_c(\mu, \sigma^2) + p_f m_b m_s p_e N_1(\mu, \sigma^2) \end{pmatrix} n_t \tag{1}$$

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

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

$$e_{\tau_{z_t,g,v}^k} = \frac{\tau_{z_t,g,v}^k}{\lambda} \frac{\partial \lambda}{\partial \tau_{z_t,g,v}^k} \tag{2}$$

In which the kth demographic rate (τ) can be a function of ramet size (z_t), grazing intensity (g) and a resource gradient (v). To unravel any changes in λ along the grazing and resource gradients, we applied the variance decomposition technique LTRE (life table response experiment; Horvitz et al. 1997; Jongejans and de Kroon 2005) to our integral projection models (see also Williams and Crone 2006). We used the LTRE to investigate which changes in the demographic rates cause the changes in λ along the grazing intensity gradient (both at the lowest and at the highest level of the resource gradient) and along the resource gradient (both with high grazing intensity and without grazing). As reference points, we used the halfway points among these combinations. In the LTRE, the difference between the projected population rate in a focal situation (λ^F) with that in a reference situation (λ^C) was approximated by the variable α:

$$\lambda^F \cong \lambda^C + \alpha \tag{3}$$

This λ-difference approximation α was calculated by taking the sum (over all k demographic rates τ) of the products of the differences in the demographic rates ($\tau_F - \tau_C$) and the sensitivity (s) values of those demographic rates:

$$\tilde{\alpha} = \sum_k \left(\tau_{Z_t,g_F,V_F}^k - \tau_{Z_t,g_C,V_C}^k \right) S_{\tau_{Z_t,g,V}^k} \Bigg|_{\frac{1}{2}\left(A_{g_F,V_F} + A_{g_C,V_C}\right)}. \tag{4}$$

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

Results

Growth and survival of ramets

The survival and growth of ramets in 2003 (year $t + 1$) were both significantly positively explained by size in 2002 (year t; Fig. 1a, b; Table 1). Flowering at the time of each of the two censuses was also significantly explained by plant size in those years (Fig. 1c). Both the grazing intensity gradient (i.e. the number of pellet group counts) and the resource gradient (based on DCA-axis 1, see ESM, Appendix 1) affected these demographic processes (Tables 1 and 2). Increasing grazing intensity reduced the survival and growth of ramets as well as the flowering probability, whereas an increasing resource level affected the survival and flowering probabilities negatively but growth positively. Significant interactions of size and both grazing intensity and resource levels in the model for growth emphasises that grazing and resources affected small and large plants differently. The size of clonal offspring (Fig. 1d) was positively affected by both increasing grazing intensities and increasing resource levels, and the significant interaction between them indicated that the effect of the variables were not independent of each other (Tables 1 and 2). On average, 1 out of 10 shoots produced a new clonal shoot ($m_c = 0.100$, $n = 30$). The number of berries per flowering shoot (m_b) was 1.95 ($n = 66$).

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

Population growth rate

The variation in the projected population growth rate (λ) showed the synthesised effect of the variation in grazing intensities and resource levels on all demographic rates

Fig. 1 Survival (**a** from 2002 till 2003), growth (**b** from 2002 till 2003), flowering (**c** at the time of the census, combining 2002 and 2003 data) and clonal offspring size (**d** in 2003) of *Vaccinium myrtillus* from all plots in the population at the island Svanøy in western Norway. The regression lines were fitted to the plotted data and are therefore not the same as the analyses that included grazing and resource parameters (Table 1) used in the population models. Size is dry mass expressed as $\log_2$
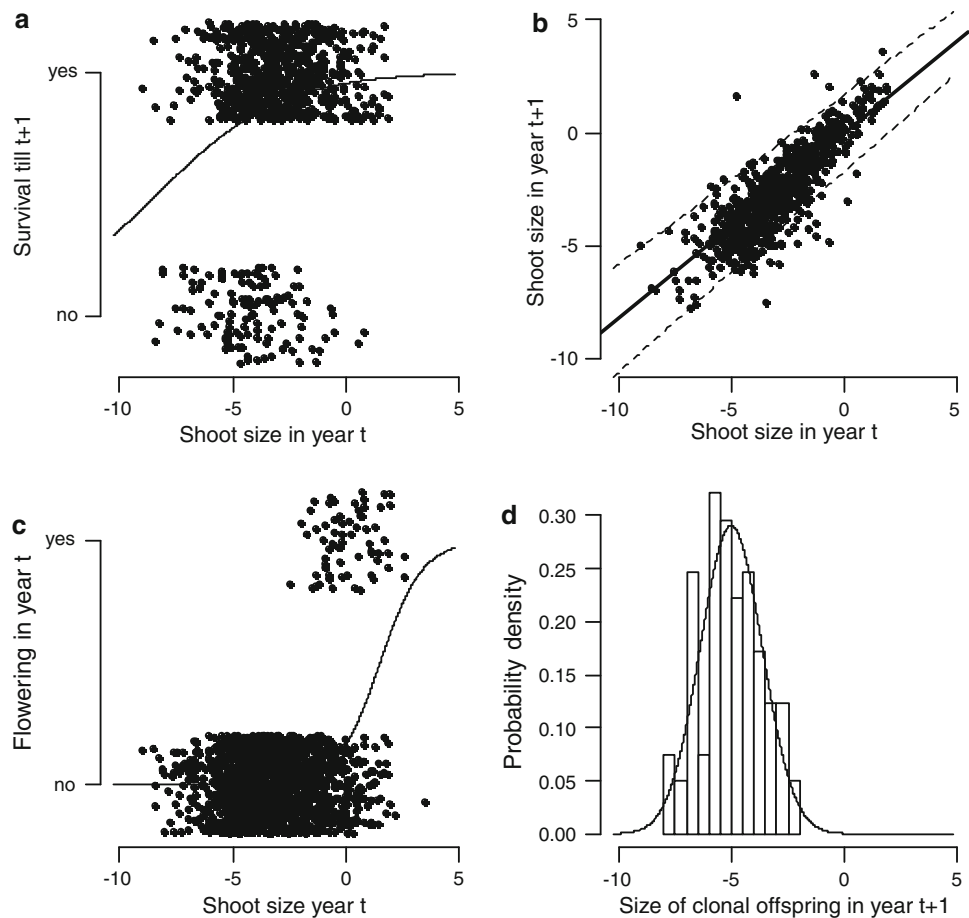
Table 2 Mixed-effects models (lmer) fitted to the survival and flowering data of *Vaccinium myrtillus* ramets

Fixed effects	Estimate	SE	z value	P value
Survival probability[a]				
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
Flowering probability[b]				
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

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 "Materials and methods" for details)

[a] Logit (p_s), $n = 813$, $P < 0.001$

[b] Logit (p_f), $n = 1,583$, $P < 0.001$

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

The relative importance of demographic processes for population growth rate

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

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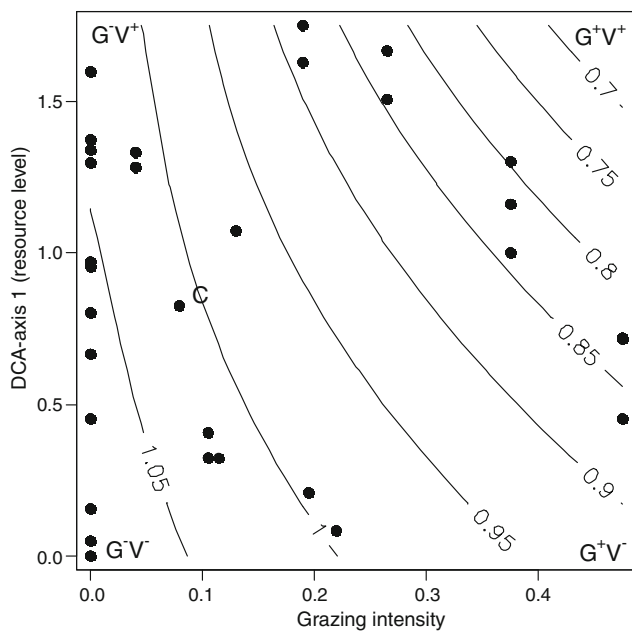
Fig. 2 The population growth rate (λ) of *Vaccinium myrtillus* as projected with the integral projection models, which included the responses to the gradients of grazing intensity and resource levels (DCA-axis 1, proxy for resource levels), within the pine forest on the island of Svanøy. The *black dots*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

'landscape' plotted in Fig. 2. Along a gradient of grazing intensity at low resource levels (Fig. 4a), as well as along the grazing gradient at high resource levels (Fig. 4b), growth reductions were most important for the decrease in λ (i.e. consistently decreasing lines). Reduced flowering also affected λ along the grazing gradient, but only when both grazing and resources were low (Fig. 4a). Without grazing, an increase along the resource gradient reduced the flowering probability. This had a large impact on λ, although positive contributions of increased growth partly buffered this negative impact (Fig. 4c). Reductions in survival, growth and clonality (but not in flowering probability) led to a decline in λ along the resource gradient when grazing intensity was high (Fig. 4d).

Discussion

The population dynamics of the clonal shrub *Vaccinium myrtillus* was clearly affected by variation in grazing intensity of *Cervus elaphus*, and the effect was modified by the resource levels in the pine forest at Svanøy. The interplay of the two studied gradients led to several interesting findings. Indeed, the effects of grazing were different for population growth rate (Fig. 2) and vital rates (Fig. 4) at low and high resource levels for this dominant

and functionally important species. Population growth rate of *V. myrtillus* was projected to increase with decreasing intensity of grazing. The highest population growth rate (λ), however, occurred where the forest was poor in resources. There was a steady decrease in population growth rate with grazing intensity, and the decline was strongest in the most resource-rich vegetation. Such modification of grazing-effects by resource levels is not generally expected, but it appears that the growth and reproduction of woody plants often respond in such inter-acting way (Hawkes and Sullivan 2001). We found a large variation in the population growth rate, ranging from 0.65 to 1.10, along the two environmental gradients. Although we only possess data from two censuses, we believe that the pattern in λ along the gradients probably would not change considerably if we used data from a longer time-frame. It is known that long-lived species like *V. myrtillus* are expected to show a much more stable population dynamic than short-lived species (García et al. 2008). For example, Ehrlén (1995b), studying herbivory impacts on population dynamics of *Lathyrus vernus*, found little between-year variation in λ, but far more variation between sites and populations (see also Colling and Matthies 2006). Moreover, as the environmental gradients span a relatively large range, and show surprisingly little variation across years (i.e. grazing intensity, see "Materials and methods"), the relationship between the environmental gradients and λ may also be relative consistent over time.

Why does herbivory affect the population growth rate of *V. myrtillus* most profoundly in the relatively resource-rich forest? Potentially, the food preferences of herbivores could explain some of the negative effect that resource levels have on plant performance. Studies have shown that rodent herbivores graze preferentially on *V. myrtillus* shoots that were damaged and had received supplemental nitrogen (Dahlgren et al. 2007; Grellmann 2002; Strengbom et al. 2003), perhaps because fertilised shoots may have lower concentrations of phenolic compounds (Strengbom et al. 2003). However, as *C. elaphus* graze at similar intensity in both resource-rich and -poor sites on Svanøy (i.e. points with similar positions along *x*-axis in Fig. 2; and lack of correlation, $r = 0.05$, between average DCA-score per site and grazing intensities per site), herbivore preferences cannot directly explain the response of the population growth rate. *V. myrtillus* may also possess competitive advantage through a relative higher tolerance to ungulate grazing than the surrounding plant species. The species has an efficient clonal propagation after major environmental disturbances (Schimmel and Granström 1996), and this may be one character that provides *V. myrtillus* with such an advantage. Competitive advantages generally explain why some species dominate certain grazing influenced systems (e.g. Fornara and Du Toit 2007).

Fig. 3 Contour plots of the lambda (λ)-elasticity values at the stable population dynamics at point C in Fig. 2. The integrated elasticity values of sexual reproduction (**b**) and clonal propagation (**c**) are much lower than of the survival and growth of shoots (**a**), which therefore dominated the combined elasticity plot (**d**). The missing 0.0041 is the combined elasticity value of the transition involving the seed bank. Size is dry mass expressed as $\log_2$. The *contour lines* indicate isoclines of different orders of λ-elasticity densities
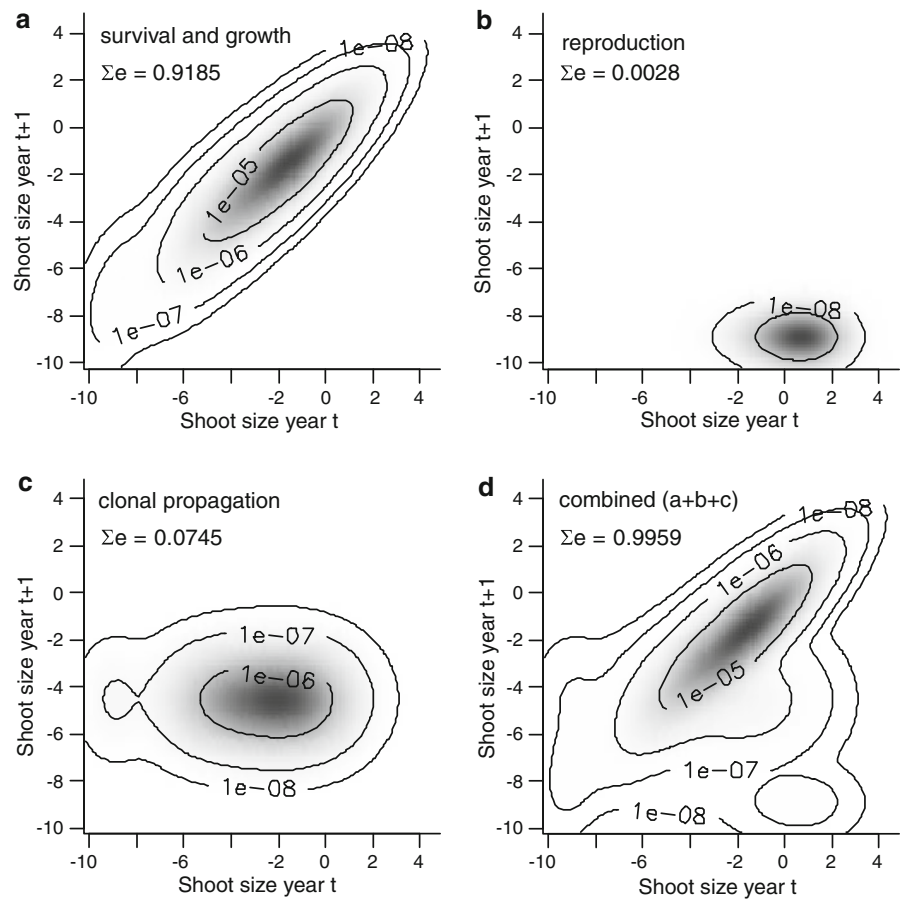
Another plausible explanation can be related to the concept of a species' niche that is, at least partly, determined by environmental variables (Austin 2007). In our dataset (ESM, Appendix 1), *V. myrtillus* shows an optimum in the more resource-poor part along the inferred gradient. The niche concept may explain the better performance and tolerance to grazing here. Further support for the niche explanation can be found through the higher abundance of *V. myrtillus* in the intermediate to resource-poor parts of the boreal forest (Rydgren 1993, 1996; Økland 1996). The latter explanation justifies the investigations of plant population dynamics along major environmental gradients.

The projected population growth rate of *V. myrtillus* populations stays >1.0 until a certain level of grazing intensity. We cannot relate our measure of grazing intensity to a distinct level of *C. elaphus* density (see "Materials and methods" for some approximations), but as long as the grazing intensity did not exceed the mean grazing intensity on the island, ca 0.2 on the relative scale excluding zero-grazing areas (Fig. 2), the population growth rate was >1.0 or close to 1.0. Such grazing intensity is equal to a grazing pressure of ca. 5–10% of the annual shoots on *V. myrtillus* ramets (Hegland et al., unpublished results). Rodent grazing has also been shown to increase the production of new

ramets in *V. myrtillus*, although it generally reduced biomass and number of ramets in boreal forest populations (Dahlgren et al. 2007; Grellmann 2002). The populations of *V. myrtillus* at Svanøy have a population growth rate largely determined by survival and growth of ramets. The dynamic element was the emergence of clonal offspring, whereas the contribution of reproduction to the population growth rate was low and corroborates earlier findings that new plants do not emerge from seeds within closed vegetation (Eriksson and Fröborg 1996). Species with life history characteristics such as high longevity, a relatively persistent seed bank and forest dwelling, as largely the case for *V. myrtillus*, are often buffered against large reductions in population growth rate after herbivory (Maron and Crone 2006).

Integral projection models proved to be useful in this study, as the clonal shrub *V. myrtillus* cannot easily be divided into distinct size classes. A forcing of such class division on the individuals of the studied populations could have given a different result (Easterling et al. 2000; Zuidema et al. 2010). Our approach was novel in the sense that we not only treated plant size as a continuous state variable, but also analysed population dynamics along continuous gradients of important environmental factors:

grazing intensity and resource levels. This allowed us to
examine the gradual interaction effects of resources and
grazing on population dynamics. Furthermore, we applied
a continuous scale type of the life table response experi-
ment, enabling us to pinpoint how the different demo-
graphic processes contribute to the rate of change in
population growth rate within the resource-grazing land-
scape. The approach to study population dynamics of plant
species along major environmental gradients takes into
account that the performance of species varies along such
gradients (Austin 2007; Rydgren 1997). As the population
study was integrated with a vegetation-dynamical study
(Hegland et al., unpublished results) we could study the
performance of *V. myrtillus* populations along major
vegetation gradients. Demographic studies are often useful
when investigating species response to changes in envi-
ronmental and nature management-related processes
(Auestad et al. 2010; Hegland et al. 2001; Jongejans and de
Kroon 2005; Oostermeijer et al. 1996). The approach
presented here may contribute to a further knowledge on
how species respond to changes in factors that affect their
habitat.

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

We did not aim at estimating the full lifetime dynamical
response of *V. myrtillus* in this study as this would require
>10 years of sampling for a species with such high lon-
gevity. Instead, we used the data from 900 ramets, spread
across the island Svanøy, sampled in two consecutive years
to infer how *C. elaphus* grazing affected the population
growth rate of the ecological important species *V. myrtil-
lus*. *V. myrtillus* is a preferred food species for *C. elaphus*,
in particular during the part of the year when nutritious

material from grasses and herbs are less available (Latham et al. 1999). However, the grazing of *C. elaphus* on the plant species has to exceed the average grazing intensity of Svanøy to lead to serious declines in *V. myrtillus* populations. Given the high elasticity value of ramet survival, it is probable that the genet level of *V. myrtillus* is quite resistant to the current average grazing intensity on Svanøy. The highest population growth rates were found at the lower end of the resource gradient, and therefore we conclude that *V. myrtillus* populations are most vulnerable to declines due to grazing when resource levels in the forest are high.

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