

# Local environment and density-dependent feedbacks determine population growth in a forest herb

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**Abstract** Linking spatial variation in environmental factors to variation in demographic rates is essential for a mechanistic understanding of the dynamics of populations. However, we still know relatively little about such links, partly because feedbacks via intraspecific density make them difficult to observe in natural populations. We conducted a detailed field study and investigated simultaneous effects of environmental factors and the intraspecific density of individuals on the demography of the herb *Lathyrus vernus*. In regression models of vital rates we identified effects associated with spring shade on survival and growth, while density was negatively correlated with these vital rates. Density was also negatively correlated with average individual size in the study plots, which is consistent with self-thinning. In addition, average plant sizes were larger than predicted by density in plots that were less shaded by the tree canopy, indicating an environmentally determined carrying capacity. A size-structured integral projection model based on the vital rate regressions revealed that the identified effects of shade and density were strong enough to produce differences in stable population sizes similar to

those observed in the field. The results illustrate how the local environment can determine dynamics of populations and that intraspecific density may have to be more carefully considered in studies of plant demography and population viability analyses of threatened species. We conclude that demographic approaches incorporating information about both density and key environmental factors are powerful tools for understanding the processes that interact to determine population dynamics and abundances.

**Keywords** Intraspecific density · Plant demography · Population dynamics · Shade · Spatial variation

## Introduction

The abundance and distribution of organisms are determined by abiotic environmental factors as well as biotic interactions with other organisms. Moreover, sufficiently high densities can lead to impaired performance of individuals and self-regulation of population densities (e.g. Murdoch 1994). The vital rates that determine population growth will thus be determined by both intraspecific density and the abiotic and biotic environment of individuals (e.g. Maurer and Taper 2002). Although we have much evidence that both environmental conditions and intra-specific densities can have important effects on population dynamics, we know less about the interplay between these factors and about their relative importance for the dynamics of natural populations (e.g. Benton et al. 2006). A likely reason for this is that observations of spatial variation in survival, fecundity and growth of individuals cannot readily be linked to environment or density separately as these factors are interdependent. In a given habitat patch, favourable environmental conditions will have positive effects on

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vital rates when densities are below the equilibrium level, but the resulting increase in density will lead to counteracting self-regulatory effects on vital rates, causing an eventual stabilization of population size. This means that among populations close to carrying capacity, we expect population growth rate ( $r$ ) to be zero, and related neither to environmental factors nor density. However, natural populations are likely to often deviate from perfect equilibrium (Krebs 2002). As a consequence, identifying effects of local environment and density on vital rates and population growth rate should still be possible using observational field data, if effects of variation in environmental factors and density are assessed simultaneously.

The wealth of studies documenting correlations between species distributions and environmental conditions strongly suggest that environmental factors play a fundamental role for population dynamics (e.g. Guisan and Thuiller 2005). In addition, differences in vital rates among plots and sites in demographic studies suggest that environmental factors, such as light availability (Alvarez-Buylla 1994; Horvitz et al. 2005) and nutrient concentrations (Gotelli and Ellison 2002; Brys et al. 2005; Colling and Matthies 2006), do affect population growth rates of plants. Recently, several studies have explored how differences in specific environmental factors can drive spatial variation in plant population dynamics (e.g. Dahlgren and Ehrlén 2009; Mandle and Ticktin 2012; Diez et al. 2014). Also correlations between temporal variation in environmental factors and population dynamics constitute evidence of the importance of environmental conditions. For example, studies with several plant systems have identified effects of climate on population growth rate via different vital rates (e.g. Doak and Morris 2010; Nicolè et al. 2011; Salguero-Gómez et al. 2012; Sletvold et al. 2013).

To reliably establish links between environmental factors, vital rates and population dynamics, the effects of density should also be accounted for (Hubbell et al. 1990; Alvarez-Buylla 1994; Zhu et al. 2010). While observational studies frequently have found no evidence of intraspecific competition affecting demographic rates (Matos et al. 1999; Waser et al. 2010; Luo et al. 2012), several detailed longitudinal studies and studies experimentally manipulating density have identified strong effects (e.g. Fowler et al. 2006; Ramula and Buckley 2009). A number of studies with annual plants suggest that intraspecific density can indeed have important effects on population dynamics and that also established individuals are affected (e.g. Yoda et al. 1963; Freckleton and Watkinson 1998; Buckley et al. 2001). Density effects have also been identified for tropical trees (Hubbell et al. 1990; Peters 2003). Studies of effects of intraspecific density in other perennial plants are fewer and often focus on effects

during the establishment phase of the life cycle (e.g. Matos et al. 1999; Waser et al. 2010), although several studies have assessed effects during multiple life stages (e.g. Gillman et al. 1993; Alvarez-Buylla 1994; Fowler et al. 2006; Ramula and Buckley 2009). Moreover, the effects of environmental factors and intra-specific density on population dynamics may be interactive. In recent years, several studies have provided evidence that the importance of intra-specific competition depends on the degree of abiotic stress (Goldenheim et al. 2008; Fajardo and McIntire 2011). Another example of how the effects of intra-specific interactions may depend on environmental conditions is the ‘Sukatschew effect’, i.e. self-thinning being more intense under more benign conditions (Harper 1977). In spite of such evidence that both environmental factors and intra-specific density may have important effects and that effects may be interactive, studies examining the simultaneous effects of explicit environmental factors and intra-specific density on vital rates and population growth rate of perennial plants in natural environments are still largely lacking.

Here we examine relationships between spatial variation in several environmental factors, density, vital rates, and structure and dynamics in a natural population of the long-lived forest herb *Lathyrus vernus*. This species has a life history that might be expected in a moderately shade-tolerant forest herb in that individuals grow fairly slowly, have high annual survival rates and produce few, large seeds after many years of vegetative growth. In the study area, the species occurs in the forest understory and has a patchy distribution with densities ranging from low to moderate. We used demographic data consisting of 7 years of observations on marked individuals and data on multiple environmental factors from 72 permanent plots distributed over a 0.5-km<sup>2</sup> study area, consisting of deciduous forests and wooded meadows. To identify the drivers of vital rates, we used hierarchical regression models in combination with the least absolute shrinkage and selection operator (lasso) variable shrinkage technique. Our focus in this study was on spatial variation and we did not explicitly consider temporal variation. Based on the previous studies of environmental factors and density as drivers of population dynamics reviewed above, we hypothesized that environmental factors cause differences in carrying capacities among suitable habitat patches, that effects of environmental factors on vital rates can be determined using regression analyses with observational data when controlling for density, and vice versa, and that population sizes are regulated by density-dependent environmental effects on vital rates. We conducted analyses both at the individual level and at the plot level to test the following specific predictions:

1. Variation in environmental factors, such as shade, is correlated with variation in vital rates.
2. Variation in density is correlated with variation in vital rates.
3. Relationships of vital rates with environmental factors and density are interdependent and density effects are stronger in less favourable environments.
4. Individuals of different sizes are influenced differently by intra-specific density, and effects of density and environmental factors at the level of individuals should translate into effects on the mean size of individuals at the plot level.

Finally, we used the statistically optimal regression models of environment and density effects on vital rates to parameterize density-dependent integral projection models (IPMs). With these models we examine how individual-level relationships translate to effects on populations, and whether these effects lead to equilibrium densities that correspond to those observed in different local environments.

## Materials and methods

### Study system

*Lathyrus vernus* (L.) Bernh. (Fabaceae) is a long-lived forest understory herb distributed across Europe and parts of northern Asia. It is non-clonal and one or several shoots emerge from the rhizome early in spring (Ehrlén 1995). The aboveground parts of the plant die back in autumn each year. Some plants may be dormant in one season and reappear only in the following year. Flowering plants usually produce five to 30 large flowers that are pollinated by bumblebees. Individuals produce a small number of relatively large seeds that are ballistically dispersed and may remain viable for several years in the soil. Seedlings are able to survive for many years also under very low light conditions. Recruitment is seed limited and the emergence and survival of seedlings does not depend on intra-specific density (Ehrlén and Eriksson 1996). Increases in size between years are small and seedlings frequently take more than 10 years before they first flower (J. E., unpublished data). Individuals that reach maturity have been estimated to have a mean total life span of 44 years (Ehrlén and Lehtilä 2002). A detailed description of the study species' biology is provided in Ehrlén (2002).

In the study area *L. vernus* occurs in deciduous forests and wooded meadows varying in tree species composition and canopy cover. The distribution of *L. vernus* in the study area is patchy and densities of individuals may vary by several orders of magnitude, but very high densities (higher than 50 % cover) or mono-specific stands do not occur.

The forest floor appears in many respects to constitute a relatively stable environment and changes in densities of *L. vernus* are slow (Crone et al. 2013). Annual variability in vital rates is therefore assumed to be small (which was also found during this study; J. P. Dahlgren, H. Östergård and J. Ehrlén, unpublished data).

### Demographic data collection

In 1999, we mapped plants in 72 plots in a 5-km × 5-km area (66°73'N, 16°13'W, WGS 89) in the province of Uppland, central eastern Sweden. The plots constituted a random sample of the parts of the area with *L. vernus*, and varied in size between 1 and 85 m<sup>2</sup> as a result of our aim to include ca. 30 individuals per plot. During the entire study 2,376 plants were tagged and numbered. Individual plants were easily identified in the following years. The plots were revisited once a year at the time of fruit maturity from 1999 up to and including 2005 and all seedlings and previously dormant individuals appearing above ground in the plots were included. For each individual we recorded the number of shoots and measured the height of the largest shoot. The base diameter was measured if shoots were grazed. Previous studies have shown that above-ground volume estimated as shoot number × diameter<sup>2</sup> × height is a good non-destructive measure of total plant biomass (Ehrlén 2002). To be able to translate our measures of shoot number, height (in intact individuals) and diameter (in grazed individuals) into this measure of total above-ground size, we measured shoot height and shoot diameter in a subset of undamaged individuals. We then used the observed relationship between these two measures to convert shoot heights and diameters into measures of shoot volumes. For fruiting individuals, the number of fruits was recorded. Individuals that did not produce above-ground shoots in 2 consecutive years were never seen to produce sprouts in later years, and were considered dead. On average 15 % of the shoots were damaged by grazers each year. The incidence and level of damage was not correlated to measured abiotic factors or density (all  $r^2 < 0.003$ ). We did not further consider effects of grazing in this study that focuses on density and abiotic conditions. The collected data were used to build statistical models of vital rates. For seedling establishment rate, we first calculated it as the yearly average of total number of observed seedlings in a given year divided by the number of fruits the previous year. As seedlings are sometimes difficult to identify and this estimate was very low compared to previous more detailed studies of recruitment of this species (Ehrlén 1995), we increased this vital rate from the estimated value of 0.17 to 0.30 in order to produce a stable modelled population density corresponding to the mean observed density (4.3 individuals m<sup>-2</sup>) for the mean shade environment (30 % shade).

## Environmental variables

Environmental variables were estimated in each plot once during the study. Although absolute values of some of the environmental variables likely vary among years, we judged that in this forest environment relative differences in most variables are likely to remain relatively stable over the limited period of time that this study was carried out. As a measure of shading, canopy cover was estimated 50 cm above ground by the proportion of pixels obscuring the sky in an upwards-directed digital picture taken with a 0.63× wide-angle converter at the plot centre at the initiation of flowering (spring shade), and when the canopy was in full leaf (summer shade).

Soil samples were collected before the growing season started. Each sample consisted of four cores (one from each corner of the plot) taken by pushing a metal cylinder 10 cm into the soil below the litter layer. For each soil sample, concentrations of N ( $\text{NO}_3^-$  plus  $\text{NH}_4^+$ ; mg N  $\text{kg}^{-1}$ ),  $\text{PO}_4^{3-}$ , K, Mg, Ca (mg 100  $\text{g}^{-1}$ ) and total C (percentage of dry weight) were determined by the Soil Fertility and Plant Nutrition lab at the Department of Soil Sciences, Swedish University of Agricultural Sciences. For the analyses in the present study we only considered the effect of ‘nutrient availability’ (the first axis from a principal components analysis of all standardized nutrient variables, explaining 68 % of the variation; Online Resource 1) since we did not know what nutrients affected this species and did not have a large enough sample size to include all nutrient variables. We also recorded the soil temperature at each plot centre (except for in five plots where the data loggers were not recovered; in the analyses we assumed these plots to have average temperature values), using temperature loggers buried at 5-cm depth. Recordings were made continuously for 7 weeks and started just before flowering. We calculated the mean temperature and the range in temperature over this time period, as measures of microclimate.

Lastly, we estimated soil depth, density of heterospecific field layer plants and shrub layer cover in each plot. Soil depth was measured below the litter layer down to a maximum of 30 cm at 20 randomly assigned points with a metal stick. The height of the field layer was measured at five randomly assigned points. Field layer cover was recorded as the number of hits on a 50-cm-long stick dropped vertically at the same five points. Density of heterospecific field layer plants was then approximated by multiplying average height with average cover. It was interpreted as an estimate of the biomass of competing species. Shrub layer cover was categorized in five classes from none to complete cover and was included because it could affect both light availability and microclimate. All variables were included in subsequent variable selection analyses because the correlation

between them was relatively weak (all Spearman  $\rho < 0.5$ ; Online Resource 2).

## Intraspecific density

Intraspecific density was estimated by the number of individuals per square metre in the entire plots. More elaborate measures at the individual level, based on the size of and distance to neighbouring individuals within a certain distance, gave practically identical results regarding the impact of density on vital rates (results not shown).

## Analyses of vital rates and plot-level patterns

Relationships between vital rates (growth, survival, flowering and fruit production), intraspecific density, and environmental factors were investigated in regression models in R (R Core Team 2013). In generalized linear models with dichotomous response variables (survival and flowering), a binomial error distribution and a logit link function were used. In models of fruit number a Poisson error distribution and a log link function were used. In the other models, with continuous variables, a Gaussian error distribution was assumed and no link function was used. For the models of individual survival, growth, flowering and fruit number, random effects were included in hierarchical (mixed) models to account for the fact that environmental factors were measured at the plot level and that observations spanned several years. Thus, repeated observation of individuals was accounted for in the analyses, but we did not further consider temporal variation here. Hierarchical models were fitted using the R package lme4 and, when done in combination with the Bayesian lasso technique described below, in the package R2OpenBUGS and OpenBUGS (Lunn et al. 2009). For models of plot-level patterns, data for all years were pooled as differences between study years were very small.

To estimate effects and also attempt to identify important environmental variables, the lasso regression shrinkage and variable selection method was employed (Tibshirani 1996). For analyses at the plot level we used the glmnet R package [commented code is available in the help file of the package (Friedman et al. 2010)]. For the individual vital rate models we combined hierarchical models and the Bayesian version of the lasso. The lasso has been shown to be a reliable method of variable selection, working by penalizing models with a larger sum of absolute values of regression coefficients, and shrinking coefficients towards zero (Tibshirani 1996; Dahlgren 2010). A Bayesian equivalent of the lasso can be achieved by specifying double exponential (Laplacian) prior distributions with modes of zero for the parameters in question (Tibshirani 1996). It is thus straightforward, in theory, to include the lasso in a

hierarchical model in OpenBUGS (e.g. McMahon and Diez 2007), by using Laplacian priors on parameters varying at any hierarchical level. OpenBUGS code for this was based on that used by Yi and Xu (2008). Hierarchical models were fitted using R code in Gelman and Hill (2007). Optimal shrinkage was determined by cross-validation in glmnet and as part of the model-fitting Gibbs-sampling Markov chain Monte Carlo procedure in OpenBUGS (cf. Friedman et al. 2010; Gelman and Hill 2007).

The Bayesian lasso was used in models of vital rates including all environmental factors as predictor variables. In a second step, the environmental variables that were identified to potentially have effects were included in a generalized additive mixed model (GAMM) that allowed non-monotonic relationships and also included interactive effects between individual size and density and between environmental variables and density (these models were fitted using the gamm4 R package). These interactions were tested because we hypothesized that density effects on individuals might differ between individuals of different size, and that environmental factors might modify density dependence. Parameters were excluded if this decreased the model Akaike information criterion.

At the plot level, the variation in (log) mean size of individuals not explained by (log) density of individuals was regressed on the measured environmental variables, and statistically significantly correlated variables were identified using the lasso method. Relationships between residual variation in size and environmental variables were interpreted as effects of local environment on carrying capacity.

### Analyses of population dynamics

In order to analyse population-level effects of density and environment we used non-linear size-structured IPMs, specified based on the regression models of vital rates as in Ellner and Rees (2006) and Dahlgren and Ehrlén (2009). However, in this study we allowed also current population density to affect vital rates of established plants. IPMs are discrete-time, structured population models where state transitions are given by a kernel function based on vital rates. Seedling establishment rate per fruit was assumed to be 0.30 (cf. demographic data collection). The size distribution of seedlings was assumed to be normal with a mean of  $2.5 \log(\text{mm}^3)$  and a variance of 1. The model was

$$n(y, t+1) = \int_L^U (s(x, z)g(y, x, z) + f_p(x)f_n(x)e_p e_d(y))n(x, t)dx,$$

where  $n$  is the population function,  $y$  is size year  $t+1$ ,  $x$  size year  $t$  and  $z$  is density year  $t$ , with effects on the vital rate functions  $s$  (survival),  $g$  (growth),  $f_p$  (flowering probability), and  $f_n$  (fruit number).  $e_p$  is the probability of seedling establishment per fruit and  $e_d$  is the size (normal)

distribution of established individuals.  $U$  and  $L$  are the upper and lower bounds of the range of sizes and were set to 1.1 times the largest observed size of an individual in this study and 0.9 times the smallest observed size, respectively. As growth to sizes beyond these limits could still occur in the model, i.e. the growth kernel did not integrate to 1, we forced growth to sizes outside the boundaries to give the extreme values [ $U$  and  $L$  (cf. Dahlgren and Ehrlén 2009)]. Previous studies have shown that the contributions of survival in and germination from the seed bank to population growth rate are very small in this species (Ehrlén 1995), and a seed bank was therefore not included in the model.

The IPM was parameterized for different environments, based on the effects of the environmental variables (see Results). We included interactive effects of size and density if these were identified in the regression models, but we assumed potential positive effects on large individuals to be model artefacts. In such cases, density effects were capped at the effect of density in models not including interactions with size, or set to zero if density was suggested to have positive effects. For fecundity, where positive density effects were suggested by the regression models for practically all combinations of other predictor variables (see Results), vital rates were assumed to always correspond to those for the average density value. We used the model to forecast density-dependent growth in different environments, by iterating the model until stable population densities were reached.

## Results

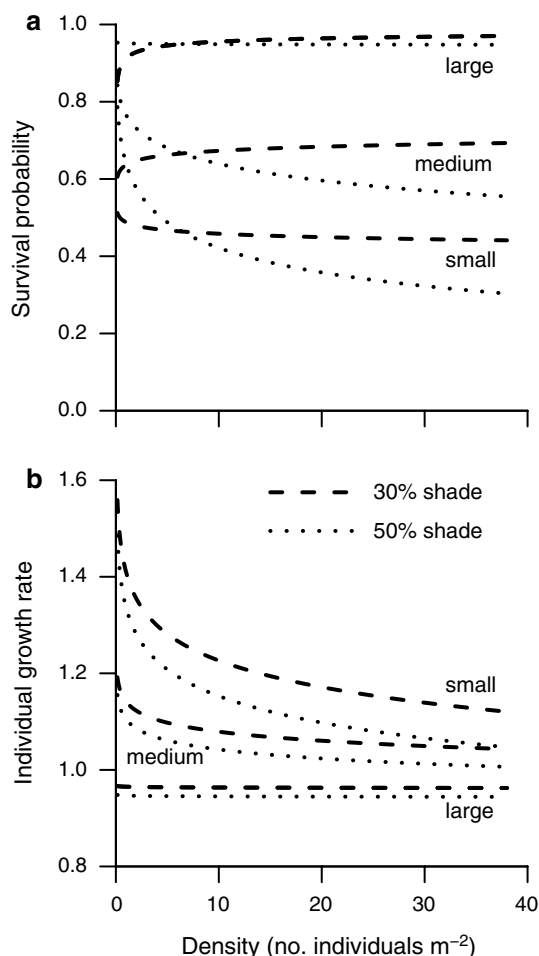
### Effects on individual vital rates

Bayesian lasso analyses did not clearly identify a specific environmental factor as being related to any vital rate, but suggested a relationship between vital rates and variables associated with shade, in particular spring shade, shrub cover and summer shade (Online Resource 3). Spring shade varied between 0.6 and 50.5 % (mean = 30.0, median = 30.5, SD = 11.8) of the sky being obscured in canopy photographs. Increasing spring shade was positively related to flowering ( $b = 0.012$ ,  $P = 0.024$ ), negatively to growth ( $b = -0.007$ ,  $P < 0.001$ ) and marginally significantly positively to survival ( $b = 0.013$ ,  $P = 0.05$ ), but there was no significant relationship with fruit production ( $b = 0.004$ ,  $p = 0.46$ ) in GAMMS including only size and spring shade.

Density was negatively related to growth and survival of small and medium-sized individuals (Fig. 1). Flowering probability and fruit number per capita were positively related to density (Online Resource 4).

To find evidence of potential simultaneous effects of environment and density, we used models including spring





**Fig. 1** Fitted relationships for effects of density on **a** survival and **b** growth rate for *Lathyrus vernus* individuals of different sizes and for two levels of spring shade (see Table 1 for statistical analysis). Summed shoot sizes (log mm<sup>3</sup>) are: large = 8, medium = 4, small = 2. Confidence bands are presented in Online Resource 6

shade as the only environmental factor, based on the results of the analyses of environmental effects on both individual and plot levels. For survival, there was a statistically significant negative effect of spring shade when accounting for density (Table 1). There was also a significant interaction between the two variables, suggesting more negative effects of density in more shaded environments (Fig. 1). Relationships with density and spring shade for growth, flowering probability and fruit number were similar when accounting for spring shade and density simultaneously, compared to when they were examined separately.

#### Plot-level relationships

The negative relationship between mean (log) plot density and mean (log) plant size of individuals was well described

**Table 1** Fixed-effects coefficients from the generalized additive mixed models of survival and growth on size (log), density (log) and spring shade

	Coefficient	SE	df	P-value
Logistic model for survival. Proportion explained deviance = 0.132				
Intercept	0.832	0.366	1	0.023
Size	NA	NA	3.3	<0.001
Spring shade	0.031	0.011	1	0.004
Density	0.329	0.279	1	0.24
Size × density	0.061	0.021	1	0.004
Spring shade × density	−0.016	0.008	1	0.030
Gaussian model for growth. Adjusted $R^2$ = 0.697				
Intercept	7.054	0.086	1	<0.001
Size	NA	NA	7.9	<0.001
Spring shade	−0.007	0.002	1	<0.001
Density	−0.210	0.056	1	<0.001
Size × density	0.026	0.007	1	0.001

df Estimated for smoothed terms. The models are presented graphically in Online Resource 5

NA Not applicable

by a linear model with a slope of  $-0.69$  ( $SE = 0.13$ ). Plot densities were right-skewed, with a mean of 4.0 individuals m<sup>-2</sup> and a median of 3.0 individuals m<sup>-2</sup>. The least dense plot during the study contained 0.15 individuals m<sup>-2</sup> and the densest plot 38 individuals m<sup>-2</sup>. Mean plant sizes in plots (log) were slightly left-skewed with a mean of 6.7 and a median of 6.8.

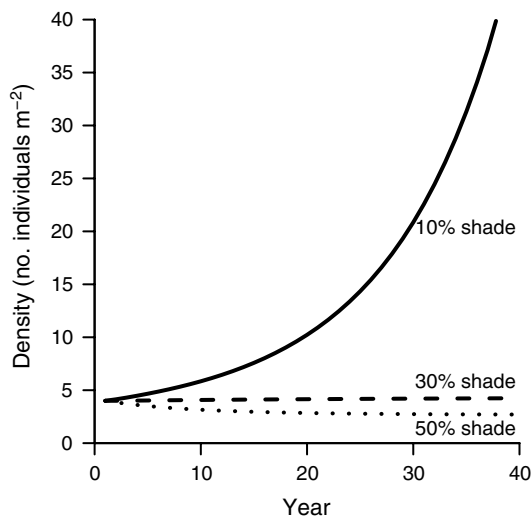
Approximately 17 % of the variation in (log) mean size that could not be explained by (log) density could be explained by environmental variables, suggesting that the measured environmental factors influenced carrying capacity (Table 2). A negative effect of spring shade could explain most of the residual variation in size.

#### Effects on population dynamics

The IPM analyses showed that the local environmental (in terms of negative effects of spring shade) and density effects on survival and growth indicated by the regression models had strong effects on population growth rate. These effects resulted in modelled differences in densities of individuals among environments with different degree of shading that were consistent with those observed among plots (Fig. 2). The effect of shade on individual growth was the main cause of these differences, but there was also an effect via survival (Fig. 3). The large effect of shade via individual growth appeared to be the result of that population growth rate was more sensitive to changes in growth than to changes in the other vital rates (Online Resource 7).

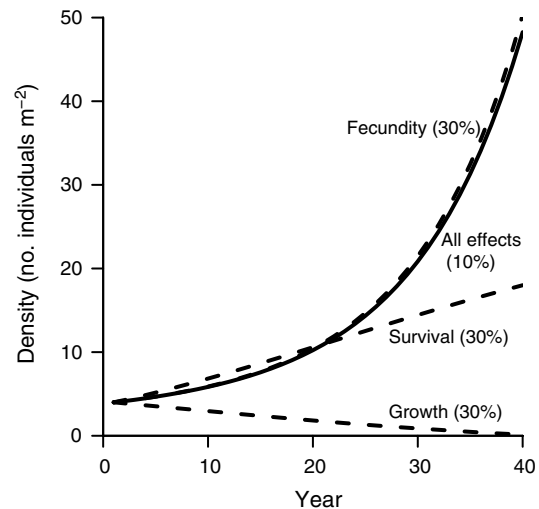
**Table 2** Summary statistics for a regression of residual variation in individual size (after controlling for density) on environmental factors

	Coefficient	SE	P-value
Including all environmental factors chosen using the lasso regression. $R^2 = 0.169$			
Intercept	−0.260	0.393	0.51
Spring shade	−0.010	0.005	0.047
Competing vegetation	0.087	0.057	0.13
Temperature range	0.063	0.070	0.37
Reduced by backwards stepwise removal of variables with $P > 0.05$ . $R^2 = 0.105$			
Intercept	0.386	0.144	0.009
Spring shade	−0.013	0.004	0.006

**Fig. 2** Density-dependent population trajectories of *L. vernus* in three spring shade environments, predicted by an integral projection model based on regression models of vital rates over individual size, population density and spring shade

## Discussion

In this study on the demography of the forest herb *Lathyrus vernus*, we quantified correlations between vital rates, and intraspecific density and local environmental factors. Our results suggest that environmental factors and density often need to be considered simultaneously to detect effects on vital rates and population growth rates. In our study system, modelled effects of shade and density on individual survival and growth resulted in population growth rates that stabilized at higher densities at higher light levels. These relationships, together with observed differences among plots, are in agreement with our hypothesis that environmental factors cause differences in carrying capacity among habitat patches.

**Fig. 3** Influence of spring shade effects on different vital rates on the modelled population trajectory of *L. vernus*. Solid line depicts the modelled trajectory in a low (10 %) spring shade environment. Dashed lines are trajectories resulting from setting spring shade to the mean value (30 %) for each vital rate

The mechanisms underlying the observed relationship between shading and vital rates are unclear. Several different combinations of predictor variables explained variation in vital rates equally well. Still, the results strongly suggest that competition for light or another correlated resource is an important driver of population dynamics in this system. The effect of the environment on vital rates that had the strongest impact on population size was the decreased growth and survival of individuals associated with increases in spring shade. Our analyses suggested an increased fecundity under low-light conditions. This is in contrast to observations that plants grow larger and are more fecund in newly formed canopy gaps, but consistent with long-term field observations showing that the positive effects of increased light availability after tree falls are temporary, and that increased competition from other field-layer species often counteracts the initial positive effect after some years (J. E., unpublished data). Light conditions have previously been found to affect population dynamics of plants (e.g. Alvarez-Buylla 1994; Svenning 2002; Scanga and Leopold 2010). Effects of primary resources are intuitive, but identified associations between spatial variation in vital rates and specific environmental factors in other systems have typically been weak (Dahlgren and Ehrlén 2009; Nicolè et al. 2011; Diez et al. 2014). Despite the uncertainties regarding the exact mechanisms of how a shaded environment impacts survival and growth of *L. vernus*, the impact of the local environment was large in this study.

In this study we used natural variation in densities. We hypothesized that because populations will often not be at

equilibrium densities, it should be possible to detect effects of density in data on natural variation if the relevant variation environmental factors are accounted for. In agreement with this, our results did indicate strong effects of intraspecific density on vital rates. This lends support to the notion that density dependence needs to be considered when interpreting estimates of plant population growth rates (Matos et al. 1999; Freckleton et al. 2003; Zeigler et al. 2013). Apart from in studies of invasive weeds, most published plant demographic models implicitly assume that densities remain constant at the levels of the time of data collection (Crone et al. 2011). As a result, we currently know relatively little about the role of density-dependent processes in plant population dynamics in general. A possible reason for why density dependence is usually not included in plant demographic models is that preliminary analyses have failed to detect any relationship between intraspecific density and vital rates or population growth rates. However, without accounting for the local environment, density effects are likely to go undetected. In fact, cross-sectional studies may often be expected to suggest positive density dependence if density is higher in more favourable patches (e.g. Menges and Dolan 1998). For this reason, destructive and labour-intensive manipulations of plant density and long monitoring periods are typically assumed to be needed to experimentally assess density effects in long-lived perennials (Fowler et al. 2006; Ramula and Buckley 2009). However, our study suggests that cross-sectional data can still be useful, at least if relevant differences in local environment are characterized. We detected density effects also in models not accounting for environmental variation, but effect sizes did depend on the local environment, with density having strong effects on survival in environments with high spring shade but weak effects in less shaded environments.

Just as environmental effects can obscure effects of density, the reverse is also true. One important result of this study was that some relationships between environmental factors and vital rates were not detectable without accounting for density. Our approach of statistically correcting for density and local environment while estimating their relative effects is of course flawed if the negative correlation between environmental and density effects is very strong. However, in our study correlations were not that strong and, in general, natural populations are likely to rarely be in perfect equilibrium due to temporal variation in environmental conditions (e.g. Tuljapurkar 1989; Krebs 2002). We therefore suggest that our approach could be useful also in other systems for determining what factors shape the dynamics of natural populations and thereby constitute the mechanisms underlying distribution patterns.

Relationships of local environment and density with vital rates corresponded to relationships between environment, density and size structure across study plots. The mean size

of individuals was clearly correlated to density, and there was also a strong correlation between spring shade and the residual variation in the size-density regression. Even though we expected a relationship between mean plant size and density, the identified patterns indicating self-thinning were surprisingly strong. Density has been shown to affect seedlings in several natural systems but effects on established individuals have often not been detected (e.g. Matos et al. 1999; Waser et al. 2010; Luo et al. 2012). Our results on both the individual and plot levels strongly suggest that also established individuals can be affected by density. As may be typical of a forest herb inhabiting stressful low-light forest understory environments, *L. vernus* densities were often low and close neighbours were often heterospecifics. Under such circumstances, self-thinning might at first glance not be expected. However, the substantial spread of fine roots observed in many plants (Casper et al. 2003), may result in effects on vital rates of established plants also at relatively low intraspecific densities.

Differing carrying capacities of habitat patches result from differences in effects of local environmental quality on population growth rate and on feedback mechanisms via density. The population model for *L. vernus* showed that the effects of shade and density on vital rates identified from field data in this study are sufficient to result in observed variation in equilibrium densities, although observed variation of plot densities indicates that also unmeasured aspects of the environment had strong effects. Demographic mechanisms of spatial variation in population sizes associated with variation in the timing of catastrophic events, such as fire (Menges and Quintana-Ascencio 2004) or hurricanes (Horvitz et al. 2005) have previously been identified. Our results illustrate how spatial environmental variation in more stable environments can lead to differences in carrying capacities.

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