










Drivers of large-scale spatial demographic variation in a perennial plant

GESA RÖMER ^{1,2,†} DITTE M. CHRISTIANSEN ^{3,4} HENDRIK DE BUHR ⁵ KRISTOFFER HYLANDER ^{3,4}
OWEN R. JONES ^{1,2} SONIA MERINERO ^{3,4,6} KASPER REITZEL ² JOHAN EHRLÉN ^{3,4} AND
JOHAN P. DAHLGREN ^{1,2}

¹Interdisciplinary Centre on Population Dynamics (CPop), University of Southern Denmark, Campusvej 55, Odense M 5230 Denmark

²Department of Biology, University of Southern Denmark, Campusvej 55, Odense M 5230 Denmark

³Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm SE-106 91 Sweden

⁴Bolin Centre for Climate Research, Stockholm University, Stockholm SE-106 91 Sweden

⁵Department of Medical Microbiology, University Medical Center Utrecht, Heidelberglaan 100, Utrecht 3584 CX The Netherlands

⁶Department of Ecology, Swedish University of Agricultural Sciences, PO Box 7044, Uppsala SE-750 07 Sweden

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Abstract. To understand how the environment drives spatial variation in population dynamics, we need to assess the effects of a large number of potential drivers on vital rates (survival, growth, and reproduction) and explore these relationships over large geographical areas and broad environmental gradients. In this study, we examined the effects of a wide variety of abiotic and biotic environmental factors on the demography of the forest understory herb *Actaea spicata* between 2017 and 2019 at 40 sites across Sweden, including the northern range margin of its distribution. We assessed the effects of potential environmental drivers on vital rates using generalized linear mixed models (GLMMs) and then quantified the impact of each important driver on population growth rate (λ) using integral projection models (IPMs). Population dynamics of *A. spicata* were mostly driven by environmental factors affecting survival and growth, such as air humidity, soil depth, and forest tree species composition, and thus, those drivers jointly determined the realized niche of the species. Soil pH had a strong effect on the flowering probability, while the effect on λ was relatively small. In addition to identifying specific drivers for *A. spicata*'s population dynamics, our study illustrates the impact that spatial variation in environmental conditions can have on λ . Assessing the effects of a broad range of potential drivers, as done in this study, is important not only to quantify the relative importance of different drivers for population dynamics but also to understand species distributions and abundance patterns.

Key words: environmental drivers; integral projection model; perennial herb; plant demography; population dynamics; population growth rate; spatial variation.

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† **E-mail:** gesa.roemer@gmail.com

INTRODUCTION

Abiotic and biotic environmental conditions such as climate and competition vary across time and space and drive the population dynamics of species through effects on vital rates such as survival, growth, and reproduction (Bruna and Oli

2005, Doak and Morris 2010). These vital rates vary both with regard to how sensitive they are to different environmental factors and to how much they influence population dynamics (Silvertown et al. 1993, Pfister 1998, Nicolè et al. 2011, Ehrlén and Morris 2015). Yet, underlying demographic mechanisms are not accounted for

in standard models of species distributions and abundances (Guisan and Thuiller 2005, Araújo and Rahbek 2006, Elith and Leathwick 2009) even though more mechanistic models are available and are increasingly used (e.g., Evans et al. 2016, Merow et al. 2017). Moreover, species distribution models based on occurrence patterns are typically based on the assumption that species are in equilibrium with their environment and thus do not capture ongoing or recent changes in environmental drivers. To achieve an in-depth understanding of the population dynamics of a species, and to describe and predict distributions and abundances, we need to assess how environmental variation is linked to demographic variation (Ehrlén and Morris 2015). Using environmentally explicit demographic models allows us to disentangle which vital rates are most affected by the environment, and how those vital rates contribute to population growth rate (λ). Such a more mechanistic understanding of the processes underlying a species' distribution and abundance allows for more accurate predictions of species responses to environmental and climate changes (Doak and Morris 2010, Csergő et al. 2017). Environmentally explicit demographic models also provide a means to identify the drivers of the short-term dynamics and of the realized niches of species.

There are likely many aspects of the environment that govern the distribution of most species, and to avoid relying only on preconceived notions about which drivers are important, assessments of environmental effects on population dynamics could benefit from including a broad range of potential drivers, if enough observations are available to reliably test relationships statistically. Such assessments should ideally include climatic and other abiotic factors, as well as biotic and anthropogenic factors such as land use (Ehrlén et al. 2016). In addition to assessing many potential drivers, data collection along a large proportion of the environmental gradient (s) occupied by a species should allow for detection of nonlinear relationships between environmental drivers and vital rates (Ehrlén et al. 2016). Meeting these needs regarding the number of drivers and accurately estimating their variation will likely often mean that data must be collected over large geographical areas. However, although the modeling tools for assessing the

effects of environmental conditions on population dynamics and distributions are available (Merow et al. 2014a, 2014b), few studies have investigated the relationships between multiple vital rates and environmental drivers on large geographical scales (but see Merow et al. 2017).

We conducted a large-scale study of the environment-driven demography of the long-lived understory forest herb *Actaea spicata* based on data from a large geographical extent. We collected demographic data and data on 16 putative environmental drivers, from 40 populations throughout the Swedish distributional range of *A. spicata* from 2017 to 2019. The putative drivers were 13 abiotic factors related to climate, topography and soil nutrient richness, and three biotic factors concerning plant community structure and intraspecific population density. We asked the following questions: (1) How do the various environmental factors influence the vital rates of *A. spicata*? We expected strong effects of both the abiotic environment, in terms of nutrient levels, and the biotic environment, in terms of shading by other plants, in line with previous smaller-scale studies (Dahlgren and Ehrlén 2009, 2011). Specifically, we expected soil potassium concentrations to positively influence growth and increasing proportion of coniferous trees to negatively influence growth (Dahlgren and Ehrlén 2009, 2011). Furthermore, we expected strong climatic effects due to the large geographical range of the study, and the fact that the study was conducted at the northern range limit of *A. spicata*. (2) How do detected effects of environmental drivers on vital rates influence the population growth rate of *A. spicata*? We expected that the environmental drivers affecting survival and growth would have a larger effect on population growth rate than those affecting reproduction, because the population growth rate is more sensitive to survival and growth than reproduction in this species (Dahlgren and Ehrlén 2009), as is the case in other long-lived herbs (Silvertown et al. 1993). We used generalized linear mixed models (GLMMs) to link the environmental drivers to vital rates describing survival, individual growth, flowering probability, and fruit number. We then incorporated the GLMMs into an integral projection model (IPM; Easterling et al. 2000) to assess the effects of environmental drivers on the population growth rate of *A. spicata*.

METHODS

Study species

Baneberry (*Actaea spicata* L., Ranunculaceae) is distributed over most of Europe and parts of Asia and North America (Anderberg and Anderberg 2017). In northern Europe, it occurs in shady, well-drained and nutrient-rich forests, often on limestone (Pellmyr 1984). The plant is common throughout Sweden but does not occur in the far north (Mossberg and Stenberg 2014). *Actaea spicata* has a morphology typical of many early summer flowering forest herbs, with a greater height than spring ephemerals and an umbrella-like leaf display (cf. Givnish 1987). Previous studies have found that individuals can produce several shoots, each typically bearing up to four inflorescences (Eriksson 1995), with the first, top inflorescence, typically bearing most flowers and fruits. Each black berry contains 8–16 seeds (Zeipel et al. 2006) which germinate below ground one year after release, and cotyledons emerge one year thereafter (Ehrlén and Eriksson 2000, Fröborg and Eriksson 2003). The entire plant is toxic (Anderberg and Anderberg 2017). Estimated mean life span of individuals surviving to reproduction is 20.2 yr (J. Ehrlén and J. P. Dahlgren, *unpublished data*). Population growth rate is more sensitive to survival and growth than to reproduction (Dahlgren and Ehrlén 2009), as is typical for long-lived herbs (Silvertown et al. 1993).

Study area

We selected potential study populations using Artportalen¹, an online reporting system for species observations (including citizen science observations) and information about Swedish flora and fauna developed by the Swedish University of Agricultural Sciences (SLU). We visited more than 100 populations across the country distributed with the aim of covering the entire Swedish distribution of the species and to obtain a representative sample of the environments experienced by the species (favoring reported occurrences with more exact coordinates). We aimed for populations with at least 50 established non-seedling individuals, but occasionally populations with fewer individuals were included in the study to guarantee a good spatial coverage. We identified 43 suitable

populations across Sweden (Fig. 1, Appendix S1: Fig. S1) and recorded exact latitude and longitude positions with a Garmin GPS Map 64s. In each of these populations, one permanent plot was established in 2017 and followed until 2019. Over the course of the study, we lost three populations due to grazing and wild boar activity, leaving 40 study populations in which data was collected in all three years. Distance to nearest population ranged between 30 and 139 km (mean distance = 73 km) and plot size depended on the plant density, aiming to include 50 non-seedling individuals, and ranged from 6 to 363 m². The habitat varied substantially between sites, with some sites located in pure broadleaf forest and others in pure coniferous forests.

Demographic data collection

All plants were marked by placing a small flag (steel wire with a piece of tape) in the soil and mapped to enable relocation in following years. All seedlings were counted and followed individually from the year after emergence. In total, 2263 plants were surveyed over the course of the study. Presence (1 or 0), state (flowering or vegetative), plant height, shoot diameter, and fruit number per inflorescence were recorded for all established plants between July and August in all years. An individual was considered dead in 2018 if it lacked above-ground structures in both 2018 and 2019. Individuals that were only missing in 2018 had either been dormant or the above-ground tissues had been damaged before the demographic census. Because damage/dormancy in one year could only be detected in retrospect after revisiting the site in the following year, we assumed the same proportion (3.6%) of individuals lacking above-ground structures were damaged/dormant in 2019. In the statistical analyses of survival, we therefore used a weighted regression, where the weight of death observations was 3.6% lower than the weight of survival observations. Plant size was defined as the natural logarithm of the product of plant height and squared shoot diameter, where height is the distance from the ground to the horizontal plane formed by the largest leaves (as in Dahlgren and Ehrlén 2009; see Appendix S2: section 1). Growth was defined as the difference in size between censuses.

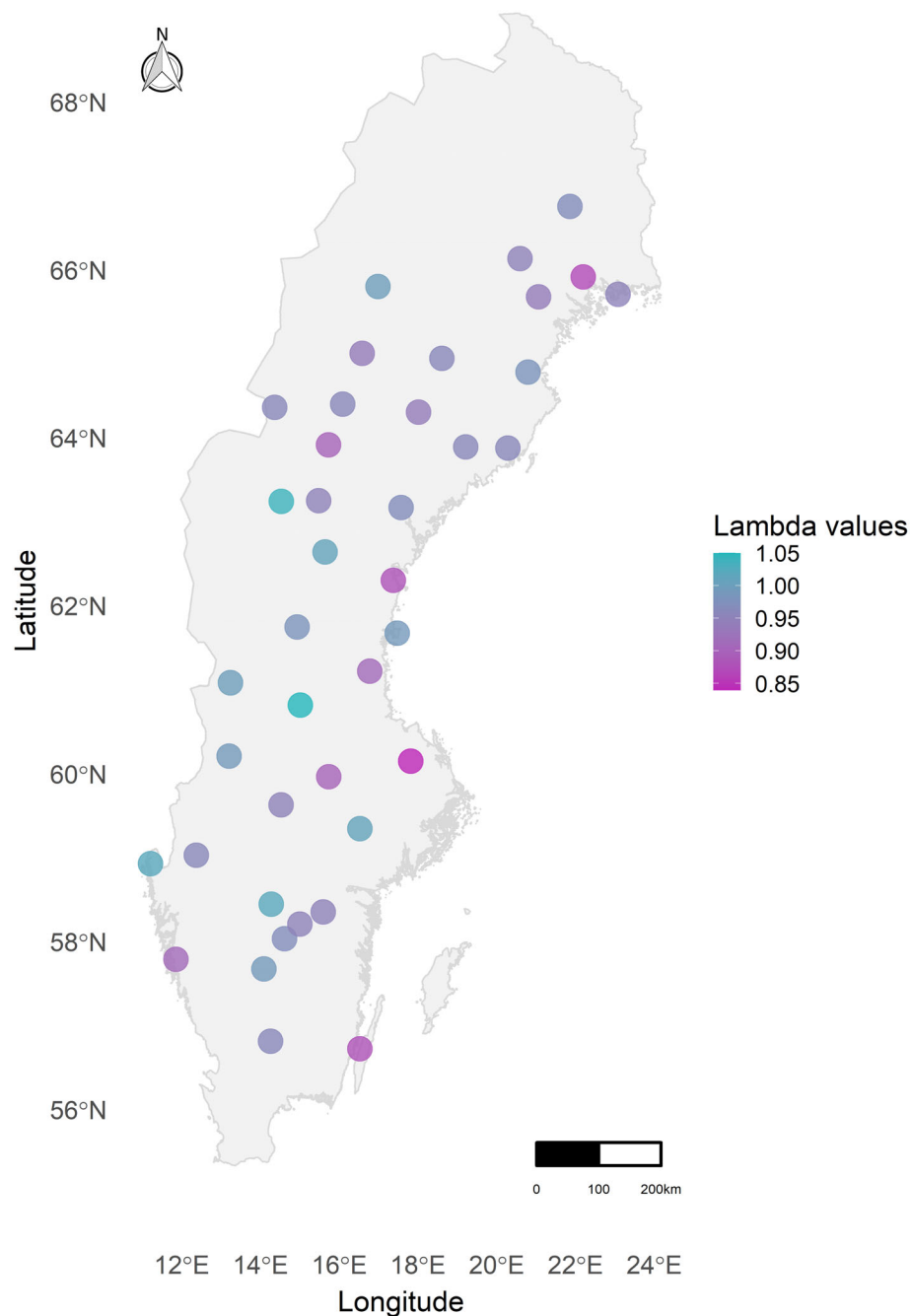


Fig. 1. Map of Sweden showing all study sites and the population growth rate (λ) of *Actaea spicata* at the corresponding sites for the time period 2017–2019.

Environmental data collection

We collected a range of 16 environmental variables (below) including 13 abiotic factors related to climate, topography and soil properties, and

three biotic factors concerning plant community structure and intraspecific population density. We collected weather data throughout the whole study period, with (1) air-temperature and (2)

humidity data loggers (EasyLog EL-USB-2, Lascar Electronics, Erie, Pennsylvania, USA) placed at the center of each plot and covered with a plastic cup to protect them from direct sunlight and rain. We used the logger data to calculate (3) growing degree days (base temperature: 5°C) for the spring period 15 May–15 June 2006, (4) the start of spring, using the definition from the Swedish meteorological office (SMHI 2011) and (5) vapor pressure deficit (hereafter VPD), the difference between the actual vapor pressure in the air and that of saturated air, where vapor pressure is a temperature corrected measure for moisture (Anderson 1936, Jones 2014). VPD was calculated for the summer period (15 June–15 August) using the R package *plantecophys* (Duursma 2015). We measured slope inclination and slope aspect and used them to calculate (6) the extent to which the ground was slanted toward the sun, as an additional indicator of the exposure to light and moisture (hereafter “slope”). In addition, we estimated (7) site area and calculated (8) intraspecific plant density for each site as the number of individuals per m². In 2018, we collected soil samples and analyzed the concentrations of (9–14) nitrate (NO₃⁻), exchangeable ammonia (NH₄⁺), plant available phosphorus (P), phosphate (PO₄³⁻), plant available potassium (K), and soil pH. Lastly, we collected data on the plant community structure at each site: To determine the (15) percentage of trees that were coniferous (as opposed to broadleaf), we recorded the abundance of each tree species using a relascope, a forestry instrument to measure basal area, for each tree visible from the center of the site. We took canopy cover pictures using the back camera of a Sony Xperia L1 with an attached fisheye lens (180° Supreme Fisheye Lens, Model MFE4, MPOW) which were then processed in ImageJ (Schneider et al. 2012) using the plugin Hemispherical 2.0 (Beckschäfer 2015) to calculate the (16) gap fraction (see Appendix S2: section 2 for further details on the environmental data collection). In Table 1, we present the minimum, the maximum, and the mean observed values on our 40 field sites for each environmental driver.

Statistical analyses

To avoid the effects of overfitting (Harrell 2001), we did not evaluate interaction effects and

Table 1. Observed values of environmental drivers in the field.

Environmental driver	Min value	Max value	Mean value
Growing degree days	142.5	430	310.1
First spring date	3/6/2018	7/19/2018	4/23/2018
Vapor pressure deficiency	-0.038 kPa	0.929 kPa	0.55 kPa
Potassium concentration	0.03 mg/g TV	1.54 mg/g TV	0.28 mg/g TV
pH in the soil	4.77	7.73	5.91
Soil depth	4.8 cm	42.8 cm	11.59 cm
Percentage of coniferous trees	1%	100%	49%
Gap fraction	6.31%	38.28%	18.08%
Aspect distance to South	0°	190°	101.72°
Slope	0°	-388°	-18.84°

Note: For each environmental driver, we present minimum and maximum observed value on our 40 field sites as well as the mean of all observations.

limited the number of environmental variables included in the regression models based on bivariate correlations. If two environmental variables had a Pearson $r > 0.7$, we omitted the variable we expected less likely to have an effect on the population growth rate of *A. spicata* based on knowledge of the system (Appendix S1: Fig. S2). To further reduce the number of putative drivers, we performed a principal component analysis (PCA) on the soil variables. All soil variables except pH were aligned with the first PCA-axis, which explained 46.8% of the variation, and soil pH was aligned with the second PCA-axis, which explained 22.3% of the variation (Appendix S1: Fig. S3). Based on this, we chose to retain only soil potassium and pH as soil potassium has previously been shown to have important effects on *A. spicata* (Dahlgren and Ehrlén 2009, 2011). Final models thus included the following environmental variables in the vital rate regression models: VPD, soil potassium concentration, soil pH, soil depth, percentage of coniferous trees, intraspecific density, canopy gap fraction, and slope.

We assessed effects of environmental variables on vital rates (probability of survival, growth, probability of flowering, and number of fruits) using generalized linear mixed models (GLMM) and linear mixed models (LMM) in the R

package lme4 (Bates et al. 2015). Predicted values and 95% confidence intervals were generated with the R package effects (Fox and Weisberg 2018). We standardized all variables by subtracting the arithmetic mean and dividing by the standard deviation to ease interpretation when comparing effect sizes and to improve model convergence. For modeling the probability of survival and flowering, we used logistic regressions with binomial error distributions and logit link functions. Growth was modeled with an ordinary Gaussian linear model, and fruit number was modeled using a Poisson error distribution and log link function. Model fit was evaluated based on visual inspection of the residuals. We pooled the data for both annual transitions for analysis and accounted for the spatial structure of the data and repeated measurements of individuals by including site and plant ID as random effects. We also analyzed the two years separately, to investigate the consistency of effects. In all models, we included plant size in year t as a fixed effect.

We first included all environmental variables and intraspecific population density as both linear and quadratic fixed-effect terms. To ease interpretation and avoid effects of overfitting (Harrell 2001), we then created a reduced model, which only included those quadratic terms that were statistically significant following strict cutoff points (for the GLMMs: $P < 0.05$; for the LMMs: No P -values are provided by the lme4 package, we therefore used $-1.96 < t < 1.96$ which corresponds to a P -value of < 0.05 in models with high degrees of freedom). We then used this reduced model to assess the statistical significance of remaining linear and quadratic terms and evaluated the statistical significance of effects according to the same criteria as above. We conducted all modeling, data exploration, and visualization using R version 3.5.1 (R Core Team 2018).

Integral projection modeling

An IPM is a population model with similar properties as a matrix population model but with continuous instead of discrete stage classes and a projection kernel instead of a projection matrix (Easterling et al. 2000). We constructed the IPM in this study as described in Dahlgren and Ehrlén (2009) based on R code presented in Merow et al. (2014a, Appendix F). To allow for a delay of

seedling establishment (see *Study species*) and treatment of seeds and seedlings as discrete classes (cf. Rees et al. 2006), our environmentally explicit IPM consisted of three coupled equations:

$$n_{t+1}(x') = p_s p_d(x') S_{2(t)} + \int_L^U s(x, \theta) g(x', x, \theta) n_t(x) dx \quad (1)$$

$$S_{2(t+1)} = p_e S_{1(t)} \quad (2)$$

$$S_{1(t+1)} = \int_L^U p_f(x, \theta) f_n(x, \theta) f_s(x_t) dx. \quad (3)$$

Each relevant component of the IPM included a vector θ for the significant environmental drivers identified in the regression models as covariates. $n(x_t) dx$ is the distribution of size x at time t while L and U are the upper and lower bounds of possible sizes. In Eq. 1, p_s is the probability of seedling survival and p_d the probability density function of sizes of surviving seedlings. S_1 is the number of seeds and S_2 the number of seedlings. The function $s(x, \theta)$ describes survival and $g(x', x, \theta)$ is the growth function, describing individuals of size x at time t which survive reaching size x' in time $t + 1$. In Eq. 2, p_e is the probability of seedling establishment given the survival of seeds (S_1). In Eq. 3, $p_f(x)$ is the probability of flowering and f_n the number of fruits. f_s is the number of seeds per fruit, which was assumed to be 9.61, as in Dahlgren and Ehrlén (2009).

We first used the IPM to calculate the population growth rate (λ) for each study site as the dominant eigenvalue of the kernel approximated by a 100×100 matrix (Ellner and Rees 2006, Ellner et al. 2016). We used a simple linear regression model to identify a possible correlation between the latitude of each site and population growth rate, obtained as described above. However, we found no significant relationship between λ and latitude ($P = 0.77$).

To evaluate and compare the effects of each significant environmental variable on λ , we constructed a separate kernel for each environmental variable and calculated λ for the observed mean values of the tested variable and for a range corresponding to three standard deviations away from the mean (i.e., ranging from -3 to 3) while holding all other variables constant at their mean value.

RESULTS

Over the two observed transitions, the average yearly survival of individuals was 91%. On average, 24% of all individuals flowered and the number of fruits per individual ranged from 0 to 90 (mean = 16.15). Individual plant size was correlated with all four investigated vital rates; survival, growth, probability of flowering, and number of fruits (Appendix S1: Figs. S4, S5, and Table S1). Soil depth, soil pH, VPD, intraspecific density, and percentage of coniferous trees were significantly related to one or several vital rates (Fig. 2, Appendix S1: Fig. S6). Most environment–vital rate relationships were linear, but density and percentage of coniferous trees had significant quadratic relationships with fruit number (Fig. 2d). In our regression models, the

percentage of coniferous trees affected survival positively (Fig. 2a) whereas fruit number was highest at average values of percentage of coniferous trees (Fig. 2d). VPD negatively influenced growth and flowering probability (Fig. 2b, c). Soil depth had a positive relationship on growth (Fig. 2b). Soil pH was negatively related to flowering probability (Fig. 2c), and the effect of intraspecific density on number of fruits was u-shaped with higher fruit production at lowest and highest density values (Fig. 2d). The effects of environmental variables were similar in both transitions (Appendix S1: Table S4).

Our IPMs showed that coniferous trees and VPD had the largest influence on population growth rate, closely followed by the effect of soil depth (Fig. 3, Appendix S1: Figs. S6, S8, and Table S3). While the effects of increasing

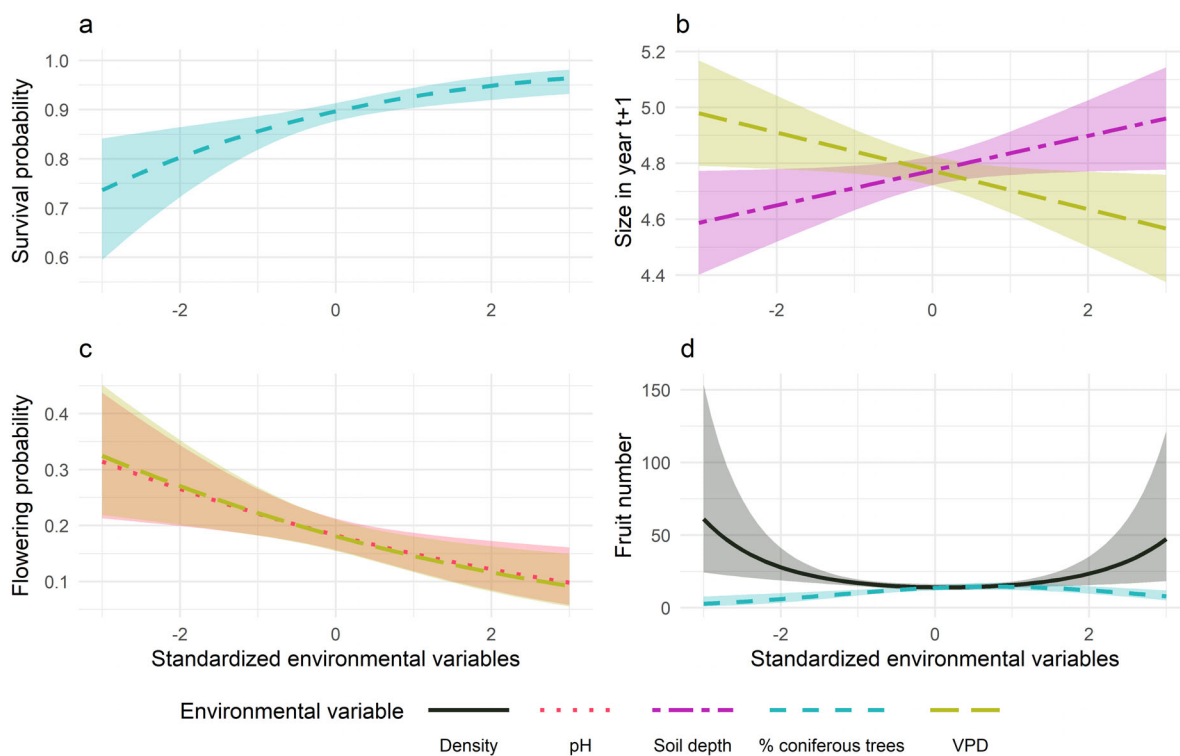


Fig. 2. Influence of environmental drivers on vital rates of *A. spicata*. Values correspond to the vital rates of mean sized plants. Panel (a) shows the influence of coniferous trees ($\beta = 0.38 \pm 0.11$ [mean \pm SE], $P < 0.01$) on survival, (b) VPD ($\beta = -0.07 \pm 0.03$, $t = -2.209$) and soil depth ($\beta = 0.06 \pm 0.03$, $t = 2.071$) on growth, (c) pH ($\beta = -0.24 \pm 0.09$, $P < 0.01$) and VPD ($\beta = -0.26 \pm 0.09$, $P < 0.01$) on the probability of flowering, and (d) density ($\beta = 0.17 \pm 0.07$, $P = 0.01$; $\beta = -0.12 \pm 0.04$, $P < 0.01$ for density and density², respectively) and percentage of coniferous trees ($\beta = -0.04 \pm 0.04$, $P = 0.25$; $\beta = 0.15 \pm 0.06$, $P < 0.01$, for coniferous trees and coniferous trees², respectively) on the number of fruits. Polygons show 95% confidence intervals.

percentage of coniferous trees and soil depth were positive, increasing VPD had a negative association with λ . The influence of increasing pH was also negative but smaller than the effect of VPD. The effect of density was negligible. For VPD and percentage of coniferous trees, that affected several vital rates, the influence on population growth rate via growth and survival, respectively, was stronger than the influence via reproduction, as shown by only including the effect on one vital rate at the time in the model (Appendix S1: Fig. S7).

The mean population growth rate was 0.96 over all transitions and sites. However, populations were on average increasing during the first transition (mean $\lambda_{2017-2018} = 1.04$, $SD = 0.05$), but decreasing during the second transition (mean $\lambda_{2018-2019} = 0.87$, $SD = 0.05$). Population growth rates also varied between sites (Fig. 1) and ranged from 0.84 to 1.05 per site over the study period ($SD = 0.05$, Appendix S1: Table S2).

DISCUSSION

Our results demonstrate substantial effects of climatic, non-climatic abiotic, and biotic environmental drivers on the population dynamics of

the perennial herb *Actaea spicata*. Specifically, we showed that population growth rate is strongly influenced by vapor pressure deficit (VPD), soil depth, and tree composition. There was also a substantial difference in the relative importance of the various environmental drivers on the different vital rates. The three environmental factors influencing survival and growth had large effects on overall population dynamics, illustrating that the population growth rate of *A. spicata*, as well as other long-lived plants, is more sensitive to changes in those vital rates (Silvertown et al. 1993, Dahlgren and Ehrlén 2009). In accordance with the low influence of reproduction on population growth rate of *A. spicata*, soil pH had small effects on population dynamics, even though it had a strong negative effect on the probability of flowering. The effect of intraspecific density on fruit number translated to an even smaller effect on population growth rate. These results illustrate how effects of environmental factors and the sensitivity to the affected vital rates jointly determine the realized niches of species by putting limits on population growth.

The negative effects of VPD on several vital rates and population performance are particularly interesting in the context of ongoing

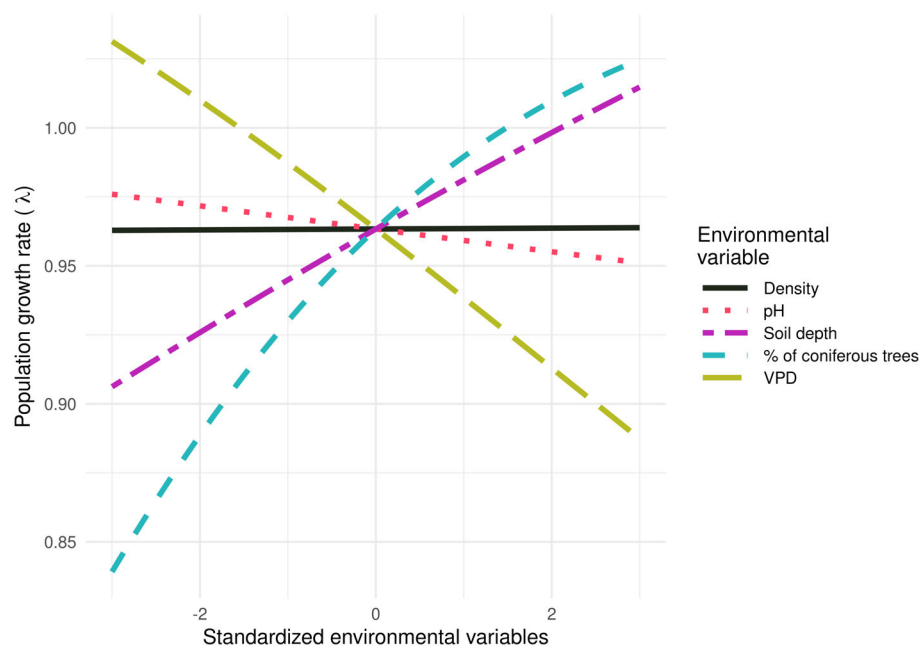


Fig. 3. Influence of the environmental drivers of vital rates on the population growth rate (λ).

climatic changes. If humidity in Sweden will increase at the same rate as it has during the last 50 yr (Wern 2013), and temperature increases as predicted by Sjökvist et al. (2015), the predicted average population growth rate of *A. spicata* across Sweden would increase from $\lambda = 0.97$ to $\lambda = 1.01$ by the end of the century (see Appendix S3 for details). The positive influence of lower VPD values on population growth rate, and the expectation of a future decrease, highlights the importance of understanding the effects of climate change on plant populations. Like several previous studies in temperate areas (Nicolè et al. 2011, Sletvold et al. 2013), we found that direct effects of climate change on plant populations will likely be positive. In addition to direct effects on *A. spicata* and its competitors, changes in climate might affect forest community structure and soil composition (e.g., Lükewille and Wright 1997, Garten et al. 1999), which in turn affect its population dynamics. In a changing climate, a combination of these factors will lead to a shift in the geographical distribution of suitable conditions for *A. spicata*.

Some of the effects that we detected contrasted with our expectations. The positive effect of a high percentage of coniferous trees on individual survival and population growth rates is the opposite of the effect found in previous studies with the same species (Fröborg and Eriksson 2003, Dahlgren and Ehrlén 2011). It also contrasts with that *A. spicata* tends to be more common in broadleaf forests (Mossberg and Stenberg 2014). It is possible that the percentage of coniferous trees in our study was correlated with, for example, high soil moisture, low maximum temperatures or other not tested environmental factors. This could explain why its effect on population growth was stronger in the 2018–2019 transition following an extremely warm and dry year in 2018, suggesting the positive effect of coniferous trees on survival may have been due to a buffering of the drought. Previous studies also detected effects of soil potassium, but no effects of soil pH, soil depth, and variables related to soil moisture and temperature (Dahlgren and Ehrlén 2009, 2011). The differences in detected effects are likely due to the different spatial scale of the studies, where the previous were focused on patterns at a few sites close to each other while this study covers the Swedish distribution of the

species. The difference in results highlights the importance of scale for demographic studies. Large-scale studies are likely to cover larger environmental gradients and therefore more likely to detect responses to an environmental driver (e.g., Levin 1992, Chave 2013).

We detected significant effects of both biotic and abiotic drivers and several of these might alter due to anthropogenic influences, such as effects of forestry might alter tree species composition. Our findings are in line with other studies that have assessed the effects of multiple drivers of population dynamics (e.g., Nicolè et al. 2011, Diez et al. 2014). Further, a recent study found that the impact of abiotic, biotic, and anthropogenic factors on population growth rate are equally important and should therefore all be considered in environmentally explicit population models (Morris et al. 2020). Like Morris et al. (2020) our results emphasize that the performance of a species is affected by multiple environmental drivers and that we should consider evaluating as many of them as possible, given considerations of sample size and potential overfitting, when predicting how environmental change will affect species. We conclude that environmentally explicit demographic models, fitted to data over large geographical scales, and including a broad variety of environmental drivers are a valuable tool for identifying species' niches. We also assert that these analyses can be valuable for designing management strategies for species of special interest. Finally, combining these demographic models with classical species distribution models (e.g., Greiser et al. 2020) has the potential to lead to a deeper understanding of the drivers of changes in species abundances and distributions.

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designed fieldwork. GR and HdB conducted fieldwork. KR conducted soil analyses. GR analyzed data with assistance from DMC and JPD. GR, JPD, and JE led the writing of the manuscript, with input from all authors.

NOTE

¹www.artportalen.se

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