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Christiansen, Ditte M.; Römer, Gesa; Dahlgren, Johan P.; Borg, Malin; Jones, Owen R.; Merinero, Sonia; Hylander, Kristoffer; Ehrlén, Johan

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ARTICLE

High-resolution data are necessary to understand the effects of climate on plant population dynamics of a forest herb

Ditte M. Christiansen^{1,2}  | Gesa Römer^{3,4}  | Johan P. Dahlgren^{3,4}  |
 Malin Borg¹ | Owen R. Jones^{3,4}  | Sonia Merinero^{1,2}  |
 Kristoffer Hylander^{1,2}  | Johan Ehrlén^{1,2} 

¹Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden

²Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

³Interdisciplinary Centre on Population Dynamics (CPop), University of Southern Denmark, Odense M, Denmark

⁴Department of Biology, University of Southern Denmark, Odense M, Denmark

Correspondence

Ditte M. Christiansen
 Email: dittechristiansen@live.dk

Present addresses

Ditte M. Christiansen, Department of Plant and Environmental Sciences, University of Copenhagen, Frederiksberg, Denmark; and Sonia Merinero, Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain.

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Abstract

Climate is assumed to strongly influence species distribution and abundance. Although the performance of many organisms is influenced by the climate in their immediate proximity, the climate data used to model their distributions often have a coarse spatial resolution. This is problematic because the local climate experienced by individuals might deviate substantially from the regional average. This problem is likely to be particularly important for sessile organisms like plants and in environments where small-scale variation in climate is large. To quantify the effect of local temperature on vital rates and population growth rates, we used temperature values measured at the local scale (in situ logger measures) and integral projection models with demographic data from 37 populations of the forest herb *Lathyrus vernus* across a wide latitudinal gradient in Sweden. To assess how the spatial resolution of temperature data influences assessments of climate effects, we compared effects from models using local data with models using regionally aggregated temperature data at several spatial resolutions (≥ 1 km). Using local temperature data, we found that spring frost reduced the asymptotic population growth rate in the first of two annual transitions and influenced survival in both transitions. Only one of the four regional estimates showed a similar negative effect of spring frost on population growth rate. Our results for a perennial forest herb show that analyses using regionally aggregated data often fail to identify the effects of climate on population dynamics. This emphasizes the importance of using organism-relevant estimates of climate when examining effects on individual performance and population dynamics, as well as when modeling species distributions. For sessile organisms that experience the environment over small spatial scales, this will require climate data at high spatial resolutions.

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KEYWORDS

climate change, climate scale, demography, integral projection model, *Lathyrus vernus*, microclimate, plant population dynamics, population growth rate, species distributions, spring frost

INTRODUCTION

To assess the importance of climate as a driver of population dynamics and species distributions, researchers have often used climate data aggregated on regional scales (kilometer spatial resolution) (Bennie et al., 2014; Compagnoni et al., 2021; Thuiller et al., 2005). The relevance of such analyses rests on the assumption that regionally aggregated climate data adequately reflect the conditions experienced by the focal organisms. There is, however, an increasing awareness that locally measured climate can differ considerably from the regional average (Lembrechts et al., 2018, 2019) and, thus, that organisms with restricted mobility experience climatic conditions differing from those suggested by regionally aggregated data (Blonder et al., 2018; Greiser et al., 2020). Differences between regionally aggregated and local climate can be particularly pronounced in topographically heterogeneous environments and in forest understories where canopy density influences the buffering of extreme temperatures (De Frenne et al., 2021; Greiser et al., 2018; Zellweger et al., 2019). Yet, we still know little about how such local deviations from regionally aggregated climate data influence our ability to identify and quantify the effects of climate on organism performance.

A given change in a climatic driver might affect an individual differently during different phases of its life cycle (Doak & Morris, 2010; Oldfather & Ackerly, 2018). Therefore, to assess the overall effects of climate on individual performance and the consequent population growth rate, we need approaches that integrate information about the effects of climate during all phases of the life cycle (Ehrlén & Morris, 2015). For plants in seasonal environments, the timing of key life-cycle events, such as emergence, development, and reproduction, to suitable climate conditions in spring has important effects on demographic vital rates (Iler et al., 2021). Early spring development is associated with a longer growing season, which could increase resource acquisition and reproductive success (Ehrlén & Valdés, 2020). However, early development might also increase exposure to frost damage on developing leaves and flowers (Augsburger, 2011; Inouye, 2008). Spring temperature, in terms of both the frequency and severity of frost events and in terms of accumulated heat, are thus likely to be important for population dynamics of many early-emerging organisms in seasonal environments.

We used local temperature data from in situ loggers and demographic data collected from individuals in 37 populations over a 3-year period to explore how spring temperature influenced vital rates and the asymptotic population growth rate of the understory forest herb *Lathyrus vernus*. We also explored whether models using regionally aggregated temperature data (≥ 1 km spatial resolution) captured the effects identified using local temperatures. *Lathyrus vernus* emerges and flowers as soon as conditions are suitable for growth in spring, and favorable conditions for resource acquisition occur only during a relatively short period before canopy closure. We therefore focused on the effects of two aspects of spring temperature that we judged to be particularly important for the study species: accumulated frost (freezing degree days [FDDs]) and accumulated heat (growing degree days [GDDs]). We also included other potentially important drivers of population dynamics: light availability, grazing, and intraspecific density (Dahlgren et al., 2014; Ehrlén, 1995a; Greiser et al., 2020). We asked three specific questions: (1) How does locally measured spring temperature affect among-population variation in population growth rate? (2) Are regionally aggregated temperature data sufficient to identify the effects of temperature on population dynamics indicated by locally measured temperatures? (3) Which vital rates contribute most to the effects of spring temperature on population growth rate?

METHODS**Study system**

Lathyrus vernus (L.) Bernh. (Fabaceae) is a long-lived herb growing in mesic forests on nutrient-rich soils in central and northern Europe (Hultén & Fries, 1986). In Sweden, *L. vernus* occurs mainly in southern parts but is also seen further north along the coast and in valleys (Mossberg & Stenberg, 2010, Appendix S1: Figure S1). Resources accumulated during one growing season are stored in overwintering rhizomes and used for growth in the following season (Ehrlén, 2002). One to several shoots emerge from the rhizome in spring, and flowering occurs before canopy closure (Ehrlén, 1995a). All aboveground parts senesce in autumn. *Lathyrus vernus* is slow growing and flowers only after 10–15 years. Flowers are pollinated by bumblebees. Fruits

contain few large seeds that are sometimes predated by the larvae of the beetle *Bruchus atomarius* (Ehrlén, 1995b). Mammal grazers sometimes consume most of the above-ground parts in spring (Ehrlén, 1995b).

Demographic data

During the summer of 2017, we established a permanent plot in each of 37 different populations evenly spread across the species' Swedish distribution range (Appendix S1: Figure S1). The distribution of *L. vernus* is patchy, and we defined a population as a patch of individuals clearly separated from other patches. The minimum distance between two populations included in the study was 24 km. Plot size was chosen to include an adequate number of individuals in each plot and ranged from 3 to 94.5 m² (mean $\pm$ SD = 28.5 $\pm$ 23). The number of individuals at the first census ranged from 14 to 72 (mean $\pm$ SD = 49 $\pm$ 12) (Appendix S1: Table S1).

We collected demographic data yearly from 2017 to 2020 (summarized in Appendix S1: Table S2). Each population was recorded after the growth and development of seeds were completed, that is, between late June and late August. We marked all individuals in each plot with numbered flags during the first census and mapped their position. For each shoot, we noted flowering state (flowering vs. nonflowering), size, grazing (having visible mammal grazing damage of shoot stem or being intact), number of fruits, number of seeds per fruit, and number of predator entrance holes per fruit. Size was calculated as the natural logarithm of the sum of the products of cross-sectional area (in square millimeters) and height (in millimeters) of each shoot. This aboveground volume estimate strongly correlates with dry biomass (Ehrlén, 1995a). We imputed diameter from height for shoot diameters <0.5 to avoid damaging the stem when measuring (Appendix S1: Table S3). Growth was estimated by changes in size between years. To estimate the effects of grazing as accurately as possible, we assigned the effects to the year subsequent to the incidence of the damage, that is, as the change in state and size to the recording the year after damage. We therefore imputed shoot height for grazed individuals in the year of damage using shoot diameters of grazed shoots and the allometric relationship between height and stem diameter in nongrazed shoots (Appendix S1: Table S4). New recruits (distinguished based on size) and individuals dormant at the first recording were included in the study from the year in which they were first recorded.

Individuals reappearing after being absent in a given year were recorded as alive and dormant in that year. For individuals that lacked aboveground structures in the

final census year (2020), we assumed that the proportion that was dormant equaled the average in 2018 and 2019, and we imputed their status (dormant or dead) based on size (Appendix S1: Table S5). Individuals that lacked aboveground structures in two consecutive censuses were considered dead as individuals of this species are almost never dormant in more than one season (Ehrlén, 2002).

We counted the total number of seeds and the number of predated seeds in up to three random fruits per shoot. The total number of seeds produced by an individual and the number of predated seeds were estimated by the products of the total number of fruits and the average number of seeds per fruit and the total number of fruits and the average number of predated seeds per fruit, respectively. After counting, the seeds were dispersed in the near vicinity of the individual. Opened fruits were collected, and seed number was determined in the lab based on the number of indentations in the fruit walls. The number of predated seeds in opened fruits was estimated using the number of entrance holes on the fruits and a previously estimated relationship between the number of predated seeds, the total number of seeds, and the number of entrance holes in fruits for *L. vernus* (Fogelström & Ehrlén, 2019). Recruitment in terms of the probability that a seed produced in a given year resulted in a surviving seedling in the next year was calculated as the number of new individuals below a threshold size divided by the total number of intact seeds produced in the previous year. The threshold size chosen, 15 mm³, corresponds to the maximum observed size of newly emerged seedlings (Ehrlén, unpublished data). We calculated recruitment probability and seedling sizes across years with one estimate per population.

Spring temperature and other potential drivers of population dynamics

We estimated local spring temperature, light, grazing, and intraspecific density for each plot. Local measures of temperature were recorded hourly by loggers (EasyLog EL-USB-2, Lascar Electronics, Erie, Pennsylvania, USA) placed about 20 cm above ground at the center of each plot and shielded from direct sunlight and rain with white plastic pots. We calculated accumulated heat in terms of growing degree days (GDDs) and accumulated spring frost in terms of freezing degree days (FDDs). To capture the temperature conditions during relevant and similar periods of plant development across the wide latitudinal gradient represented by the populations, we calculated GDDs and FDDs for a 60-day period from the first day of the year's first week with a minimum of 5°C daily mean temperature for each population and year

using temperature logger data. We calculated local GDDs as the sum of daily mean temperatures above 5°C (Forrest & Thomson, 2011) and daily mean temperatures as the average of daily maximum and minimum temperatures (Appendix S1: Equation S1). We calculated local FDDs as the absolute sum of daily minimum temperatures below 0° (Greiser et al., 2020) (Appendix S1: Equation S2). Some plots (four in 2018, eight in 2019) lacked local temperature measurements for part of the period due to logger failure. For these plots, we predicted local first spring day as well as local FDD and GDD values using linear regressions including ERA5-Land temperature values as predictors (Appendix S1: Tables S6–S8). We estimated light availability in terms of canopy gap fraction in summer 2018 by analyzing hemispherical photos taken with a Sony Xperia L1 camera with a fisheye lens (180° Supreme Fisheye Lens, Model MFE4, MPOW) in Image J with the plugin Hemispherical 2.0 (Beckschäfer, 2015). Intraspecific density in each plot and year was calculated as the summed size of all individuals divided by plot area.

To examine whether the effects of spring temperature on population dynamics detected using locally measured temperature data could be identified also using regionally aggregated temperature data, we used four different commonly used regional estimates: (1) European reanalysis of hourly temperatures at a height of 2 m with a spatial resolution of c. 11 km, using atmospheric forcing and elevation correction (ERA5-Land, Muñoz Sabater, 2019); (2) daily minimum and maximum values from E-OBS (Cornes et al., 2018), interpolated data from a dense network of weather stations in Europe (c. 10 km resolution); (3) daily minimum and maximum temperatures from a topographically downscaled version of ERA5-Land using the KrigR R package for statistical downscaling of spatial resolution values of c. 11 to 2 km (Kusch & Davy, 2022) (abbreviation KrigERA); (4) daily minimum and maximum estimates at a 1-km resolution from CHELSA, which are based on ERA-Interim data and statistically downscaled using topography (Karger et al., 2017). From these four sources we calculated GDD and FDD values using the same method and the same first spring day as for the locally measured data (see Appendix S1: Tables S9 and S10 for an overview of all variables).

Vital rate regressions

To assess the effect of temperature and nonclimatic factors on vital rates, we modeled the probability of survival, growth, probability of flowering, number of seeds in flowering individuals, and proportion of seeds damaged as functions of local FDD, local GDD, light, grazing, and

intraspecific density, as well as size. To examine whether models using regionally aggregated temperature data identified the same patterns as models using locally measured temperature, we repeated these analyses, replacing local FDD and GDD estimates with each of the four different regional estimates (AIC_c comparison in Appendix S2: Table S7).

We did all analyses in R version 4.0.5 (R Core Team, 2021). To fit the vital rate regressions, we used linear mixed models and generalized linear mixed models using the functions “lmer” and “glmer” from the lme4 package (Bates et al., 2015). We checked the models for multicollinearity with the function “vif” from the car package (Fox & Weisberg, 2019) with a threshold of 3 and examined model diagnostics with the DHARMa package (Hartig, 2021).

We modeled growth as a regression of size on size the prior year, with a Gaussian distribution and identity-link function. The probabilities of survival and flowering were modeled with binomial error distributions and logit-link functions. We modeled square-root-transformed number of seeds with a Gaussian distribution and identity-link function due to model diagnostics on prior models using Poisson or negative binomial distributions. We modeled the proportion of seeds damaged with binomial error distribution, a logit-link function, and included a prior weight of the total number of seeds to account for total number of seeds. We included plant size in the prior year in the survival model and size in the same year in models of probability of flowering, number of seeds, and the proportion of seeds damaged. We added a quadratic term for plant size to allow for a nonlinear relationship between plant size and vital rates. To include previously dormant individuals, size of dormant individuals in the year of dormancy was assigned a value corresponding to the mean of sizes in the years immediately before and after the year of dormancy. The rationale for using this approach was that a considerable part of the total biomass of *L. vernus* individuals is belowground and that the imputed aboveground biomass in the year of dormancy is likely to be a reasonable proxy for total biomass. For more details on the decision for including dormant individuals, see Appendix S1: Section S1.

The growth of *L. vernus* individuals within a season is determinate and draws on resources accumulated in the previous growing season (Ehrlén, 2002). Furthermore, leaves and flower buds are also formed during the previous growing season (Ehrlén, 2002). Therefore, we assumed that spring temperature conditions, as well as grazing and intraspecific density, in a given year affected survival, size, and reproduction mainly in the transition to the next year (see Appendix S1: Table S11 for model comparison with models including temperature values with no lag). In all vital rate regressions, we therefore

included grazing in the prior year, light (constant across years), local FDD and GDD in the spring leading up to the prior year (1 year lag), and intraspecific population density in the prior year. Accounting for time-lagged effects in this way enabled us to only explore effects on demographics from 2018 to 2020. Information about grazing was available at the level of individuals, and we estimated the effect of grazing on vital rates at the individual rather than the plot level. We included plot (one plot per population) as a random intercept in all models and scaled plant size and all other continuous predictor variables to unit variance and mean-centered across years before conducting our analyses.

We modeled vital rates separately per year because preliminary models using data pooled across years showed significant interactions between predictor variables and year. Models including interactions with year also performed better than models without interactions but with quadratic terms for each driver (AIC_c comparison of models in Appendix S1: Table S12). To ensure that our results were not dependent on the imputed values for FDD and GDD, we repeated the vital rate regressions excluding the populations with missing logger measurements, which showed no qualitative difference in the coefficients (Appendix S1: Table S13). See Appendix S2: Tables S2–S6 for full summaries of vital rate regressions.

Integral projection modeling

To calculate the effects of local FDD, local GDD, light, grazing, and intraspecific density on asymptotic population growth rates (λ), we used the estimates obtained from the vital rate regressions to construct deterministic integral projection models (IPMs). IPMs are size-structured population models with continuous state variables (Easterling et al., 2000). To estimate the effects of the environmental drivers on population growth rates across populations, we included all estimated relationships between vital rates and environmental factors, regardless of their statistical significance. We estimated the effect of a focal environmental factor in IPMs where it was allowed to vary, while all nonfocal factors were kept at their mean (across populations) levels. Thus, we did not estimate the effects of environmental factors on the growth rate of each population. We used the proportion of individuals grazed in each population as estimates of grazing in these analyses. We modeled λ for each environmental predictor's minimum to maximum range with 100 equal distance levels. Lastly, to assess the extent to which models using the four regionally aggregated temperature data sets were able to detect the same effects on λ as models using locally measured temperature, we

reran the previously described analysis with estimates from vital rate regressions that used each of the regional estimates instead of local FDD and GDD.

To construct the deterministic IPMs, we used two functions that represent the state transitions from one census (time t) to the following census ($t + 1$), driven by growth and survival ($\mathbf{P}$, Equation 1) and fecundity ($\mathbf{F}$, Equation 2), respectively. These sum to the IPM kernel, $\mathbf{K}$ (Equation 3), which is part of the transition model (Equation 4):

$$\mathbf{P} = S(x, \theta) G(x', x, \theta), \quad (1)$$

$$\mathbf{F} = p_f(x, \theta) [s_i(x, \theta) - s_p(x, \theta)] p_e p_d(x'), \quad (2)$$

$$\mathbf{K} = \mathbf{P} + \mathbf{F}, \quad (3)$$

$$n_{t+1}(x') = \int_L^U K(x', x, \theta) n_t(x) dx, \quad (4)$$

where θ denotes the vector of environmental covariates included in the vital rate models; $\mathbf{P}$ (Equation 1) is the state transition function, consisting of the probability of survival, $S(x, \theta)$, multiplied by growth, $G(x, x', \theta)$; $\mathbf{F}$ (Equation 2) is the fecundity function, which consists of the seedling size distribution (p_d) multiplied by the number of seedlings. The number of seedlings was derived by multiplying the probability of flowering, $p_f(x, \theta)$, by the number of intact seeds produced by flowering plants, i.e., the total number of seeds, $s_i(x, \theta)$, minus the number of damaged seeds (proportion of damaged seeds multiplied by the total number of seeds, $s_p[x, \theta]$) and seedling establishment rate, p_e . Seedling sizes were assumed to follow a Gaussian distribution with mean and variance estimated across years for each plot (mean $\pm$ SD = -1.37 ± 0.36 SD). The growth variance was taken as the residual variance from the growth vital rate regression model. The kernel $\mathbf{K}$ (Equation 3) is the summed product of $\mathbf{P}$ and $\mathbf{F}$ and represents the transition of individuals from time t to time $t + 1$. Equation (4) describes the entire transition model, with $n_t(x)$ being the size distribution at time t ; $n_{t+1}(x')$ is the size distribution at time $t + 1$; and U and L are the upper (3.16) and lower (-3.77) size range limits in units of SD from the mean, corresponding to 10% above and below the observed size range, respectively (cf. Merow et al., 2014). For individuals with size estimates above or below these values, we adjusted their size to the maximum or minimum limits, respectively (Williams et al., 2012). We implemented the model using the midpoint rule of integration to construct a 100×100 matrix, representing a discretized IPM kernel, and 100-element vectors to represent size distributions.

To assess the uncertainty of our estimates and obtain confidence intervals of the effects of the environmental variables on the overall population growth rate, we reran the five vital rate regressions using 1000 bootstrapped samples. For the bootstrapping procedure, we randomly sampled our 37 plots 1000 times with replacement. For a few iterations, the seed predation model did not converge, and for those iterations we set seed predation rate to the mean across populations in that transition year. We used the re-estimated coefficients of the bootstrapped vital rate regressions in the IPM and extracted the mean and the 0.025 and 0.975 quantiles of the resulting λ values to derive estimates of 95% CIs. Effects on λ were interpreted as significant if the confidence intervals of the λ values for the minimum and maximum values of the environmental variable did not overlap. To be able to compare effects on λ among predictors, we show the effects on λ for each predictor's 15th–85th quantile interval. For comparison, the effects of FDD and GDD for the different temperature data sets are shown as deviations from the overall population growth rate when all predictors are at their mean, $\Delta\lambda$.

Life table response experiment

To determine how spring temperature contribute to differences in population growth rate through their effects on vital rates, we conducted a one-way fixed life table response experiment (LTRE) analysis (Caswell, 2001) using the function LTRE from the popbio R package (Stubben & Milligan, 2007). First, we constructed three kernel matrices using the values of the 15th quantile, mean, and 85th quantile of the focal predictor (FDD or GDD), respectively, in models of the focal vital rate, while keeping all other predictors at their mean and all predictors at their mean in nonfocal vital rates. Second, we calculated difference matrices between the 15th quantile and the mean, and the mean and the 85th quantile matrices, for each focal predictor and focal vital rate. Third, we calculated sensitivity matrices corresponding to the averages of the mean matrix and the matrices representing the 15th and the 85th quantile, respectively. Fourth, we multiplied the two difference matrices with the respective sensitivity matrix. Fifth, we summed these two products to get the total contributions of differences in λ between the 15th and 85th quantiles for each focal predictor and focal vital rate. Finally, we reran step 1–5 using bootstrapped estimates of the vital rate regressions to generate 95% CIs of the estimated contributions. Contributions were interpreted as significant if the CIs did not overlap zero. We ran the LTRE analyses for FDD and GDD from the temperature data sources

that showed a significant effect of FDD or GDD on the overall asymptotic population growth rate.

RESULTS

Effects of locally measured spring temperature on population growth rate

The total variation explained in the vital rate regressions were high for growth and flowering (0.75–0.92, R^2 -marginal) but generally lower for survival, number of seeds, and proportion of damaged seeds (0.21–0.79, R^2 -marginal, see also Appendix S2: Table S1; Figures S1–S7). The mean asymptotic population growth rate (λ) differed between the two transition intervals (Figure 1). In models with local temperature estimates, FDD had the largest impact on the population growth rate of environmental variables in both transition intervals. FDD had a negative effect on λ in the first transition (effect size between the 15th and 85th quantiles, $\Delta\lambda = -0.15$), but the slope was more shallow and not significant in the 2019–2020 period ($\Delta\lambda = -0.10$) (Figure 1; Appendix S2: Figure S9). In the first transition that included the warm summer of 2018 (mean local GDD = 553), there was a trend of decreasing λ with increasing GDD ($\Delta\lambda = -0.13$, Figure 1; Appendix S2: Figure S9). In the second transition with cooler conditions (mean GDD = 396), the effect of GDD was positive but not significant ($\Delta\lambda = 0.08$) (Figure 1; Appendix S2: Figure S9). Light had a significant positive effect on λ in 2018–2019 ($\Delta\lambda = 0.09$), but not in 2019–2020. Grazing and intraspecific density had no effects in either transition interval (Appendix S2: Figure S9).

Do models based on regionally aggregated temperature data identify the same effects of temperature on population dynamics as models based on locally measured temperatures?

CHELSEA (at 1-km resolution) was the only regional temperature data that showed a significant negative effect of FDD on λ similar to that found for locally estimated FDD, but the effect was smaller (Figure 2; Appendix S2: Figure S10). In the second transition, none of the FDD estimates from the four regional climate data sets had an effect on λ similar to that found for local FDD. In the first transition, none of the regional GDD values yielded a slope similar to the local GDD, but in the second transition, all showed a similar slope.

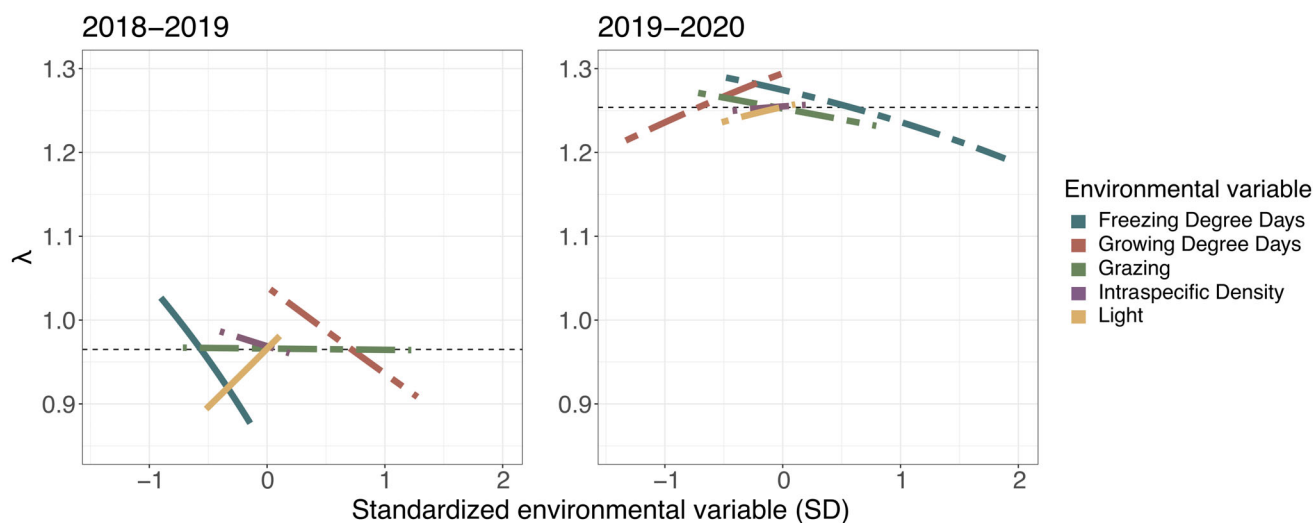


FIGURE 1 Mean of predictions of 1000 bootstrap resamples of effects of local spring temperature (freezing degree days and growing degree days) and other nonclimatic drivers on asymptotic population growth rate under conditions in which all drivers are at their mean for two transition intervals, based on integral projection models. Each colored line represents the relationship between λ and a predictor from the 15th to 85th quantiles of the range of the focal predictor while keeping all other predictors at their mean. Solid lines denote significant relationships, dashed lines nonsignificant relationships. Dashed black lines denote the mean asymptotic population growth rate under mean conditions. The predictor variables are mean-centered and shown in units of SD across years.

Vital rate regression models including local temperature in most cases showed significantly lower AIC_c values than models with regional temperatures (Appendix S2: Table S7). One exception was seed predation, where models including regional temperatures in most cases had slightly lower AIC_c values (no difference larger than -1.75).

Consistent with the pattern that the agreement between effects in models with local versus regional temperature data differed between regional data sets, correlations between regional and local temperature data varied between both years and temperature variables. Correlations for FDD were stronger in 2018 than in 2019 (Appendix S2: Figure S12). Correlations between regional GDD and local GDD also varied between years, with most correlations being negative in year 2018 but positive in 2019 (Appendix S2: Figure S13).

Which vital rates contribute most to the effects of spring temperature on λ ?

The effects of local FDD and GDD on λ occurred mainly via effects on growth and survival in both transition intervals (Figure 3). Local FDD had a significant negative effect on survival, contributing -0.062 and -0.064 to the difference in λ between the 15th and 85th quantiles in the first and second transition intervals, respectively. The negative effects of local FDD on λ occurred also through growth in the 2018–2019 period ($\Delta\lambda = -0.10$). The CIs of the contributions of local GDD to λ overlapped zero for

all vital rates in both transition intervals. Both FDD and GDD contributions from the regional data set CHELSA were overall smaller than the corresponding contributions in models with locally measured temperature and overlapped zero for all vital rates.

DISCUSSION

We examined the impact of spring temperature on the asymptotic growth rate of the forest herb *L. vernus* based on individual-based data from 37 populations across a wide latitudinal range and using both locally measured and regionally aggregated temperature data. In the first transition, increasing sums of locally measured frost during spring were associated with lower asymptotic population growth rates, and higher sums of locally measured spring heat showed a trend of decreasing the asymptotic growth rate, while effects were not significant in the second transition. Interestingly, models using regionally aggregated temperature data mostly did not detect the same effects. Only spring frost estimated from CHELSA had a similarly negative effect on population growth rate as the locally estimated data, but the effect size was smaller. The effects of temperature acted mainly through survival and growth. Taken together, our results show that spring temperature can have important effects on plant population dynamics but that identifying and understanding these effects might require high-resolution temperature data.

Local spring temperature and light showed significant effects on population growth rate, although effects were

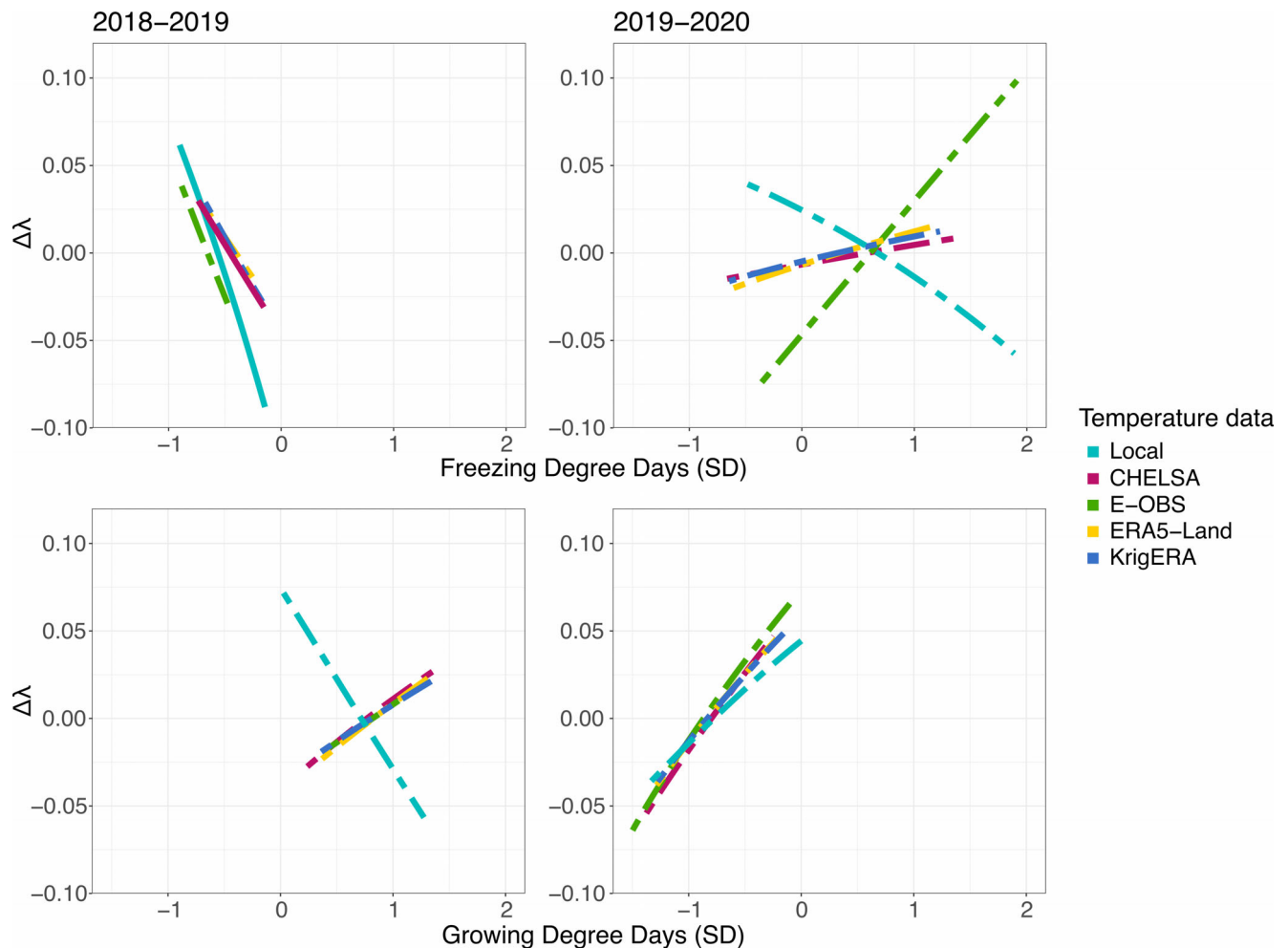


FIGURE 2 Mean of predictions of 1000 bootstrap resamples of effects of freezing degree days (FDDs) and growing degree days (GDDs) on deviation from population growth rate under conditions in which all other drivers are at their mean ($\Delta\lambda$) based on locally measured temperature and regionally aggregated temperature. Each line represents the relationship between $\Delta\lambda$ and the 15th to 85th quantiles of the range of FDDs or GDDs from the five different temperature data sources while keeping all other predictors at their mean. Solid lines denote significant relationships, dashed lines nonsignificant relationships. Predictor variables are mean-centered and shown in units of SD across years.

only significant in the first transition. For the early-emerging forest understory herb *L. vernus*, spring temperatures before canopy closure in late spring are likely to have a strong impact on plant performance, with low temperatures being potentially damaging (Augspurger, 2011; Iler et al., 2019) and high temperatures allowing rapid development and efficient resource acquisition (Blondeel et al., 2020; De Frenne et al., 2010). For many forest understory plants, light limitation is also typical, and previous studies suggested that light might be more important than climate for these species (De Pauw et al., 2021; Greiser et al., 2020). However, the relative importance of temperature and light availability in deciduous forest herbs should strongly depend on phenology. Early-emerging plants, such as our study species, might partly avoid light depletion through early

development but then instead become more exposed to frost and experience lower GDD values during the time critical for development, leading to an increased relative importance of temperature.

The fact that we found substantial differences in temperature effects between years might be explained by the fact that the relationship between species performance and temperature depends on other factors, climatic and nonclimatic, that vary among years, or the fact that the mean temperatures experienced across populations varied between years. It is also possible that the exact timing of frost events is important (Augspurger, 2011; Iler et al., 2019) and that frost events in the first transition occurred when individuals were more sensitive. Between-year differences in the effects of climate on population growth rates have been demonstrated in other systems (Nicolè

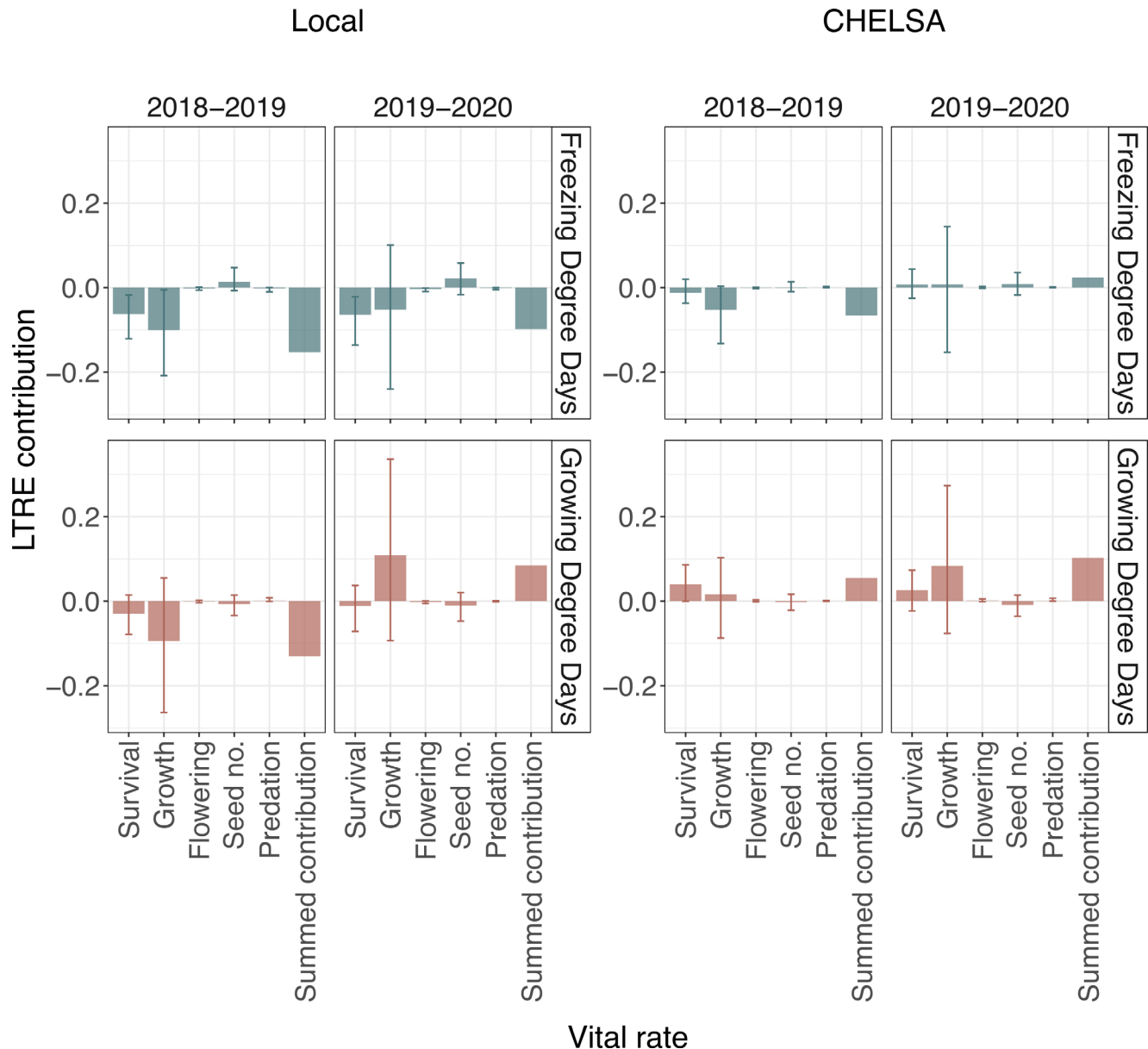


FIGURE 3 Contributions shown as $\Delta\lambda$ through different vital rates to effects of local versus regional (CHELSA) freezing degree days (FDDs) and growing degree days (GDDs) on λ , as well as summed contribution. The mean effects and 95% CIs from 1000 bootstrapped samples are shown for 15th to 85th quantiles of the range of the predictors. LTRE, life table response experiment.

et al., 2011; Peterson et al., 2021; Römer et al., 2021). An interesting implication of such between-year differences in climate effects on population growth rate is that to the extent that effects in cold and warm years are negatively correlated they will result in smaller differences in growth rate among populations over time than suggested by the effects in single years (Morris et al., 2008).

Regional temperature data did not reveal the same effects on population growth rates as locally measured data for spring temperatures. This is likely because sessile forest herbs experience the environment over very small spatial scales and because local temperatures can deviate substantially from regionally aggregated temperatures

(De Frenne et al., 2021). Since the forest canopy buffers extreme temperatures (Greiser et al., 2018; Zellweger et al., 2019), some populations under comparatively dense canopies are likely to have experienced less frost and lower heat than the regional temperature data suggested. On the other hand, some populations in sites with low canopy cover or in depressions collecting cold air might have experienced more heat or more frost, respectively (Greiser et al., 2018). Regional temperatures are thus expected to deviate more from the temperatures actually experienced by plants than locally measured temperatures, leading to lower significance levels for models using regional temperatures than for models using local temperatures. Still, the

correlations between local and regional climate were surprisingly low and sometimes even negative (Appendix S2: Figures S12–S14). The mechanisms behind such patterns are likely related to the fact that local drivers (e.g., topography and vegetation) override regional drivers and that populations occupy a narrower climatic niche in relation to their distribution limit (Ackerly et al., 2020). In the case of *L. vernus*, more northern populations are found in a subset of sites that are warmer relative to regional mean temperatures (e.g., southfacing slopes) than southern populations, and this is likely to affect the correlations between regional and local climate.

Still, spring frost estimated from CHELSA yielded a significant negative effect on λ , albeit of a smaller magnitude than frost estimated locally, and the effects in models with regionally aggregated temperatures were also relatively similar to those yielded in models with locally measured temperature data in some other cases. This suggests that regional temperature data under certain conditions might be a good proxy for the conditions actually experienced by plants but not under other conditions. Local and regional temperatures might be relatively similar during cloudy and windy days, whereas they tend to differ more under clear skies and less windy conditions as local temperatures would then be strongly influenced by topography and vegetation (De Frenne et al., 2021; Zellweger et al., 2020). Seed predation was the only vital rate regression that showed higher AIC_c values using local temperatures than using regional temperatures. This might be due to the fact that plants are only a part of the life cycles of beetles, and the population dynamics of beetles might depend on climatic conditions over a larger area and over a longer time period than captured by local temperatures during one season. Local FDD contributed to differences in population growth rate via its effects on the growth and survival of individuals, whereas regional FDD did not contribute significantly through any vital rate. That local FDD mainly acted through survival and growth is consistent with the results of previous studies of perennial plant species that examined the contributions of climate through different vital rates (Dalgleish et al., 2015; Iler et al., 2019; Nicolè et al., 2011). The estimated contributions in the LTRE analysis are the products of two terms, the change in the vital rate caused by the environmental factor and the sensitivity of the population growth rate to this change. While many studies, including the current one, have found large effects of climate on flowering probability (Czachura & Miller, 2020; Lindell et al., 2021; Tye et al., 2018), the population growth rate of long-lived perennial plants is less sensitive to changes in reproduction than to changes in survival or growth (Dalgleish et al., 2010; Franco & Silvertown, 2004). Consistent with this notion, the effects

of temperature that we found on survival and growth had larger effects on population growth rate in our long-lived study species than effects on reproduction, although spring frost also had strong effects on flowering probability (Appendix S2: Table S4). This suggests that it is the sensitivity of population growth rate to changes in vital rates, rather than the sensitivity of vital rates to climatic factors, that explains why climate often influences population growth rates primarily through its effects on survival and growth in long-lived perennials (Czachura & Miller, 2020; Iler et al., 2019).

In conclusion, our results demonstrate that spring temperature can have important effects on the population dynamics of forest herbs but that currently available regionally aggregated temperature data might not always provide sufficient information about the temperatures relevant to the performance of sessile organisms living near the ground. Downscaling of regionally aggregated temperature data with the inclusion of topography to kilometer spatial resolution have been widely used to overcome this discrepancy (Franklin et al., 2013; Randin et al., 2009). However, our study suggests that models using such spatial resolutions perform worse than locally validated climate models (Man et al., 2022; Stark & Fridley, 2022). Our findings thus underscore the need to measure climate factors at organism-relevant scales and develop even more downscaled high-resolution climate products that also take vegetation into account to better understand how climate influences species abundances and distributions and to improve predictions of the effects of ongoing climate change. A broader implication is that the many studies that have used regionally aggregated data to investigate the effects of climate on population dynamics of organisms with limited mobility might have underestimated the role of climate as a driver of population dynamics. The ecological significance of climate extremes (Stewart et al., 2021), combined with the predicted future increase in the frequency of extreme climate events (IPCC, Seneviratne et al., 2021), implies that our findings of discrepancies between the effects of local and regional temperatures on plant performance point to the urgent need to use organism-relevant estimates of climate when assessing risks and developing mitigation strategies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code (Christiansen et al., 2023) are available in Figshare at <https://doi.org/10.6084/m9.figshare.23853807>.

ORCID

Ditte M. Christiansen  <https://orcid.org/0000-0002-7020-5082>

Gesa Römer  <https://orcid.org/0000-0002-4859-5870>

Johan P. Dahlgren  <https://orcid.org/0000-0002-1125-9769>

Owen R. Jones  <https://orcid.org/0000-0001-5720-4686>

Sonia Merinero  <https://orcid.org/0000-0002-1405-6254>

Kristoffer Hylander  <https://orcid.org/0000-0002-1215-2648>

Johan Ehrlén  <https://orcid.org/0000-0001-8539-8967>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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