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Dahlgren, Johan; Bengtsson, Karin; Ehrlén, Johan

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The demography of climate-driven and density-regulated population dynamics in a perennial plant

JOHAN P. DAHLGREN,^{1,4} KARIN BENGTTSSON,² AND JOHAN EHRLÉN³

¹Department of Biology, Max-Planck Odense Center on the Biodemography of Aging, University of Southern Denmark, Campusvej 55, DK-5230, Odense M, Denmark

²Department of Ecology and Genetics, Uppsala University, Box 256, SE-751 05, Uppsala, Sweden

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

Abstract. Identifying the internal and external drivers of population dynamics is a key objective in ecology, currently accentuated by the need to forecast the effects of climate change on species distributions and abundances. The interplay between environmental and density effects is one particularly important aspect of such forecasts. We examined the simultaneous impact of climate and intraspecific density on vital rates of the dwarf shrub *Fumana procumbens* over 20 yr, using generalized additive mixed models. We then analyzed effects on population dynamics using integral projection models. The population projection models accurately captured observed fluctuations in population size. Our analyses suggested the population was intrinsically regulated but with annual fluctuations in response to variation in weather. Simulations showed that implicitly assuming variation in demographic rates to be driven solely by the environment can overestimate extinction risks if there is density dependence. We conclude that density regulation can dampen effects of climate change on *Fumana* population size, and discuss the need to quantify density dependence in predictions of population responses to environmental changes.

Key words: climate change; demography; environmental drivers; environmental stochasticity; *Fumana procumbens*; integral projection model; intraspecific density dependence; long-term monitoring.

INTRODUCTION

Assessing how environmental variation influences population dynamics is a fundamental part of ecology, and the need to understand these relationships is accentuated by recent anthropogenic environmental change such as climate warming. One important piece of this understanding is how effects of physical environmental variation are modified by density-dependent feedbacks (e.g., Sæther 1997, Benton et al. 2006, Tyler 2010, Boggs and Inouye 2012). Demographic population projection models incorporating both environmental (external) drivers and internal regulation (density dependence) of vital rates can be very useful in investigating this (Sæther et al. 2000, Coulson et al. 2001). Such models are very data demanding, however, and detailed models based on long-term empirical data are rare for species such as perennial plants with complex demography (but see, e.g., Adler et al. 2012).

Climatic fluctuations are known to be strong drivers of individual vital rates underlying population and community dynamics (e.g., Sæther et al. 2000, Coulson et al. 2001, Doak and Morris 2010, Sletvold et al. 2013). They can act directly through variation in temperature and precipitation, and indirectly via effects

on other abiotic environmental factors or biotic interactions (Klanderud 2005, Boggs and Inouye 2012, Pfeifer-Meister et al. 2013). In addition, different vital rates may be affected in opposite ways by the same climatic factors (e.g., Doak and Morris 2010, Nicolé et al. 2011). As a result, effects of climate on population dynamics may vary geographically and be complex, making detailed mechanistic models of effects on vital rates necessary to predict local population dynamics (e.g., Sæther et al. 2004, Sletvold et al. 2013).

To understand fully the effects of the physical environment, we also need to account for internal regulation (i.e., negative density dependent effects) when determining drivers of population dynamics (Coulson et al. 2001, 2008, Berryman and Lima 2006, Hone and Clutton-Brock 2007). Yet, effects of intraspecific density are often ignored in plant population models (but see e.g., Hubbell et al. 1990, Alvarez-Buylla 1994, Fowler et al. 2006, Ramula and Buckley 2009). Effects of intraspecific density-dependent regulation on vital rates and population dynamics may be confounded with effects of environmental variation unless both are investigated simultaneously (Dahlgren et al. 2014). Internal regulation may also dampen effects of environmental change, because a change leading to a smaller (larger) population size will result in a higher (lower) population growth rate. Density dependence must

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⁴E-mail: dahlgren@biology.sdu.dk

therefore be quantified to make predictions of population dynamics. Lastly, confounding density effects should be considered when specific environmental factors are not identified but variation in demographic rates is interpreted as direct responses to “environmental stochasticity”, as is often done in population viability analyses (e.g., Morris and Doak 2002).

We studied the simultaneous effects of climate and intrinsic regulation on population dynamics of the perennial plant *Fumana procumbens*, for which we have conducted detailed monitoring of plants at three sites during 20 yr on the island of Öland, Sweden. *Fumana* has a patchy distribution at the scale of meters. Individuals of *Fumana* seemingly occupy most suitable microsites in the study plots, which suggests that intraspecific competition is important. Previous work with this plant also suggests it is strongly influenced by climatic conditions in terms of negative effects of summer droughts (Bengtsson 1993b). Based on this and previous studies in other systems, we hypothesized that both climatic variables and intraspecific densities are key drivers of the population dynamics, that different vital rates are influenced by partly different factors, and thus that integrating effects of both climatic factors and density during all phases of the life cycle is important to model and understand the population dynamics. Specifically, we asked: (1) Can correlations of vital rates with climatic factors and density explain observed population dynamics? (2) Through which changes in vital rates do density and climate influence population dynamics? And (3) how does accounting for intrinsic population processes influence estimates of population viability? We quantified relationships of climatic factors and intraspecific density with size-dependent vital rates using generalized additive mixed models (GAMMs), and included fitted relationships in a size-structured integral projection model. We found that annual climate variation influenced several vital rates, resulting in fluctuations in population densities, but that to predict the climate-driven population dynamics of *Fumana* it was necessary to account for density dependence of vital rates.

METHODS

Study system

Fumana procumbens (Dunal) Gren. and Godr., Cistaceae, is a long-lived perennial dwarf shrub with its main distribution in southern Europe, extending eastwards to the Caspian Sea. North of the main distribution area, on the Baltic Sea islands Öland and Gotland, disjunct populations occur (Hultén 1971). The study species grows in open and well-drained habitats on weathered limestone or calcareous sand. The root system often penetrates limestone crevices and the above-ground parts spread horizontally over sparsely vegetated ground or bare rock. *Fumana*

procumbens plants are sensitive to overgrowth (Bengtsson 1993a) and to disturbance in terms of grazing and trampling (Pettersson 1958, Bengtsson 1993a). We studied *F. procumbens* at three sites within the Öland population, which is restricted to sites in the northeastern part of the 25 000 ha area of steppe-like alvar grasslands on calcareous bedrock called Stora Alvaret. In the study area (56.587°N, 16.583°E) the species is found mainly on small south-facing stony slopes or fissured limestone habitats with a mosaic character in a patchy distribution on the scale of ca 5 to 100 m. A pilot study by Lindahl (2000) showed higher population density in larger patches of suitable habitat, while the species was present at low densities or absent in smaller habitat patches with slightly taller vegetation. There was no difference between occupied small and large patches in the proportion of reproductive individuals.

Fumana procumbens is reported to be self-fertilized (e.g., Vestergren 1909, Pettersson 1958) but small bees (e.g., *Halictus* spp., *Lasioglossum* spp.) and hoverflies (Syrphidae) visit flowers (K. Bengtsson, unpublished data). Mature seed capsules normally detach to fall right beneath the plant but may be transported by strong winds or local flooding, and single seeds have occasionally been observed carried by ants (Bengtsson 1993a, K. Bengtsson unpublished data). Observations from 1985 to present indicate that individuals that die are often replaced by new individuals in the same spots, suggesting that the most important factor for establishment is the occurrence of micro-sites with suitable conditions for germination and growth.

Field studies

We collected data on life-cycle stage, size, fecundity and survival of *Fumana procumbens* individuals in permanent plots (0.5 m × 0.5 m) at three sites within an 0.7 × 0.5 km area on Öland. Data were collected in the second half of August each year from 1985 to 2012, except in 1996 and from 2000 to 2006. For the period 1985–1995, a total of 33 plots were observed several times every year. The period 1997–2012 included yearly observations of 14 to 27 plots. The number of plots recorded each year decreased because disturbance associated with an alvar grassland restoration project between 1998 and 2002 made some plots impossible to find. All individuals in each monitored plot were depicted on a 1:4 scale map and the numbers of buds, flowers, and fruits (seed capsules) were recorded for each reproductive plant. *Fumana* is not clonal, and all shoots originate from one main stem, making it straightforward to identify individuals in the field. From 1985 to 1989, all individuals in the plots were classified into six life cycle stages based on size and reproductive status: seedling, small vegetative (≤ 2 shoots), intermediate vegetative (> 2 shoots), small reproductive (≤ 3 capsules produced), large reproductive

(>3 capsules produced), and temporarily non-reproductive. From 1989 a continuous estimate of size, total branch length, was calculated from measurements on the maps for each individual. Sizes for individuals in 1985–1988, when only stage was recorded, were assumed to be the mean size of each respective stage in the three following years when fitting the statistical models. In total, 871 non-seedling individuals were included in the study.

Weather data

Information on daily precipitation and mean temperature from 1982 to 2012 were retrieved from the local weather station at the Ecological Research Station/Station Linné in Ölands Skogsby. For periods of missing observations in the data series from the research station, we used data from SMHI (The Swedish Meteorological and Hydrological Institute), collected at the two stations closest to the study populations; Norra Möckleby (precipitation) and Skede Mosse (temperature). Before analysis, the SMHI daily values for each parameter were corrected by adding or subtracting a term corresponding to the average deviance from the research station values.

Data analysis

We hypothesized that increased temperatures early and late in the season extend the growing season and results in higher survival, growth and flowering. We also hypothesized that higher precipitation during the warm summer months results in less drought stress and better plant performance. We thus predicted that annual survival, growth, and flowering were positively related to high spring temperature, high summer precipitation, and high autumn temperature in the previous year, as well as to high spring temperature and high summer precipitation in the same year. We further hypothesized that fruit number was positively affected by summer temperature in the year fruits are produced and that seedling establishment was positively affected by summer temperature in the year following seed dispersal. Finally, since *Fumana* individuals seemingly occupy most micro-sites that allow individual plants to establish, grow and reproduce, we hypothesized that all vital rates were density dependent and that intraspecific competition is more important than interspecific competition for our particular study system.

We used the monitoring data to estimate size-dependent vital rates that together describe life cycle transitions between two yearly censuses. These vital rates were: survival of individuals, flowering, and shoot growth of surviving individuals, number of fruits per flowering individual and probability of seedling establishment per fruit. To describe the yearly weather, we used mean values for temperature and precipitation

in three different periods: spring (April–May); summer (June–July); autumn (August–October). The values for daily precipitation were square root transformed in order to reduce the effect of rare events of extreme rainfall. We assumed that carrying capacities varied among plots in our study system primarily due to differences in the microsite-dependent water availability, thus density estimates were standardized to allow comparisons across plots. Assuming that maximum plot densities observed during the study period were proportional to carrying capacity, density was calculated for each plot and year as the proportion of the maximum recorded sum of all individual sizes per plot. Five plots where individuals were observed in fewer than 5 yr were assumed to have a maximum sum of individual sizes equal to the mean over all other plots at the respective site.

Survival, growth, flowering, and fruit production were modeled as functions of size, density and climatic variables in generalized additive mixed models (GAMMs), using the `gamm4` function in R (R Development Core Team 2013). We chose this function so that nonmonotonic relationships between variables and random effects, taking into account the structure of the data with predictor variables varying over plots and years, could both be included. Error distributions and link-functions were specified to correspond to standard logistic regression for survival and flowering, ordinary least squares regression for growth, and Poisson regression for fruit number. In accordance with the hypotheses, effects of spring temperature and summer precipitation in years t and $t + 1$, and autumn temperature and density in year t , were tested for survival and growth from t to $t + 1$ and flowering in year $t + 1$, by including these variables as covariates in the regression models and determining their statistical significance. For fruit number of flowering individuals and seedling establishment rate in year $t + 1$ we tested effects of autumn temperature in year t , and spring temperature, summer temperature, summer precipitation and density in year $t + 1$. For each vital rate, “site” was included as a fixed factor, and relationships between individual size and vital rates were also allowed to have different shapes for the three sites. Climatic and density effects were assumed to affect individuals equally across sites (but as described earlier, estimates of density accounted for different carrying capacities among plots).

Non-monotonic relationships were allowed for all covariates, using the default thin-plate spline option in the `gamm4` function. The penalized smoothing splines in `gamm4` are similar to restricted cubic splines (cf. Dahlgren et al. 2011), but the function chooses curve complexity based on the data. We set the maximum complexity of the smoothed relationship to $k = 3$, which corresponds to a three-knotted spline and basically means that the overall slope of the fitted curve can change only once. Seedling establishment

was modeled using mixed-effects logistic regression with the `glmer` function in R as there were not sufficient data to model nonmonotonic relationships for this rate.

The choice of included variables and model complexity was a trade-off between realism and ensuring convergence of the model fitting algorithm. The resulting “full” models (including all hypothesized effects of density and climatic covariates) were still difficult to fit, and the full models were simplified by removing parameters (variables or nonlinear components) when this did not affect predictions. Parameters were thus removed when this did not increase the Akaike information criterion (AIC). In addition, a linear model was chosen over a statistically optimal model that included positive effects of extreme weather conditions in both directions, if effects on population growth rate were deemed negligible.

Population model

The regression models of vital rates were included as components in a size-structured integral projection model (IPM), following standard methods (Easterling et al. 2000, Ellner and Rees 2006, Merow et al. 2014, see Supplement 1 for the R code used in the IPM analyses). In the IPM, survival probability, flowering probability, fruit number in flowering individuals, and mean size next year were modeled as functions of size, climatic factors, and density according to the fitted regression functions. The probability of reaching a size other than the mean predicted size was assumed to follow a normal distribution, with variance equal to the fitted variance in the growth regression. Seedling establishment rate was given by the fitted effects of climatic factors and density. In addition, we assumed that size distributions of seedlings were normal and estimated the mean and variance from the data. Together these six functions described all possible annual life cycle transitions in the model, and formed the ‘transition kernel’ of the IPM. An IPM is analogous to a matrix population projection model, in that it projects population structure over a discrete time-step, but the population is modeled as a distribution function rather than a population vector and the continuous kernel replaces the discrete matrix. Structured models in general are assumed to model population dynamics more realistically, because life cycle transitions are explicitly included (Caswell 2001) and because fluctuations in structure can have large effects on population dynamics (e.g., Pelletier et al. 2012).

We used the IPM to investigate how effects of density and climatic factors on vital rates translate to effects on population dynamics, using the different projection kernels resulting from differences in climatic factors and density. We mainly examined responses in terms of changes in total shoot length, which we

judged to be a better measure of the abundance of *Fumana* than number of individuals (for the same reason our measure of density was also based on total shoot length). Effects on the number of individuals were similar, but modeled dynamics corresponded less well with observations (see Appendix S1). Estimates of extinction risk were made based on number of surviving individuals. In simulations of dynamics based on the observed years, population projections started with the population density observed in 1989, the first year in which the sizes of individuals were measured. Parameters were then modified one by one to investigate their effects on the observed dynamics. In analyses of asymptotic properties of the model, i.e., calculations of the asymptotic population growth rate and the elasticity (proportional sensitivity) of this growth rate to perturbations in vital rates, a kernel corresponding to mean climatic factors and the stable population density was used.

To examine how the explicit inclusion of density regulation influenced predictions of population viability, we compared forecasts made using the explicitly density-dependent model described earlier, where all observed annual variation in transition kernels (vital rates) was assumed to be caused by both environmental variation and density, with forecasts using a density-implicit parameterization of the model where annual variation in transition kernels was implicitly assumed to be caused by only environmental variation. For these comparisons, we assumed that the true effects of density and climatic variables were identified in our regression models, and simulated population growth in a variable environment to estimate extinction risks. Climatic states were drawn randomly from the observed years for both simulations, which corresponds to a commonly used method for calculating stochastic population growth rates and extinction risks in population viability analyses (Morris and Doak 2002). In the “density explicit” case, we randomly drew years, and combined information about environmental states from these years with the modeled population density to predict vital rates with the GAMMs. In the “density implicit” case, we assumed that all variation was caused by the environment and used the same sequence of years as in the density explicit case, but used both observed environmental states and observed density in each year to calculate vital rates with the GAMMs, without accounting for the actual density in the modeled population. For both types of simulations, we estimated the risk of extinction over 30 yr, starting with the population structure observed in 1989. A population was considered extinct if it reached a quasi-extinction threshold of 10 established individuals within the study plots (corresponding to 4.7% of the population size in 1989). The models were iterated 10 000 times to calculate the probability of extinction over the modeled years. In addition, we included two different environmental scenarios for both simulation

types: in scenario 1, we modeled effects of observed environmental variation, and in scenario 2, we assumed the probability of encountering the driest observed year was twice as high (8% rather than 4%) as observed. Scenario 2 was used to investigate how incorporating density dependence could affect predictions of effects of climate change on population dynamics, but was not based on actual predictions of climatological models for the study area. We did not include between-year variability that was not explained by climate or density in any of these simulations, but results were qualitatively the same when we also incorporated the fitted random effects into these simulations (not shown).

RESULTS

Vital rates, and as a consequence population size (Fig. 1A), fluctuated markedly over the observation period. The observed synchrony in dynamics across sites suggested that strong, common, large-scale environmental drivers were acting on the entire population (see Appendix S2). The statistical models showed that all vital rates were correlated with climatic variables

and also negatively correlated with intraspecific density, at least at high densities (Table 1, see Appendix S3). Survival was highest in years with intermediate precipitation. Increasing precipitation had a negative relationship with growth but a positive relationship with flowering. Both growth and flowering were positively correlated to autumn temperature. Intermediate summer temperatures were correlated with maximum fruit development, whereas intermediate spring temperatures were correlated with minimum fruit number. Seedling establishment was positively correlated with spring temperature and negatively correlated with summer temperature. Density was not correlated with annual climate variation, resulting in effects of climate on vital rates that were similar in models with or without density.

Modeled population dynamics integrating effects of climatic variables and density on all vital rates corresponded well with observations (Fig. 1B), even though the modeled dynamics were less pronounced than the observed time series (underestimating high densities and overestimating low densities, see Appendix S4). The model accurately captured the three major observed oscillations in total shoot length, and predicted a rise

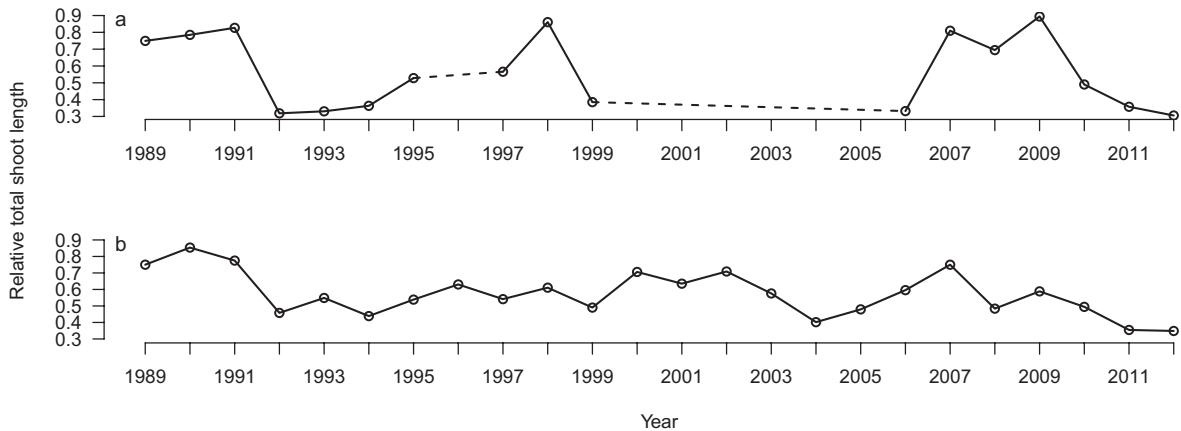


FIG. 1. Observed *Fumana procumbens* density (total shoot length relative to the maximum observed) from 1989 to 2012 on Öland, Sweden (A), and the density predicted by an integral projection model (B). Dashed lines indicate years with missing observations.

TABLE 1. Relationships of density and climatic variables with vital rates of *Fumana procumbens*.

	Survival	Growth	Flowering	Fruit	Seedling est.
Spring temperature				Min.	+
Summer temperature				Opt.	-
Summer precipitation	Opt.	-	+		
Autumn temperature		+	+		
Density	-	-	-	Opt.	-

Notes. Relationships with an entry were statistically significantly correlated at $p < 0.05$ in additive mixed models (GAMMs). '+' equals primarily positive effect of an increase in temperature or precipitation, '-' equals primarily negative effect, Opt., Min. equals an optimum or minimum exists within the observed range of the variable. Seedling est. equals Seedling establishment. Effect sizes and relationships with plant size are shown graphically in Appendix S3.

and fall during the unobserved period between 1999 to 2006 (comparing Fig. 1 A and B). The asymptotic population growth rate in the mean environment was most sensitive to survival (elasticity = 0.94) and growth (0.88), whereas the summed elasticity to the reproductive rates was smaller (0.12).

The effects of density on vital rates were important for regulating the modeled population. When ignoring density effects, the modeled population grew almost geometrically (Fig. 2). Fluctuations in population size were caused by the climatic variables. Models assuming climatic variables to be constant at the mean observed values stabilized quickly at a constant density (not shown). Assuming a stable (density-independent) population growth rate, high spring and autumn temperatures had positive net effects on long-term population growth rate (see Appendix S5). High summer temperatures had negative effects, and population growth was highest at mean levels of summer precipitation. To quantify how variation in the climatic factors affected the population during the study years, dynamics predicted by IPMs where each climatic variable was set to the mean observed value were compared to the full model including among-year variation in all climatic factors. These analyses showed that observed deviations from a stable population density resulted from combined effects of all climatic factors. Holding precipitation constant at the mean observed value had a slightly larger effect on population dynamics than keeping spring, summer, or autumn temperature constant (Fig. 3). Years with either high or low precipitation (see Appendix S6) affected population size negatively in the model. As an example, large population declines in 1992, when there was a drought, and in 2010 when summer rainfall was high, were both absent when keeping precipitation constant in the model.

Leaving out density effects had a large impact on predictions of population growth rate and extinction risk (Fig. 4). In the density-explicit model, population size stabilized quickly (with an average population

growth rate, λ , of 1). In the density-implicit simulations, where variation in the annual vital rates caused by both environmental variation and density dependence was assumed to depend solely on environmental stochasticity, average growth rate stabilized at 0.98, i.e., predicting a decrease in population size. This underestimation in population growth rate caused a predicted extinction risk after 30 yr of 7.6% in the density-implicit simulations. In the density-explicit simulation, there was no risk of extinction, because reductions in population size following bad years led to a release from negative density effects and higher population growth rate. The scenario with a doubled risk of drought-years resulted in an extinction risk of 23% in the density-implicit simulations but still zero risk in the density-explicit model.

DISCUSSION

Our results for the long-lived plant *Fumana procumbens* indicate that climatic variation drives variation in vital rates but that these effects are modified by density-dependent feedbacks. To understand how environmental variation drives population dynamics in this system, we thus need to quantify density effects. An important implication of our results is that if plant population densities are high enough to have intrinsic regulation, then forecasts of effects of climate change on populations and communities that do not account for density dependence might be misleading. In accordance with this, extinction risks based on predictions of stochastic population growth were overly pessimistic unless density was explicitly included in the models used in the simulations.

The significant correlations of individual vital rates with climate and density identified in our analyses translated into modeled population dynamics that agreed overall with the observed dynamics in the study populations. The concurrence between predictions and observations suggests that the main drivers of

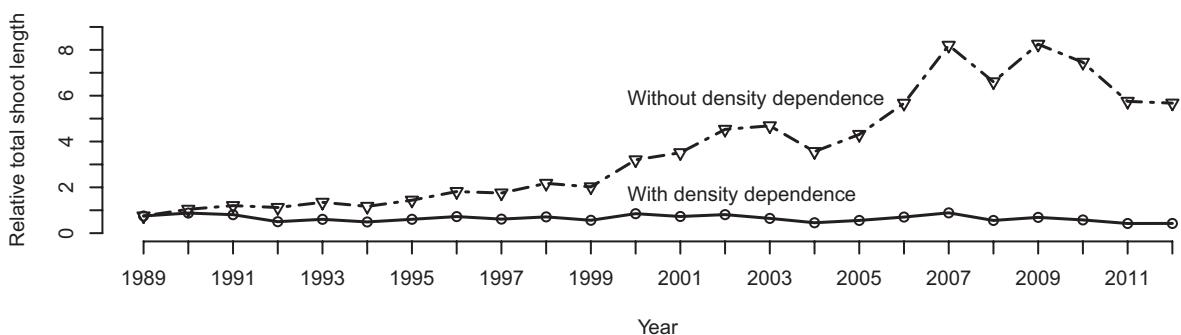


FIG. 2. The effect of intraspecific density dependence of vital rates on the dynamics of *Fumana procumbens* population size over the study years. The predicted dynamics with density dependence are the same as in Fig. 1. The predicted dynamics without density dependence was calculated using the same IPM, but setting the density parameter to the mean observed value of density. Population size is presented as the predicted density relative to maximum observed density (note that the predicted density much exceeds the observed when density dependence is not included).

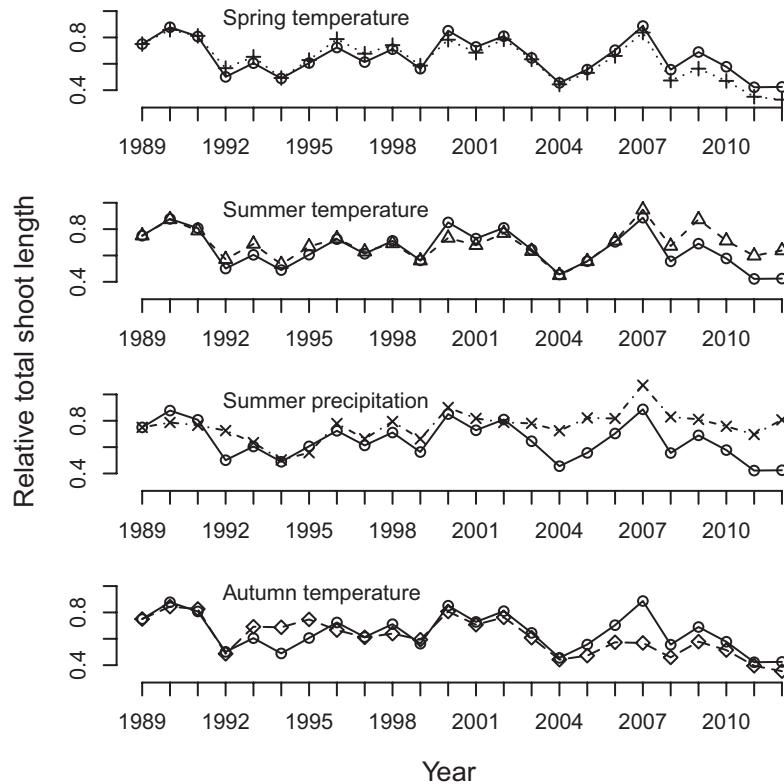


FIG 3. Modeled population dynamics of *Fumana procumbens*, including yearly variation in all four studied climatic variables (solid lines in all panels), and keeping each of spring, summer, and autumn temperature ($^{\circ}\text{C}$) and summer precipitation ($\sqrt{\text{mm}}$) constant at the mean observed values (dashed lines).

population dynamics in *Fumana* were identified, and that the regression approach employed here can be used to disentangle simultaneous effects of environmental drivers and density dependence in long-term data. Since climate variation was not correlated with density in our data, effects of climate were correctly identified even when not accounting for density. Both climate and density had to be included in the IPM to explain the observed population dynamics, however. Long-term data have been used for similar analyses for animals (e.g., Sæther et al. 2000, Coulson et al. 2008) and long-term demographic data are also becoming increasingly available for perennial plants (e.g., Hutchings 2010, Sletvold et al. 2013). Previous demographic studies with plants, most of them covering a lower number of years, have identified important environmental effects on population dynamics (e.g., Riba et al. 2002, Lucas et al. 2008, Toräng et al. 2010, Nicolè et al. 2011, Bucharová et al. 2012). These studies have typically not quantified density effects (Crone et al. 2011), however, possibly because effects of density might be hard to detect in short-term observational studies with only small to moderate variation in densities (Fowler et al. 2006, but see Dahlgren et al. 2014). Results from the present study indicate that longer monitoring periods, comprising

larger variation in density, allow estimation of density effects and thereby enable more accurate assessments of the drivers of population dynamics.

Our analyses suggest that the size of *Fumana procumbens* populations fluctuated in response to variation in summer precipitation and other climatic factors, but that intraspecific density-dependence regulated the resulting dynamics. Low precipitation had a negative effect on survival and flowering but a positive effect on growth. Such opposing effects of climatic factors on different vital rates have been observed also in several other systems and may be common (e.g., Doak and Morris 2010). This highlights the need to study effects on all life cycle stages as well as to assess how different vital rates contribute to population growth rates. In *Fumana*, population growth rate was most sensitive to variation in survival and moderately sensitive to growth, whereas reproductive rates had the smallest effects. As a consequence, effects of drought on survival had a large impact on population growth. In addition, our analyses suggested that precipitation affected survival more than the other vital rates. This was somewhat surprising given that many plants are thought to survive harsh conditions such as droughts by shrinking (e.g., Vega and Montaña 2004). Likewise, the strong negative effect of density

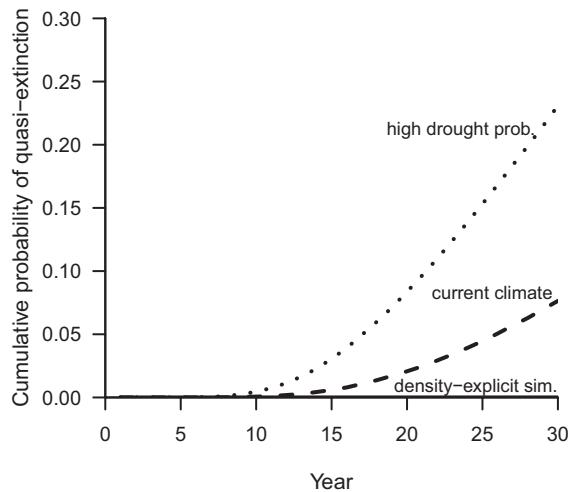


FIG. 4. Quasi-extinction risk (the probability of the observed population shrinking to 10 established individuals) of *Fumana procumbens* over 30 yr based on “density-explicit” and “density-implicit” population projections. Extinction risks in two climatic scenarios are presented for the density implicit simulations (observed climate, and a high drought probability scenario where drought years are twice as common as observed; see text). In the density-explicit projections, extinction risk was constant at zero in both scenarios. The density-implicit and density-explicit projections were both made using the climate and density dependent IPM presented in the text, but in the density-implicit projections it was assumed that all variation was caused by the environment (see text).

on the survival of established plants is interesting. Relatively little is known about the mechanisms of density regulation of plant populations, and it has previously been suggested that primarily the recruitment phase may be affected by density dependence (e.g., Matos et al. 1999, but see Dahlgren et al. 2014). Overall, interplay between density regulation and climate effects, as observed in our study, has important consequences for predictions of effects of climate change. In our study system, the observed patterns suggest that despite the strong sensitivity to climatic fluctuations, *Fumana* populations are resilient to climate change. This is because negative effects of climate will lead to lower population densities, release from negative density effects, and higher population growth rates than at higher densities.

Density regulation can also have important consequences for assessments of how environmental stochasticity influences population viability, although this has received relatively little attention. In many population viability analyses for plants, annual variation in vital rates is implicitly assumed to be caused only by environmental variation. For density-regulated populations this is not true, however. Our simulations illustrate that analyses where it is assumed that vital rate variation is driven solely by external factors may overestimate effects of environmental variation and, as a consequence the extinction risk. Explicitly including

environmental factors and density in projection models should thus result in more accurate forecasts. Since it is not known how often natural plant populations reach sizes that result in intrinsic regulation, the significance of this issue with PVAs is also unknown. It should be noted, however, that even for rare and threatened species, local densities may be high, and that even sparse populations in stressful environments can experience strong density effects (Rodenhouse et al. 1997, Dahlgren et al. 2014). In conclusion, we suggest that density dependence needs to be more carefully considered in models of plant population dynamics. By simultaneously investigating both external and internal drivers of populations, we can get a better basic understanding of plant population dynamics, as well as a better basis for predicting the effects of anthropogenic changes of the environment on biodiversity.

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