Do we need demographic data to forecast the state of plant populations?

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Summary

1 Rapid environmental change has generated growing interest in forecasts of future population trajectories. Traditional population models built with detailed demographic observations from one study site can address the impacts of environmental change at particular locations, but are difficult to scale up to the landscape and regional scales relevant to management decisions.

2 An alternative is to build models using population-level data which are much easier to collect than individual-level data over broad spatial scales. However, it is unknown whether models built using population-level data adequately capture the effects of density-dependence and environmental forcing that are necessary to generate skillful forecasts.

3 Here, we test the consequences of aggregating individual responses when forecasting the

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population states and trajectories of four perennial grass species in a semi-arid grassland in Montana, USA. We parameterized two population models for each species, one based on individual-level data (survival, growth and recruitment) and one on population-level data (percent cover), and compared their forecasting skill and forecast horizons with and without the inclusion of climate covariates. For both models we used Bayesian ridge regression to weight the influence of climate covariates for optimal prediction.

4 In the absence of climate effects, we found no significant difference between the forecasting skill of models based on individual-level data and models based on population-level data. Climate effects were weak, but increased forecasting skill for two species. Increases in skill with climate covariates were similar between model types.

5 For our focal species at this particular location, and using our particular statistical models, percent cover models generated forecasts as skillful as those from a demographic model. We conclude that models based on aggregated individual-level data offer a practical alternative to data-intensive demographic models.

Key-words: forecasting, climate change, grassland, integral projection model, population model, statistical regularization, ridge regression

Introduction

Perhaps the greatest challenge for ecology in the 21st century is to forecast the impacts of environmental change (Clark et al. 2001, Petchey et al. 2015). Forecasts require sophisticated modeling approaches that fully account for uncertainty and variability in both ecological process and model parameters (Luo et al. 2011, but see Perretti et al. 2013). The increasing statistical sophistication of population models (Rees and Ellner 2009) makes them promising tools for predicting the impacts of environmental change on species persistence and abundance. But reconciling the scales at which population models are parameterized and the scales at which environmental

changes play out remains a challenge (Clark et al. 2010, 2012, Freckleton et al. 2011, Queenborough et al. 2011). Most population models are built using demographic data from a single study site because tracking the fates of individuals is so difficult. The resulting models cannot be applied to the landscape and regional scales relevant to decision-making without information about how the estimated parameters respond to spatial variation in biotic and abiotic drivers (Sæther et al. 2007). The limited spatial extent of individual-level demographic datasets constrains our ability to use population models to address applied questions about the consequences of climate change.

Aggregate measures of population status, rather than individual performance, offer an intriguing alternative for modeling populations (Clark and Bjørnstad 2004, Freckleton et al. 2011). Population-level data cannot provide inference about demographic mechanisms, but might be sufficient for modeling future population states, especially because such data are feasible to collect across broad spatial extents (e.g., Queenborough et al. 2011). The choice between individual and population-level data involves a difficult trade-off: while individual-level data are necessary for mechanistic models, population-level data enable models that can be applied over greater spatial and temporal extents. An open question is how much forecasting skill is lost when we build models based on population rather than individual-level data.

To date, most empirical population modelers have relied on individual-level data, with few attempts to capitalize on population-level measures. An important exception was an effort by Taylor and Hastings (2004) to model the population growth rate of an invasive species to identify the best strategies for invasion control. They used a "density-structured" model where the state variable is a discrete density state rather than a continuous density measure. Such models do not require individual-level demographic data and can adequately describe population dynamics. Building on Taylor and Hastings (2004), Freckleton et al. (2011) showed that density-structured models compare well to continuous models in theory, and Queenborough et al. (2011) provide empirical evidence that density-structured models are capable of reproducing population dynamics at landscape spatial scales, even if some precision is lost when compared to fully continuous

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models. However, previous tests of density-structured models have yet to assess their ability to forecast out-of-sample observations, and they have not included environmental covariates, which are necessary to forecast population responses to climate change.

Addressing climate change questions with models fit to population-level data is potentially problematic. Population growth (or decline) is the outcome of demographic processes such as survival, growth, and recruitment that occur at the level of individual plants. Climate can affect each demographic process in unique, potentially opposing, ways (Dalgleish et al. 2011). These unique climate responses may be difficult to resolve in statistical models based on population-level data where demographic processes are not identifiable. Futhermore, models based on aggregated data may reflect short-term effects of one vital rate more than others whose importance may only emerge over the long-term. For example, a one-year change in a plant species' cover or biomass might reflect individual growth or shrinkage, whereas the long-term trajectory of the population might be more influenced by recruitment. The same is true for density dependence: intraspecific density depedence may act most strongly on vital rates, like recruitment, that are difficult to identify from population-level data. If density dependence and/or important climate effects are missed because of the aggregation inherent in in population-level data, then population models built with such data will make uninformative or unreliable forecasts.

We compared the forecasting skill of statistical and population models based on aggregated, population-level data with the skill of models based on individual-level data. We used a demographic dataset that tracks the fates of individual plants from four species over 14 years to build two kinds of single-species population models, traditional models using individual growth, survival, and recruitment data and alternative models based on basal cover. We simulated the models to answer two questions motivated by the fact that the effects of intraspecific competition (density dependence) and interannual weather variability act at the level of the individual (Clark et al. 2011). First, can population models fit using aggregated individual-level data (percent cover) adequately capture density dependence to produce forecasts as skillful as those from models fit to demographic data? Second, can population models fit using aggregated data adequately capture

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the influence of climate on population growth and, in turn, produce forecasts as skillful as those from models fit to demographic data?

Materials and Methods

Study site and data

Our demographic data come from a northern mixed grass prairie at the Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana, USA ($46°$ 19' N, $105°$ 48' W). The dataset is available on Ecological Archives[1] (Anderson et al. 2011), and interested readers should refer to the metadata for a complete description. The site is 800 m above sea level and mean annual precipitation (1878-2009) is 334 mm, with most annual precipitation falling from April through September. The community is grass-dominated, and we focused on the four most abundant grass species: *Bouteloua gracilis* (BOGR), *Hesperostipa comata* (HECO), *Pascopyrum smithii* (PASM), and *Poa secunda* (POSE) (Fig. 1). *B. gracilis* is a warm-season perennial grass, whereas *H. comata*, *P. smithii*, and *Poa secunda* are cool-season perennial grasses. The growing season begins in early spring (typically in April) and lasts through mid-summer (typically in June).

From 1932 to 1945, individual plants were identified and mapped annually in 44 1-m^2 quadrats using a pantograph. The quadrats were distributed among six pastures, each assigned a grazing treatment of light (1.24 ha/animal unit month), moderate (0.92 ha/aum), and heavy (0.76 ha/aum) stocking rates (two pastures per treatment). In this analysis, we accounted for potential differences among the grazing treatments, but do not focus on grazing$\times$climate interactions. The annual maps of the quadrats were digitized and the fates of individual plants tracked and extracted using a computer program (Lauenroth and Adler 2008, Chu et al. 2014). The permanent quadrats have not been relocated, but their distribution in six different pastures means the data represent a broad spatial distribution for the study area. Daily climate data are available for the duration of

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[1]http://esapubs.org/archive/ecol/E092/143/

124 the data collection period (1932 - 1945) from the Miles City airport, Wiley Field, 9 km from the

125 study site.

126 We modeled each grass population based on two levels of data: individual and quadrat. The

127 individual data are the "raw" data. For the quadrat-level data we simply sum individual basal

128 cover for each quadrat by species. This is equivalent to a near-perfect census of quadrat percent

129 cover because measurement error at the individual-level is small (Chu and Adler 2014). Based on

130 these two datasets of 13 year-to-year transitions, we can compare population models built using

131 individual-level data and aggregated, quadrat-level data. At the individual level, we explicitly

132 model three vital rates: growth, survival, and recruitment. At the quadrat level, we model popula-

133 tion growth as change in percent cover of quadrats with non-zero cover in year *t* and in year *t-1*,

134 ignoring within-quadrat extirpation and colonization events because they are very rare in our time

135 series ($N = 16$ and $N = 13$, respectively, across all species). Sample sizes for each species and

136 vital rate model are shown in Table 1.

137 All R code and data necessary to reproduce our analysis is archived on GitHub as release v1.0[2]

138 (http://github.com/atredennick/MicroMesoForecast/releases). We have also deposited the v1.0

139 release on Dryad (*link here after acceptance*).

Stastical models of vital rates

141 At both levels of inference (individual and quadrat), the building blocks of our population models

142 are vital rate regressions. For individual-level data, we fit regressions for survival, growth, and

143 recruitment for each species. At the quadrat-level, we fit a single regression model for population

144 growth. We describe the statistical models separately because they required different approaches.

145 For both model types, we fit vital rate models with and without climate covariates. Models with

146 climate effects contain five climate covariates that we chose *a priori* based on previous model se-

147 lection efforts using these data (Chu et al. *in press*) and expert advice (Lance Vermeire, *personal*

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[2]*Note to reviewers*: so that v1.0 will be associated with the published version of the manuscript, we have re-
leased v0.2 to be associated with this review version.

$_{148}$ *communication*): "water year" precipitation at *t*-2 (lagppt); April through June precipitation at *t*-1

$_{149}$ and *t* (ppt1 and ppt2, respectively) and April through June temperature at *t*-1 and *t* (TmeanSpr1

$_{150}$ and TmeanSpr2, respectively), where *t*-1 to *t* is the transition of interest. We also include interac-

$_{151}$ tions among same-year climate covariates (e.g., ppt1 × TmeansSpr1), resulting in a total of seven

$_{152}$ climate covariates.

$_{153}$ We fit all models using a hierarchical Bayesian approach. We focus on the main process and the

$_{154}$ model likelihood in what follows (full model descriptions are in the Supporting Information). For

$_{155}$ the likelihood models, $\mathbf{y}^X$ is always the relevant vector of observations for vital rate X ($X = S$, G,

$_{156}$ R, or P) for survival, growth, recruitment, or population growth). For example, $\mathbf{y}^S$ is a vector of

$_{157}$ 0s and 1s indicating whether a genet survives from *t* to *t+1*, or not, for all observation years and

$_{158}$ quadrats. All model parameters are species-specific, but we omit subscripts for species in model

$_{159}$ descriptions below to reduce visual clutter. For brevity, we only describe models with climate

$_{160}$ covariates included, but models without climate covariates are simply the models described below

$_{161}$ with the climate effects removed.

$_{162}$ **Vital rate models at the individual level**   We used logistic regression to model the proba-

$_{163}$ bility that genet *i* in quadrat *q* survives from time *t* to *t+1* ($s_{i,q,t}$):

$$y_{i,q,t}^S \sim \text{Bernoulli}(s_{i,q,t}), \tag{1}$$

$$\text{logit}(s_{i,q,t}) = \beta_{0,t} + \beta_{s,t}x_{i,q,t} + \beta_Q + \mathbf{z}_t'\boldsymbol{\beta}_c + \beta_{d,1}w_{i,t} + \beta_{d,2}(x_{i,q,t}w_{i,q,t}), \tag{2}$$

$_{164}$
$_{165}$ where $x_{i,q,t}$ is the log of genet *i* basal area at time *t*, $\beta_{0,t}$ is a year specific intercept, β_Q is the

$_{166}$ random effect of quadrat group location, $\beta_{s,t}$ is the year-specific slope parameter for size, $\mathbf{z}$ is a

$_{167}$ vector of *p* climate covariates specific to year *t*, $\boldsymbol{\beta}_c$ is a vector of fixed climate effects of length

$_{168}$ *p*, $\beta_{d,1}$ is the effect of intraspecific crowding experienced by the focal genet at time *t* ($w_{i,q,t}$), and

$_{169}$ $\beta_{d,2}$ is a size by crowding ($x_{i,q,t}w_{i,q,t}$) interaction effect.

$_{170}$ We follow the approach of Chu and Adler (2015) to estimate crowding, assuming that the crowd-

$_{171}$ ing experienced by a focal genet depends on distance to each neighbor genet and the neighbor's

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size, u:

$$w_{i,q,t} = \sum_k e^{-\delta d_{ik,q,t}^2} u_{k,q,t}. \tag{3}$$

173 In the above, $w_{i,t}$ is the crowding that genet i in year t experiences from conspecific neighbors

174 in quadrat q. The spatial scale over which conspecific neighbors exert influence on any genet is

175 determined by δ. The function is applied for all k conspecific genets that neighbor the focal genet

176 at time t, and $d_{ik,q,t}$ is the distance between genet i and conspecific genet k in quadrat q. We use

177 regression-specific (survival and growth) δ values estimated by Chu and Adler (2015).

178 We modeled growth as a Gaussian process describing log genet size ($y_{i,q,t+1}^G$) at time $t+1$ in

179 quadrat q as a function of log size at time t and climate covariates:

$$y_{i,q,t+1}^G \sim \text{Normal}(\mu_{i,q,t+1}, \sigma_{x i,q,t+1}^2 \mathbf{I}), \tag{4}$$

$$\mu_{i,q,t+1} = \beta_{0,t} + \beta_{s,t} x_{i,q,t} + \beta_Q + \mathbf{z}_t' \boldsymbol{\beta}_c + \beta_{d,1} w_{i,q,t} + \beta_{d,2} (x_{i,q,t} w_{i,q,t}), \tag{5}$$

181
180 where $\mu_{i,q,t+1}$ is log of genet is predicted size at time $t + 1$, and all other parameters are as de-

182 scribed for the survival regression. We capture non-constant error variance in growth by mod-

183 eling the variance in the growth regression ($\sigma_{x i,q,t+1}^2$) as a nonlinear function of predicted genet

184 size:

$$\sigma_{x i,q,t+1}^2 = a \exp[b \times \mu_{i,q,t+1}], \tag{6}$$

186
185 where $\mu_{i,q,t+1}$ is log of predicted genet size predicted from the growth regression (Eq. 4), and a

187 and b are constants.

188 Our data allows us to track new recruits, but we cannot assign a specific parent to new genets.

189 Therefore, we model recruitment at the quadrat level. We assume the number of individuals,

190 $y_{q,t+1}^R$, recruiting at time $t + 1$ in quadrat q follows a negative binomial distribution:

$$y_{q,t+1}^R \sim \text{NegBin}(\lambda_{q,t+1}, \phi), \tag{7}$$

where λ is the mean intensity and ϕ is the size parameter. We define λ as a function of quadrat composition and climate in the previous year:

$$\lambda_{q,t+1} = \tilde{c}_{q,t} \exp\left(\beta_{0,t} + \beta_Q + \mathbf{z}'_t \boldsymbol{\beta}_c + \beta_d \sqrt{\tilde{c}_{q,t}}\right), \tag{8}$$

where $\tilde{c}_{q,t}$ is effective cover (cm^2) of the focal species in quadrat q at time t, and all other terms are as in the survival and growth regressions. Effective cover is a mixture of observed cover (c) in the focal quadrat (q) and the mean cover across the entire group ($\bar{c}$) of Q quadrats in which q is located:

$$\tilde{c}_{q,t} = pc_{q,t} + (1-p)\bar{c}_{Q,t}, \tag{9}$$

where p is a mixing fraction between 0 and 1 that is estimated when fitting model.

Population model at the quadrat level   The statistical approach used to model aggregated data depends on the type of data collected. We have percent cover data, which can easily be transformed to proportion data in our case because plant areas were scaled by plot area. An obvious choice for fitting a linear model to proportion data is beta regression because the support of the beta distribution is (0,1), which does not include true zeros or ones. However, when we used fitted model parameters from a beta regression in a quadrat-based population model, the simulated population tended toward 100% cover for all species. We therefore chose a modeling approach based on a truncated log-normal likelihood. The model for quadrat cover change from time t to $t+1$ is

$$y^P_{q,t+1} \sim \text{LogNormal}(\mu_{q,t+1}, \sigma^2)^1_0, \tag{10}$$

$$\mu_{q,t+1} = \beta_{0,t} + \beta_{s,t} x_{q,t} + \beta_Q + \mathbf{z}'_t \boldsymbol{\beta}_c, \tag{11}$$

where $\mu_{q,t+1}$ is the log of proportional cover in quadrat q at time $t+1$, and all other parameters are as in the individual-level growth model (Eq. 4) except that x now represents log of proportional cover. The log normal likelihood includes a truncation (subscript 0, superscript 1) to ensure that

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predicted values do not exceed 100% cover.

Model fitting and statistical regularization

Model fitting Our Bayesian approach to fitting the vital rate models required choosing appropriate priors for unknown parameters and deciding which, if any, of those priors should be hierarchical. For each species, we fit yearly size effects and yearly intercepts hierarchically, where year-specific coefficients were drawn from global distributions representing the mean size effect and intercept. Quadrat random effects were also fit hierarchically, with quadrat offsets being drawn from distributions with mean zero and a shared variance term (independent Gaussian priors). Climate effects were modeled as independent covariates whose prior distributions were optimized for prediction using statistical regularization (see **Statistical regularization: Bayesian ridge regression** below).

All of our analyses (model fitting and simulating) were conducted in R (R Core Team 2013). We used the 'No-U-Turn' Hamiltonian Monte Carlo sampler in Stan (Stan Development Team 2014a) to estimate the posterior distributions of model parameters using the package `rstan` (Stan Development Team 2014b). We obtained posterior distributions for all model parameters from three parallel MCMC chains run for 1,000 iterations after discarding an initial 1,000 iterations. Such short MCMC chains are possible because the Stan sampler reduces the number of iterations needed to achieve convergence. We assessed convergence visually and checked that scale reduction factors for all parameters were less than 1.1. There were six instances where the scale reduction factor for a particular parameter was greater than 1.1. In those cases, we checked the traceplots of the violating parameter and discovered that one chain, out of three, was poorly behaved. Therefore, we removed that chain from the analysis, leaving two well-mixed and converged chains for those six parameters. For the purposes of including parameter uncertainty in our population models, we retained the final 1,000 iterations from each of the three MCMC chains to be used as randomly drawn values during population simulation. We report the poste-

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239 rior mean, standard deviation, and 95% Bayesian Credible Intervals for every parameter of each
240 model for each species in the Supporting Information (Tables S5-S20).

241 **Statistical regularization: Bayesian ridge regression**   For models with climate covari-
242 ates, our objective is to model the response of our focal grass species to interannual variation in
243 climate, even if those responses are weak. Therefore, we avoid selecting among models with all
244 possible combinations of climate covariates, and instead use Bayesian ridge regression to regu-
245 late, or constrain, the posterior distributions of each climate covariate (Gerber et al. 2015, Hooten
246 and Hobbs 2015). Ridge regression is a specific application of statistical regularization that seeks
247 to optimize model generality by trading off bias and variance. As the name implies, statistical reg-
248 ularization involves the use of a regulator that constrains an optimization. The natural regulator in
249 a Bayesian application is the prior on the coefficient of interest. Each of our statistical models in-
250 cludes the effects of climate covariates via the term $\mathbf{z}'_t \boldsymbol{\beta}_c$ with prior $\boldsymbol{\beta}_c \sim \text{Normal}(\boldsymbol{\mu}_{\beta_c}, \sigma^2_{\beta_c} \mathbf{I})$. Be-
251 cause we standardized all climate covariates to have mean zero and variance one, we set $\boldsymbol{\mu}_{\beta_c} = 0$
252 and let $\sigma^2_{\beta_c}$ serve as the regulator that shrinks covariates toward zero – the smaller the prior vari-
253 ance, the more the posteriors of $\boldsymbol{\beta}_c$ are shrunk toward zero, and the stronger the penalty (Hooten
254 and Hobbs 2015).

255 To find the optimal penalty (i.e., optimal value of the hyperparameter $\sigma^2_{\beta_c}$), we fit each statistical
256 model with a range of values for $\sigma^2_{\beta_c}$ and compared predictive scores from leave-one-year-out
257 cross-validation. We performed the grid search over 24 values of $\sigma^2_{\beta_c}$, ranging from $\sigma^2_{\beta_c} = 0.01$
258 to $\sigma^2_{\beta_c} = 2.25$. For each statistical model and each species, we fit $13 \times 24 = 312$ iterations of
259 the model fitting algorithm to search $\sigma^2_{\beta_c}$ for the optimal value (13 years to leave out for cross-
260 validation and 24 values of $\sigma^2_{\beta_c}$) – a total of 4,992 model fits. We calculated the log pointwise
261 predictive density (*lppd*) to score each model's ability to predict the left-out data (Gelman et
262 al. 2014). Thus, for training data y_{train} and held-out data y_{hold} at a given value of σ^2_θ across all
263 MCMC samples $s = 1, 2, ..., S$ and all hold outs of data from year *t* to year *T*, and letting θ
264 represent all unknowns, *lppd* is

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$$\text{lppd}_{\text{CV}} = \sum_{t=1}^{T} \log_e \int [y_{t,hold}|\theta][\theta|y_{train}]d\theta, \tag{12}$$

and computed as

$$\sum_{t=1}^{T} \log_e \left(\frac{1}{S} \sum_{s=1}^{S} (y_{t,hold}|\theta_{ts}) \right). \tag{13}$$

We chose the optimal prior variance for each species-statistical model combination as the one that produced the highest *lppd* and then fit each species-statistical model combination using the full data set for each species and the optimal prior variance. We calculated the *lppd* from posterior samples using the algorithm from Vehtari et al. (2016).

Population models

Using samples from the posterior distribution of the vital rate statistical models, it is straightforward to simulate the population models. We used an Integral Projection Model (IPM) to simulate populations based on individual-level data (Ellner and Rees 2006) and a quadrat-based version of an individually-based model (Quadrat-Based Model, QBM) to simulate populations based on quadrat-level data. We describe each in turn.

Integral projection model   We use a stochastic IPM (Rees and Ellner 2009) to simulate our focal populations based on the vital rate regressions described above. In all simulations, we ignore the random year effects so that interannual variation is driven solely by climate. We fit the random year effects in the vital rate regressions to avoid over-attributing variation to climate covariates. Our IPM follows the specification of Chu and Adler (2015) where the population of species *j* is $n(u_j, t)$, giving the density of sized-*u* genets at time *t*. Genet size is on the natural log scale, so that $n(u_j, t)du$ is the number of genets whose area (on the arithmetic scale) is between e^{u_j} and $e^{u_j + du}$. The function for any size *v* at time $t + 1$ is

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$$n(v_j, t+1) = \int_{L_j}^{U_j} k_j(v_j, u_j, \bar{w}_j(u_j))n(u_j, t)du_j, \tag{14}$$

where $k_j(v_j, u_j, \bar{w}_j)$ is the population kernel that describes all possible transitions from size u to v and $\bar{w}_j$ is a scalar representing the average intraspecific crowding experienced by a genet of size u_j and species j. The integral is evaluated over all possible sizes between predefined lower (L) and upper (U) size limits that extend beyond the range of observed genet sizes.

The IPM is spatially-implicit, thus, we cannot calculate neighborhood crowding for specific genets (w_{ij}). Instead, we use an approximation ($\bar{w}_j$) that captures the essential features of neighborhood interactions (Adler et al. 2010). This approximation relies on a 'no-overlap' rule for conspecific genets to approximate the overdispersion of large genets in space (Adler et al. 2010).

The population kernel is defined as the joint contributions of survival (S), growth (G), and recruitment (R):

$$k_j(v_j, u_j, \bar{w}_j) = S_j(u_j, \bar{w}_j(u_j))G_j(v_j, u_j, \bar{w}_j(u_j)) + R_j(v_j, u_j, \bar{w}_j), \tag{15}$$

which means we are calculating growth (G) for individuals that survive (S) from time t to $t+1$ and adding in newly recruited (R) individuals of an average sized one-year-old genet for the focal species. Note the S, G, and R are incorporated in the IPM using the fitted vital rate regressions. Our statistical model for recruitment (R, described above) returns the number of new recruits produced per quadrat. Following previous work (Adler et al. 2012, Chu and Adler 2015), we assume that fecundity increases linearly with size ($R_j(v_j, u_j, \bar{w}_j) = e^{u_j}R_j(v_j, \bar{w}_j)$) to incorporate the recruitment function in the spatially-implicit IPM.

We used random draws from the final 1,000 iterations, thinned by 10, from each of three MCMC chains for each vital rate regression to carry-through parameter uncertainty into our population models. At each time step, we randomly selected climate covariates from one of the 14 observed years. Then, we drew the full parameter set (climate effects and density-dependence fixed effects)

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from a randomly selected MCMC iteration. Relatively unimportant climate covariates (those that broadly overlap 0) will have little effect on the mean of the simulation results, but can contribute to their variation. Our focus was on the contribution of density dependence and climate covariates to population states, thus we set the random year effects and the random group effects to zero.

Quad-based model To simulate our quad-based model (QBM), we iterate the quadrat-level statistical model (Eqs. 9-10). We use the same approach for drawing parameter values as described for the IPM. After drawing the appropriate parameter set, we calculate the mean response (log cover at *t+1* is μ_{t+1}) according to Eq. 10. We make a random draw from a [0,1] truncated lognormal distribution with mean equal to μ_{t+1} from Eq. 10 and the variance estimate from the fitted model. We project the model forward by drawing a new parameter set (unique to climate year and MCMC iteration) at each timestep. As with the IPM, random year effects are ommited in our simulations.

Model validation

To test each model's ability to forecast population states, we made out-of-sample predictions using leave-one-year-out cross validation. For both levels of modeling and for models with and without climate covariates, we fit the vital rate models using observations from all years except one, and then used those fitted parameters in the population models to perform a one-step-ahead forecast for the year whose observations were withheld from model fitting. Within each observation year, several quadrats were sampled. We made predictions for each observed quadrat in each focal year, initializing each simulation with cover in the quadrat the previous year. Because we were making quadrat-specific predictions, we incorporated the group random effect on the intercept for both models. We repeated this procedure for all 13 observation years, making 100 one-step-ahead forecasts for each quadrat-year combination with parameter uncertainty included via random draw from the MCMC chain as described above. Year-specific intercepts for left-out

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334 data were drawn from the posterior distribution of the mean intercept. Thus, for some future year

335 T, β_0, $T \sim \text{Normal}(\beta_0, \sigma_{\beta_0})$.

336 This cross-validation procedure allowed us to compare accuracy and precision of the two mod-

337 eling approaches (IPM versus QBM) with and without climate covariates. We first calculated

338 the median predicted cover across the 100 simulations for each quadrat-year and then calculated

339 forecast skill as the correlation (ρ) between forecasts and observations. We calculated forecast

340 error as mean absolute error (MAE) between forecasts and observations. We compared ρ and

341 MAE between model types and within model types between models with and without climate

342 covariates using one-sided t tests with adjusted degrees of freedom following Wilcox (2009) and

343 standard errors calculated using the HC4 estimator of Cribari-Neto (2004). Statistical tests were

344 conducted using algorithms from Ye et al. (2015).

Forecast horizons

346 An important feature of any forecasting model is the rate at which forecast skill declines as the

347 time between an observation and a forecast increases; the so-called ecological forecast horizon

348 (Petchey et al. 2015). To assess the forecast horizons of our models, we initiate the forecast

349 model with the population state at some time t and make sequential forecasts of the population

350 at times $t + 1, t + 2, \ldots, t + T$ where T is the maximum number of years between the initial

351 year and the final year of our observations. For example, if we initialize the forecast model with

352 percent cover in 1940, we are able to make five forecasts up to the year 1945. Forecast models

353 are not re-initialized with observations between years. Thus, in our current example, the model

354 forecast for percent cover in 1941 has a forecast horizon of one year, the forecast in 1942 has a

355 forecast horizon of two years, and so on. We performed these simulations for all model types

356 (IPM with/without climate; QBM with/without climate) using mean parameter values for all

357 possible initial years. For a given forecast horizon, we averaged the correlation between forecasts

358 and observations. Note that these forecasts are all made using in-sample data because we used

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model fits from the full data set. Nonetheless, these simulations offer insight into the differences among model forecast horizons.

Results

The IPM and QBM generated one-step-ahead forecasts of similar skill for out-of-sample observations, with an average correlation between predictions and observations (ρ) of 0.72 across all models and species (Fig. 2). Without climate covariates, the accuracy of forecasts from the IPM were not statistically greater than the accuracy of forecasts from the QBM (Fig. 2) and overall error was similar (mean absolute error; Fig. S1, Supporting Information). With climate covariates, the best out-of-sample predictive model (highest *lppd*) for each species and vital rate typically resulted from highly constrained priors on the climate effects (Fig. S2, Supporting Information). Thus, the posterior distributions of climate effects included in our models overlapped zero and generally shrunk toward zero, though for some species-vital rate combinations, important effects (80% credible interval does not include zero) did emerge (Fig. 3).

Despite the weak climate effects, including climate covariates did increase the accuracy of forecasts for two species: *B. gracilis* and *Poa secunda* (Fig. 2). Only for *B. gracilis* were the skill increases significant for the IPM ($t_{(279)} = 1.70$, $P = 0.045$) and the QBM ($t_{(279)} = 1.80$, $P = 0.037$). Similarly, forecast error decreased significantly with the inclusion of climate covariates for the *B. gracilis* IPM ($t_{(280)} = -3.72$, $P = 0.029$) and QBM ($t_{(280)} = -3.34$, $P < 0.0001$), and for the *Poa secunda* IPM ($t_{(196)} = -1.90$, $P < 0.0001$) and QBM ($t_{(196)} = -2.47$, $P = 0.007$) (Fig. S2, Supporting Information). IPM forecasts were significantly more accurate than the QBM in only one case (Fig. 2): forecast accuracy of *P. smithii* percent cover from an IPM with climate covariates was greater than the accuracy from the QBM with climate covariates ($t_{(215)} = 1.92$, $P = 0.028$). However, including climate covariates in the IPM did not significantly increase forecast skill for *P. smithii* (Fig. 2). Results from all pairwise statistical tests are shown in Table S21 of the Supporting Information.

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With climate covariates included, the accuracy of both models' forecasts declined as the forecast horizon increased, but they did so at similar rates (Fig. 4). The only exception is for *Poa secunda*, where QBM forecast accuracy remained steady as the forecast horizon increases, whereas IPM forecast accuracy declined (Fig. 4).

Discussion

Population models built using individual-level data provide inference on demographic processes, but they can only forecast future population states across the (typically limited) spatial extent of the observations. Population-level data are much easier to collect across broad spatial extents, so models built using such data offer an appealing alternative to traditional population models (Queenborough et al. 2011). However, density-structured models rely on the aggregation of individual-level data. Given that individuals, not populations, respond to intraspecific competition and weather (Clark et al. 2011), can models based on population-level metrics generate forecasts that are as skillful as those generated from models based on individual-level data? Are models based on population-level metrics as sensitive to climate forcing as models based on individual-level data?

Our comparison of a traditional, demographic population model without environmental forcing (the IPM) to an equivalent model inspired by density-structured models (the QBM) showed that, generally, IPM forecasts of out-of-sample plant population states were no more accurate than forecasts from the QBM (Fig. 2; 'no-climate' bars). We expected the IPM to out-perform the QBM because the IPM includes more mechanistic detail on the perennial plant life cycle, but this was not the case, at least when we ignored environmental forcing. Such a finding confirms theoretical (Freckleton et al. 2011) and empirical work (Taylor and Hastings 2004, Queenborough et al. 2011) showing that density-structured models can be useful surrogates for demographic models when the goal is to estimate or forecast population states over large spatial extents.

While the models did not differ in forecast accuracy when density-dependence was the only

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driver of population dynamics, we expected the inclusion of environmental forcing to reveal more differences between the models. We expected the IPM to outperform the QBM when we included climate covariates because interannual variation in weather can affect vital rates in different ways (Dalgleish et al. 2011). Thus, estimates of climate effects on plant population growth may be biased or non-identifiable when the underlying statistical model is fit using population-level data that integrates over the potentially unique climate responses of individual vital rates. However, we found that IPM forecast accuracy was only significantly higher than the QBM for one species, *P. smithii* (Fig. 2, 'climate' bars). That the IPM outperformed the QBM with climate covariates included for *P. smithii* is a moot point, however, because including the climate covariates in the IPM did not increase forecast accuracy over an IPM without climate covariates (Fig. 2).

Acknowledgments

Tables

Table 1: Description of data. The observations span 13 year-to-year transitions.

Species	Vital Rate Model	Num. Obs.	Num. Quadrats
B. gracilis	Growth	5670	29
	Survival	10102	33
	Recruitment	304	33
	Percent cover	281	29
H. comata	Growth	1990	16
	Survival	3257	18
	Recruitment	304	18
	Percent cover	171	17
P. smithii	Growth	8052	19
	Survival	11344	19
	Recruitment	304	19
	Percent cover	217	19
Poa secunda	Growth	3018	18
	Survival	4650	18
	Recruitment	304	18
	Percent cover	197	18

Figures

Figure 1: Time series of average percent cover over all quadrats for our four focal species: *Bouteloua gracilis* (BOGR), *Hesperostipa comata* (HECO), *Pascopyrum smithii* (PASM), and *Poa secunda* (POSE). Light grey lines show trajectories of individual quadrats. Note the different y-axis scales across panels.

Figure 2: Comparison of one-step-ahead, out-of-sample forecast accuracy between the IPM and QBM models with and without the inclusion of climate covariates. Comparisons between equivalent IPM and QBM models indicate no significant difference in accuracy ($P > 0.05$ for all comparisons). Including climate covariates resulted in siginifcantly higher forecast accuracy for only one species, *Poa secunda* ($P = 0.043$). Species codes are as in Fig. 1
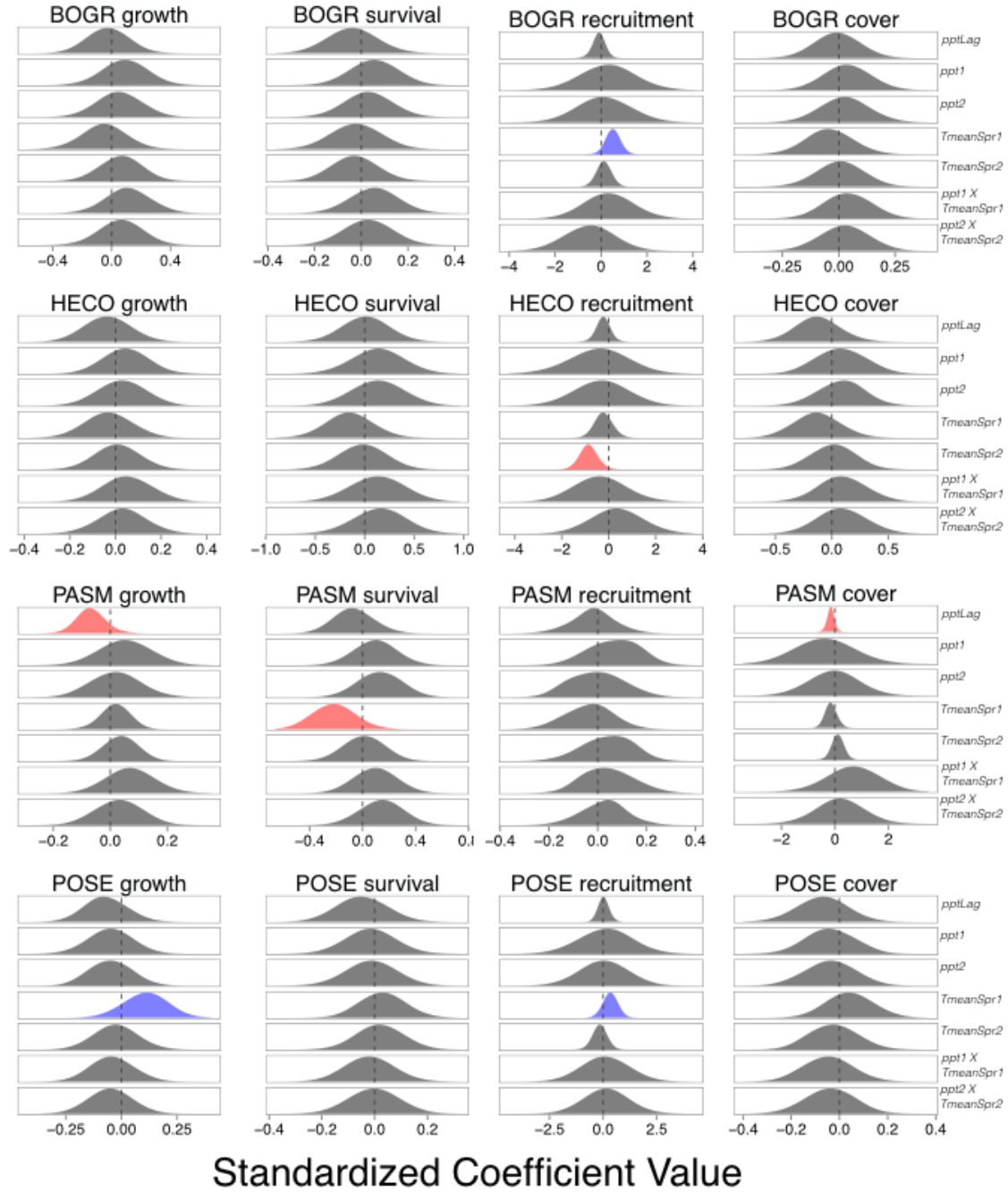
Figure 3: Posterior distributions of climate effects (β_C) for each species and vital rate statistical model. Because our priors were constrained via ridge-regression, we highlight climate effects whose 80% credible intervals do not overlap zero (red for negative coefficients, blue for positive coefficients). Kernel bandwidths of posterior densities were adjusted by a factor of 4 for visual clarity. Species codes are as in Fig. 1.
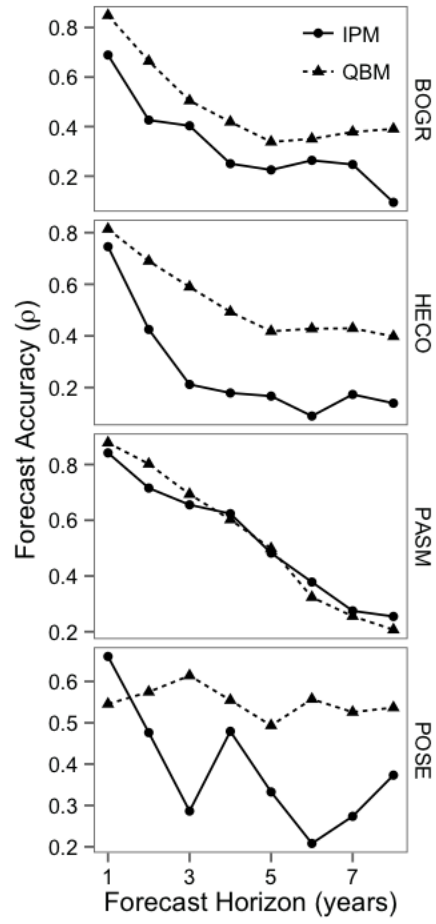
Figure 4: The forecast horizons for both models with climate covariates included. Points show the average accuracy (ρ) across all forecasts at a given time horizon. We only examine the forecast accuracy of models with climate covariates included because in no case did including climate covariates decrease accuracy (see Fig. 2). Species codes are as in Fig. 1.

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