Do we need demographic data to forecast population responses to climate change?

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Abstract

Rapid climate change has generated growing interest in forecasts of future population trajectories. Traditional population models, typically built using detailed demographic observations from one study site, can address climate change impacts at one location, but are difficult to scale up to the landscape and regional scales relevant to management decisions. An alternative is to build models using population-level data that is much easier to collect over broad spatial scales than individual-level data. However, such models ignore the fact that climate drives population growth through its influence on individual performance. Here, we test the consequences of aggregating individual responses when forecasting climate change impacts on four perennial grass species in a semi-arid grassland in Montana, USA. We parameterized two population models based on the same dataset, one based on individual-level data (survival, growth and recruitment) and one on population-level data (percent cover), and compared their accuracy, precision, and sensitivity to climate variables. The individual-level model was more accurate and precise than the aggregated model when predicting out-of-sample observations. When comparing climate effects from both models, the population-level model missed important climate effects from at least one vital rate for each species. Increasing the sample size at the population-level would not necessarily reduce forecast uncertainty; the way to reduce uncertainty is to capture unique climate dependence of individual vital rates. Our analysis indicates that there is no shortcut to forecasting climate

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change impacts on plant populations — detailed demographic data is essential. Despite the superiority of the individual-level model, the forecasts it generated still were too uncertain to be useful for decision-makers. We need new methods to collect demographic data efficiently across environmental gradients in space and time.

Key words: forecasting, climate change, grassland, integral projection model, population model

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 for an argument against modeling the ecological process). 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). The problem is that most population models are built using data from a single study site because collecting those data, which involves tracking the fates of individuals plants, is so difficult. The resulting models cannot be applied to the landscape and regional scales relevant to decision-making without information about how the fitted 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.

The inability of most population models to address landscape-scale problems may explain why land managers and conservation planners have embraced species distribution models (SDMs) (see Guisan and Thuiller 2005 for a review). SDMs typically rely on easy-to-collect presence/absence data (but see Clark et al. 2014 for new methods) and remotely-sensed environmental covariates that allow researchers to model large spatial extents (e.g., Maiorano et al. 2013). Thus, it is relatively straightforward to parameterize and project SDMs over landscapes and regions. However, the limitations of SDMs are well known (Pearson and Dawson 2003, Elith and Leathwick 2009, Araújo and Peterson 2012). Ideally, researchers would provide managers with landscape-scale population models, combining the extent of SDMs with information about dynamics and species abundances (Schurr et al. 2012, Merow et al. 2014).

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 since 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 leads to more mechanistic models, population-level data leads to 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 models. The appeal of density-structured approaches is clear. However, none of these models included environmental covariates.

Addressing climate change questions with models fit to population-level data is potentially problematic. It is individuals, not populations, that respond to climate variables (Clark et al. 2012). Ignoring this fact amounts to an "ecological fallacy", where inference about the individual relies on statistical inference on the group (Piantadosi et al. 1988). 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 opossing, 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. If 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.

Here, we compare the forecasting skill of statistical and population models based on aggregated, population-level data with models based on individual-level data. We used a unique 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. In both models, interannual variation is explained, in part, by climate covariates. We first quantify forecasting skill using cross-validation. We then performed simulations to quantify the sensitivities of species' cover to small perturbations in average precipitation and temperature. Based on the cross-validation results, predictions of individual level models were clearly better, but, unfortunately, still too uncertain to inform management decisions.

Materials and Methods

Study site and data

Our demographic data come from the Fort Keogh Livestock and Range Research Laboratory in eastern Montana's northern mixed prairie near Miles City, Montana, USA (46° 19' N, 105° 48' W). The dataset is freely available on Ecological Archives[2] (Anderson et al. 2011) , and interested readers should refer to the metadata for a complete description. The site is about 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).

From 1932 to 1945 individual plants were identified and mapped annually in 44 1-m^2 quadrats using a pantograph. The quadrats were distributed in 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 account for potential differences among the grazing treatments, but do not focus on grazing×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). Daily climate data are available for the duration of the data collection period (1932 - 1945) from the Miles City airport, Wiley Field, 9 km from the study site.

We modeled each grass population based on two levels of data: individual and quadrat (Fig. 2). The individual data is the "raw" data. For the quadrat-level we data we simply sum individual basal cover for each quadrat by species. This is equivalent to a near-perfect census of quadrat percent cover because previous analysis shows that measurement error at the individual-level is small (Chu and Adler 2014). Based on these two datasets we can compare population models built using individual-level data and aggregated, quadrat-level data.

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

All R code and data necessary to reproduce our analysis is archived on GitHub as release v1.0[3] (http://github.com/atredennick/MicroMesoForecast/releases). That stable release will remain static as a record of this analysis, but subsequent versions may appear if we update this work. We have also deposited the v1.0 release on Dryad (*link here after acceptance*).

Stastical models of vital rates

At both levels of inference (individual and quadrat), the building blocks of our population models are vital rate regressions. For individual-level data, we fit regressions for survival, growth, and recruitment for each species. At the quadrat-level, we fit a single regression model for population growth. We describe the statistical models separately since fitting the models required different approaches. All models contain five climate covariates that we chose *a priori*: "water year" precipitation at t-1 (lagppt); April through June precipitation at t-1 and t-2 (ppt1 and ppt2, respectively) and April through June temperature at t-1 and t-2 (TmeanSpr1 and TmeanSpr2, respectively), where t is the observation year. We also include interactions among same-year climate covariates (e.g., ppt1 × TmeansSpr1) and climate × size interactions. Climate × size interactions are for climate main effects only; we do not include interactions between size and pairs of interacting climate effects.

We fit all models using a hierarchical Bayesian approach. The models are fully descibed in Appendix A, so here we focus on the main process and the model likelihood. For the likelihood models, $\mathbf{y}^X$ is always the relevant vector of observations for vital rate X ($X = S, G, R, or P$ for survival, growth, recruitment, or population growth). For example, $\mathbf{y}^S$ is a vector of 0's and 1's indicating whether a genet survives from t to *t+1*, or not.

Vital rate models at the individual level We used logistic regression to model survival probability (S) of genet i from species j in quadrat group Q from time t to $t+1$:

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[3] *Note to reviewers*: so that v1.0 will be associated with the published version of the manuscript, we have released v0.1 to be associated with this review version.

$$\text{logit}(S_{ijQ,t}) = \gamma^S_{j,t} + \phi^S_{jQ} + \beta^S_{j,t} x_{ij,t} + \omega^S_j w_{ij,t} + \nu^S_j w_{ij,t} x_{ij,t} + \theta^S_{jk} C_{k,t} \tag{1}$$

$$y^S_{ijQ,t} \sim \text{Bernoulli}(S_{ijQ,t}) \tag{2}$$

where $x_{ij,t}$ is the log of genet size, $\gamma^S_{j,t}$ is a year-specific intercept, $\beta^S_{j,t}$ is the year-specific slope parameter for size, ϕ^S_{jQ} is the random effect of quadrat group location, and θ^S_k is the fixed parameter for the effect of the kth climate covariate at time t $(C_{k,t})$. Note that the vector of climate covariates $(\mathbf{C})$ includes climate variable interactions and climate×size interactions. We include density-dependence by estimating the effect of crowding on the focal individual by other individuals of the same species. ω is the effect of crowding and $w_{t,Q}$ is the crowding experienced by the focal individual at time t in quadrat group Q. We include a size×crowding interaction effect (ν^S).

We modeled growth as a Gaussian process describing genet size at time $t+1$ as a function of size at t and climate covariates:

$$x_{ijQ,t+1} = \gamma^G_{j,t} + \phi^G_{jQ} + \beta^G_{j,t} x_{ij,t} + \omega^G_j w_{ij,t} + \nu^S_j w_{ij,t} x_{ij,t} + \theta^G_{jk} C_{k,t} \tag{3}$$

$$y^G_{ijQ,t} \sim \text{Normal}(x_{ijQ,t+1}, \varepsilon_{ij,t}) \tag{4}$$

where x is log genet size and all other parameters are as described for the survival regression. We capture non-constant error variance in growth by modeling the variance around the growth regression (ε) as a nonlinear function of predicted genet size:

$$\varepsilon_{ij,t} = ae^{bx_{ijQ,t+1}} \tag{5}$$

Our data allows us to track new recruits, but we cannot assign a specific parent to new genets. THerefore, we model recruitment at the quadrat level: the number of new individuals of species j in quadrat q recruiting at time $t+1$ as a function of quadrat "effective cover" (A') in the previous year (t). Effective cover is a mixture of observed cover (A) in the focal quadrat (q) and the mean cover across the entire group ($\bar{A}$) of Q quadrats in which q is located:

$$A'_{jq,t} = p_j A_{jq,t} + (1 - p_j)\bar{A}_{jQ,t} \tag{6}$$

where p is a mixing fraction between 0 and 1 that is estimated within the model.

We assume the number of individuals, y^R, recruiting at time $t+1$ follows a negative binomial distribution:

$$y^R_{jq,t+1} \sim \text{NegBin}(\lambda_{jq,t+1}, \zeta) \tag{7}$$

where λ is the mean intensity and ζ is the size parameter. We define λ as:

$$\lambda_{jq,t+1} = A'_{jq,t} e^{(\gamma^R_{j,t} + \phi^R_{jQ} + \theta^R_{jk} C_{k,t} + \omega^R \sqrt{A'_{q,t}})} \tag{8}$$

where A' is effective cover (cm^2) of species j in quadrat q and all other terms are as in the survival and growth regressions.

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. We first considered fitting three vital rate models analagous to those we fit at the individual level: one for probability of extirpation within a quadrat (analagous to survival), one for cover change within a quadrat (analagous to growth), and one for probability of colonization within a quadrat (analagous to recruitment). However, within-quadrat extirpation and colonization events were rare in our time series ($N = 9$ and $N = 10$, respectively, across all species). Given the broad spatial distribution of the quadrats we are studying, it is safe to assume that these events are in fact rare enough to be ignored for our purposes. So we constrained our statistical modeling of vital rates at the population level to change in percent cover within quadrats. For the remaining discussion of statistical modeling, we refer to proportion data, which is simply percent cover divided by 100.

An obvious choice for fitting a linear model to proportion data is beta regression because the support of the beta distribution is [0,1], not including 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 more constrained modeling approach based on a truncated log-normal likelihood. The model for quadrat cover change from time t to $t+1$ is

$$x_{jq,t+1} = \gamma^P_{j,t} + \phi^P_{jQ} + \beta^P_{j,t} x_{jq,t} + \theta^P_{jk} C_{k,t} \tag{9}$$

$$y^P_{jq,t+1} \sim \text{LogNormal}(x_{jq,t+1}, \tau_j)\text{T}[0,1] \tag{10}$$

where $x_{jq,t}$ is the log of species' j proportional cover in quadrat q at time t and all other parameters are as in the individual-level growth model (Eq. 3). Again, note that the climate covariate vector ($\mathbf{C}$) includes the climate×cover interaction. The log normal likelihood includes a truncation (T[0,1]) to ensure that predicted values do not exceed 100% cover.

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. We decided to fit models where all terms were fit by species. Within a 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, Appendix A). Climate effects were not modeled hierarchically, and each was given a diffuse prior distribution. We used standard diffuse priors for all unknown parameters (Appendix A).

All of our analyses (model fitting and simulating) were conducted in R (R Core Development Team 2013). We used the 'No-U-Turn' MCMC 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 may surprise readers more familiar with other MCMC samplers (i.e. JAGS or WinBUGS), but the Stan sampler is exceptionally efficient, which reduces the number of iterations needed to achieve convergence. We assessed convergence visually and made sure scale reduction factors for all parameters were less than 1.01. For the purposes of including parameter uncertainty in our population models, we saved the final 1,000 iterations from each of the three MCMC chains to be used as randomly drawn values during population simulation. This step alleviates the need to reduce model parameters by model selection since sampling from the full parameter space in the MCMC ensures that if a parameter broadly overlaps zero, on average the effect in the population models will also be near zero. We report the posterior mean, standard deviation, and 95% Bayesian Credible Intervals for every parameter of each model for each species in Appendix B.

Population models

With the posterior distribution of the vital rate statistical models in hand, it is straightforward to simulate the population models. We used an Integral Projection Model (IPM) to model 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 model populations based on quadrat-level data. We describe each in turn.

Integral projection model We use a stochastic IPM (Rees and Ellner 2009) that includes the climate covariates from the vital rate statistical models. 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 a density function $n(u_j, t)$ 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 density function for any size v at time $t+1$ is

$$n(v_j, t+1) = \int_{L_j}^{U_j} k_j(v_j, u_j, \bar{w}_j(u_j))n(u_j, t) \tag{11}$$

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.

Since the IPM is spatially-implicit, 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):

$$k_j(v_j, u_j, \bar{w}_j) = S_j(u_j, \bar{w}_j(u_j))G_j(v_j, u_j, \bar{w}_j(u_j)) + R_j(v_j, u_j, \bar{w}_j), \tag{12}$$

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. Our stastical model for recruitment (R, described above) returns the number of new recruit 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 from each of three MCMC chains to introduce stochasticity 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) from a randomly selected MCMC iteration. Using this approach, rather than simply using coefficient point estimates, captures the effect of parameter uncertainty. 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. Since our focus was on the contribution of climate covariates to population states, we set the random year effects and the random group effects to zero.

Quad-based model To simulate our quad-based model (QBM), we simply 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 (population cover at *t+1* $= x_{t+1}$) according to Eq. 9. We then make a random draw from a [0,1] truncated lognormal distribution with mean equal to x_{t+1} from Eq. 9 and the variance estimate from the fitted model. We can then 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 ignored for all simulations.

Model validation

To test each model's ability to forecast population state, we made out-of-sample predictions using leave-one-year-out cross validation. For both levels of modeling, 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 the focal year, initializing each simulation with cover in the quadrat the previous year. Since 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. Random year effects were set to zero since year effects cannot be assigned to unobserved years.

This cross-validation procedure allowed us to compare accuracy and precision of the two modeling approaches (IPM versus QBM). We first calculated the median predicted cover across the 100 simulations for each quadrat-year and then calculated the absolute error as the absolute value of the difference between the observed cover for a given quadrat-year and the median prediction. To arrive at mean absolute error (MAE), we then averaged the absolute error within each species across the quadrat-year specific errors. We use MAE as our measure of accuracy. To measure precision we calculated the distance between the upper and lower 90th quantiles of the 100 predictions and averaged this value over quadrat-years for each species.

Testing sensitivity to climate covariates

With our fitted and validated models in hand, we ran simulations for each model type (IPM and QBM) under four climate perturbation scenarios: (1) observed climate, (2) precipitation increased by 1%, (3) temperature increased by 1%, and (4) precipitation and temperature increased by 1%. We ran the simulations for 2,500 time steps, enough to estimate equilibrium cover after discarding an initial 500 time steps as burn-in. Each simulation was run under two parameter scenarios: (1) using mean parameter estimates and (2) using randomly drawn parameters from the MCMC chain. We use (1) to detect the overall sensitivity of equilibrium cover to climate, and we use (2) to show the impact of model and parameter uncertainty on forecast precision.

As an effort to identify potential discrepencies between IPM and QBM forecasts, we also ran simulations designed to quantify the sensitivities of individual and combined vital rates to climate for the IPM. Specifically, we ran simulations for the above climate scenarios, but applied the perturbed climate covariates to survival, growth, or recruitment vital rates individually and in pairwise combinations. This allowed us to isolate the vital rate(s) most sensitive to climate. For this analysis, we used mean parameter estimates to reduce the sources of uncertainty in the sensitivity estimates.

We expected the IPM to produce more accurate and precise forecasts due to either (1) the smaller sample size of the quadrat level data sets compared to the individual level data sets, leading to larger parameter uncertainty for the QBM, or (2) the QBM climate effects being weakly associated with one or more vital rate climate effects at the individual level. To assess the impact of sample size on QBM parameter uncertainty we refit the QBM statistical model (Eqs. 9-10) after removing sets of 2, 5, 10, and 15 quadrats. We fit 10 models at each level of quadrat removal (2, 5, 10, 15 quadrats), removing a different randomly selected set of quadrats for each fit. We calculated the standard deviation of climate main effects (pptLag, ppt1, ppt2, TmeanSpr1, and TmeanSpr2) for each model and averaged those over replicates within each set of quadrat removals. This allowed us to regress parameter uncertainty against sample size.

To deterime if the QBM climate effects are correlated with climate effects for each vital rate model in the IPM, we simply regressed the QBM climate coefficients against each vital rate model's climate coefficients and calculated Pearson's ρ. Strong correlations indicate the QBM is capable of detecting climate effects associated with individual vital rates. A weak correlation indicates the QBM "misses" the climate effect on a particular vital rate.

Results

Comparison of forecast models

The IPM had lower overall error (MAE, mean absolute error) compared to the QBM for three species (Table 1). The IPM MAE is significantly lower at $\alpha = 0.05$ for *B. gracilis* ($P = 0.0012$), *H. comata* ($P = 4.0586 \times 10\text{-}8$), and *P. smithii* ($P = 3.183 \times 10\text{-}5$). MAEs are statistically similar between models for *P. secunda* ($P = 0.0922$). P values are highly sensitive to sample size, so not entirely appropriate in simulation exercises where we control the samples size. But, for our purposes they serve as relatively unbiased comparison metrics. In no case did the QBM significantly outperform the IPM (Table 1). The IPM was consistently more precise than the QBM, with lower distances between the 90% quantiles across all species (Table 1). In general the IPM outperformed the QBM because it had (1) lower MAE for three of the four species, (2) statistically similar MAE for the one other species, and (3) considerably more precise forecasts for all species.

Sensitivity of models to climate

The response of a population to climate change is a result of the aggregate effects of climate on individual vital rates. Since the IPM approach relies on vital rate regressions, we were able to quantify the sensitivity of each vital rate in isolation and in pairwise combinations. Across all species, climate covariates can have opposing effects on different vital rates (Fig. 3). Growth was the most sensitive vital rate for all species, showing a negative response to increased precipitation, and stronger positive response to increased temperature, and a mostly positive response when both climate factors are increased (Fig. 3). *B. gracilis* survival rates were sensitive to temperature, resulting in an increase in plant cover under increased temperature (Fig. 3a). In isolation, recruitment and survival were insensitive to climate factors for *H. comata* (Fig. 3b). Survival and recruitment of *P. smithii* were both sensitive, negatively, to temperature and precipitation (Fig. 3c). *P. secunda* equilibrium cover was sensitive to the climate effects on survival and recruitment, showing a negative effect on both vital rates for increased precipition, but a strong positive effect on survival with increased temperature (Fig. 3d). Equilibrium cover responded negatively when increased precipitation and temperature affect recruitment (Fig. 3d). At least two of three vital rates were sensitive to climate for each species (Fig. 3).

Sources of uncertainty in the QBM

Sample size had a relatively weak effect on QBM climate parameter uncertainty after the number of quadrats used in fitting exceeded about 10 (Fig. 5). Inverse-gaussian fits show that increasing sample size beyond the number of quadrats we used would result in diminishing returns in terms of parameter certainty (Fig. 5).

Climate effects estimated from the QBM are most correlated with climate effects from the growth regression at the individual level (Fig. 6). In no case does the QBM statistical model have strong correlations across all three vital rates (Fig. 6). QBM climate effects were most weakly correlated with those from individual-level recruitment models for *B. gracilis*, *H. comata*, and *P. secunda* (Fig. 6a,b,d). For *P. smithii*, QBM climate effects showed no correlation with the survival model effects (Fig. 6c).

Model forecasts

Forecasts based on 1% climate changes were extremely uncertain when we considered model error and parameter uncertainty (Fig. 6; simulations with mean parameters are in Appendix D for comparison). As expected based on model validation (Table 1), QBM projections were more uncertain than IPM projections for all species except *P. smithiii* (Fig. 6). IPM forecasts for *P. smithiii* were very uncertain due to a very high instrinsic rate of recruitment combined with uncertainty in climate coefficients which lead to high recruitment boom years and subsequent busts when young plants suffer high mortality (Appendx C). When we included model error and parameter uncertainty, forecast changes in proportional cover always spanned a wide range of negative to positive values. In other words, neither model could predict whether a climate perturbation would increase or decrease equilibrium population size.

Discussion

Population models built using individual-level data allow 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. This creates a potential problem if such models are to be used in a climate change context because it is individuals, not populations, which respond to climate (Clark et al. 2012). Are models based on population-level metrics as sensitive to climate as models based on individual-level metrics? Do these two types of models produce consistent forecasts? Do we need detailed demographic data to forecast the impacts of climate change?

The importance of demographic data

Our comparison of a traditional, demographic population model (the IPM) with a model inspired by density-structured models (the QBM) showed that the IPM outperformed the QBM: the IPM was more accurate and precise than the QBM in out-of-sample cross validation (Table 1). The superiority of the IPM could reflect either differences in sample size or the effect of averaging over unique effects of climate on each individual-level vital rate. Although increasing sample size of quadrat percent-cover observations would be easy to do in the field, we found little evidence that it would lead to higher precision of climate coefficient estimates (Fig. 4).

We did, however, find evidence that the QBM statistical model failed to identify climate dependence for some vital rates (Fig. 5). For no species were climate effects from the QBM strongly correlated with all three vital rates (Fig. 5). Freckleton et al. (2011) acknowledge that averaging over complex stage dependence will lead to poorly specified models. This is analagous to our situation, but instead of averaging over complex life histories, we are averaging over complex climate dependence. Though our work here focused on plant species, this finding is applicable to any species with vital rates that respond uniquely to weather/climate.

Our interpretation is that the QBM is "missing" climate signals associated with at least one vital rate for each species. This leads to inaccurate and imprecise forecasts because the QBM statistical model struggles to explain variation due to climate variables that have positive and negative impacts on different vital rates. When this is the case, as it is for all our species to varying degrees (Fig. 3), forecasts from models based on population-level data will fail. Our result is consistent with related work on the importance of individual-level data to forecast population responses to exogenous drivers (Clark et al. 2011a, 2011b, 2012, Galván et al. 2014).

Detailed demographic data appears to be necessary to forecast climate change impacts on plant populations when vital rates have unique climate responses. How then can we build models to make forecasts for the landscape and regional scales beyond the scope of traditional population models (Queenborough et al. 2011)? There are alternatives to density-structured models. For example, Clark et al. (2011a) use Forest Inventory and Analysis (FIA) data to parameterize a population model with multiple vital rates and climate dependence. Distributed efforts such as PlantPopNet (http://plantago.plantpopnet.com) will allow researchers to estimate variation around climate responses for widespread species by taking advantage of spatial variation in climate (e.g. Doak and Morris 2010). Finally, new approaches on the horizon that leverage photo/video of plots and advanced object recognition algorithms (e.g. Liu et al. 2014) will increase the efficiency of plant mapping and digitizing efforts.

The challenge of uncertainty

An important, but unexpected, result of our analysis was the great uncertainty in forecasts, even for our best model. The typical approach in ecology is to use point estimates of model parameters to project populations forward according to the specified model, usually allowing for some variability around the determinstic process (e.g. Battin et al. 2007, Jenouvrier et al. 2009, Adler et al. 2012). If we follow tradition and calculate the mean response to climate perturbation with only model error and interannual variation included, the IPM and the QBM produce opposing forecasts for three of four species (Fig. D1). It would be tempting to interpret this inconsistency as further evidence for the superiority of the IPM. However, if we introduce parameter uncertainty, the forecasts are actually indistinguishable (Fig. 6), though the IPM projections are generally more precise (consistent with our cross-validation results). The real story is that both models produce highly uncertain forecasts. For all species, the 90% quantiles of predicted changes in population size overlapped zero; we cannot even predict whether a change in precipitation or temperature will cause populations to increase or decrease. This result held when we tried perturbing climate by 10% and 20% as well.

Our results highlight the state of affairs in ecology when it comes to forecasting the impacts of climate change. The analysis we conducted here could be considered at the forefront of ecological forecasting with respect to the statistical approach employed (hierarchical Bayesian), the type of population model we used (density-dependent, stochastic IPM with parameter uncertainty), and the amount of high quality data we had at our disposal (14 years of individual-level data). Yet, model predictions proved so uncertain that any forecast, when bounded with model and parameter uncertainty, would be uninformative.

How might we improve on this state of affairs? First, forecasts could be improved by matching the spatial scale of predictor variables with the spatial scale of observations. One of the major limitations of the models we fit here is that the climate data are collected at a larger scale than the individual-level observations of plant size. Climate covariates only vary by year, with no spatial variability within years. Thus, even if we fit models to individual-level data, we are missing the key interaction point between weather and individual plants (Clark et al. 2011b) because all observations share the same climate covariates. Demographic studies should be designed with at least plot-level measurements of climate related variables (e.g., soil moisture). Second, accurately detecting climate signals will take even longer time series. Recent theoretical work on detecting climate signals in noisy data suggests that even advanced approaches to parameter fitting require 20-25 year time series (Teller et al. n.d.). Third, ecologists need a stronger commitment to reporting uncertainty. Although most modeling studies explicitly consider model uncertainty, parameter uncertainty is often ignored. In some cases this is because the most convenient statistical methods make it difficult to propogate parameter uncertainty. Yet even Bayesian approaches that allow integration of model fitting and forecasting (Hobbs and Hooten 2015) are not simple when using modeling approaches like integral projection models that separate the model fitting and simulation stages (Rees and Ellner 2009). However, as we have done here, it is still possible to include parameter uncertainty by drawing parameter values from MCMC iterations, taking care to draw all parameters from the same chain and iteration to account for their correlations. Only by being honest about our forecasts can we begin to produce better ones, and forecasts reported without parameter error are disingenuous. Ignoring parameter error may be justifiable when the goal is investigating basic processes, but it is indefensible when forecasting is the goal.

Conclusions

This work is not a critique of density-structured population models. We are confident that density-structured models will prove to be a valuable tool for many applications. However, our analysis represents the first comparison, to our knowledge, of population models based on individual and aggregated forms of the same data in a climate change context. Our results confirm theoretical arguments (Clark et al. 2011b) and empirical evidence (Clark et al. 2011a, 2012) that individual responses are critical for predicting species' responses to climate change. It seems there is no short cut to producing accurate and precise population forecasts: we need detailed demographic data to forecast the impacts of climate change on populations. Given the importance of demographic data and its current collection cost, we need modern methods to collect demographic data more efficiently across environmental gradients in space and time.

Our results also offer a cautionary tale because forecast uncertainty was large for both model types. Even with 14 years of detailed demographic data and sophisticated modeling techniques, our projections contained too much uncertainty to be informative. Uncertainty in demographic responses to climate can be reduced by collecting (1) longer time series and (2) climate covariates that match the scale of inference (e.g., plot rather than landscape level climate/weather metrics).

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Tables

Table 1: Accuracy (mean absolute error, MAE) and precision (90% Distance) of out of sample predictions. Forecasts were made without random year effects; only climate covariates could explain year-to-year variation. 90% Distance refers to the average distance between the upper and lower 90th percentiles of the 100 predicted values for each quadrat-year combination.

Species	Model	MAE	90% Distance	Mean Obs. Cover
BOGR	IPM	12.18	38.52	9.43
BOGR	QBM	19.66	56.50	9.26
HECO	IPM	1.22	6.47	1.15
HECO	QBM	12.35	41.11	1.18
PASM	IPM	0.19	1.65	0.42
PASM	QBM	0.55	7.78	0.42
POSE	IPM	1.37	7.64	1.25
POSE	QBM	1.79	40.59	1.27

Figures

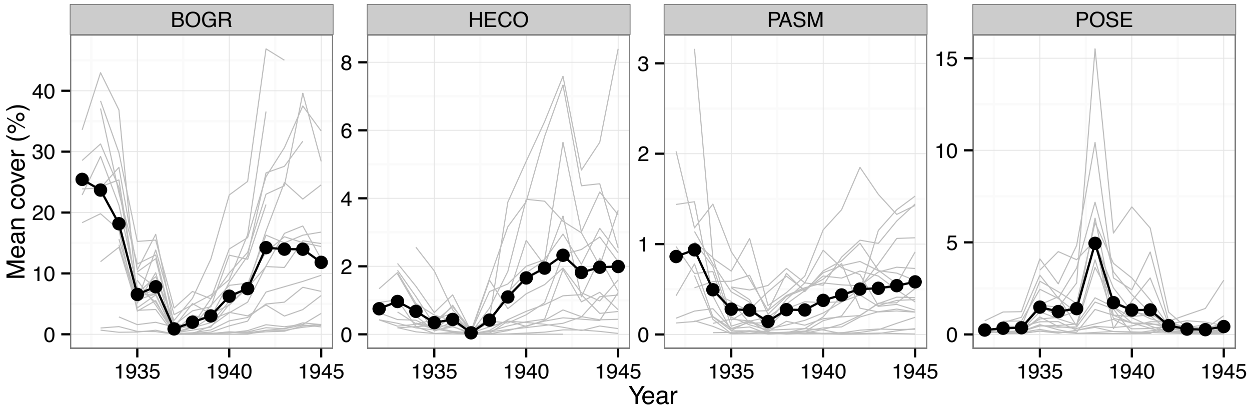

Figure 1: Time series of average percent cover over all quadrats for our four focal species: *Bouteloua gracilis* (BOGR), *Hesperostipa comata* (HECO), *Pascopyrum smithii* (PASM), and *Poa secunda* (POSE). Light grey lines show trajectories of individual quadrats. Note the different y-axis scales across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

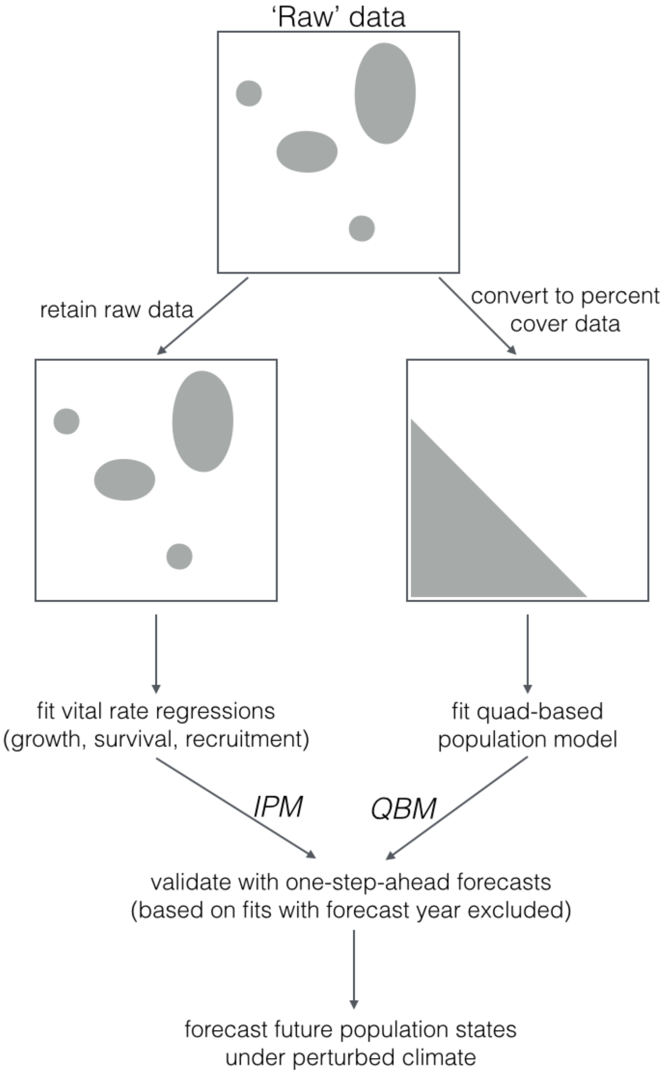

Figure 2: Work flow of the data aggregation, model fitting, and population simulating.

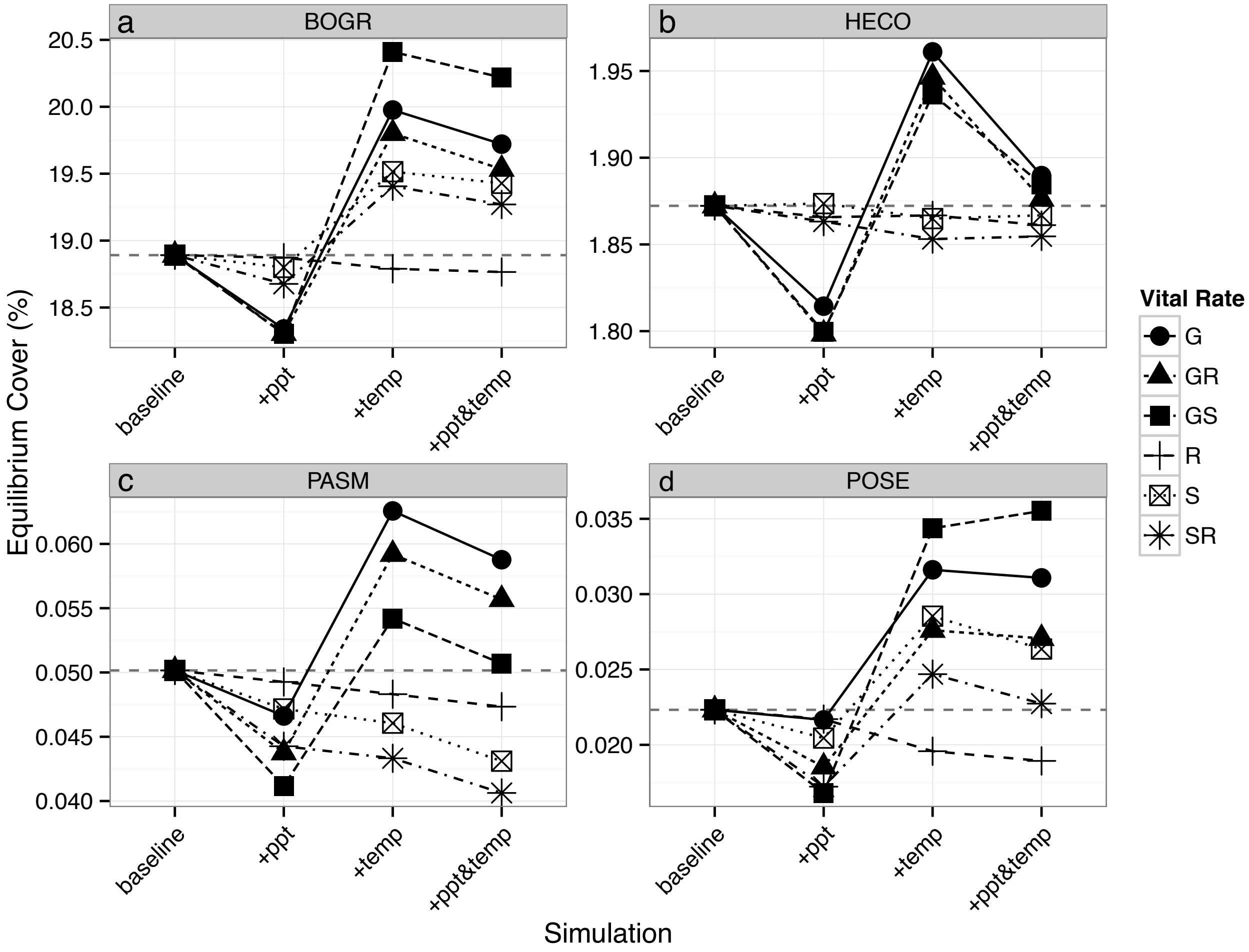

Figure 3: Sensitivity of equilibrium cover simulated from the IPM to each climate scenario applied to individual and combined vital rates. For example, the points associated with G show the median cover from IPM simulations where a climate perturbation is applied only to the growth regression climate covariates. These simulations use mean parameter values for clarity.

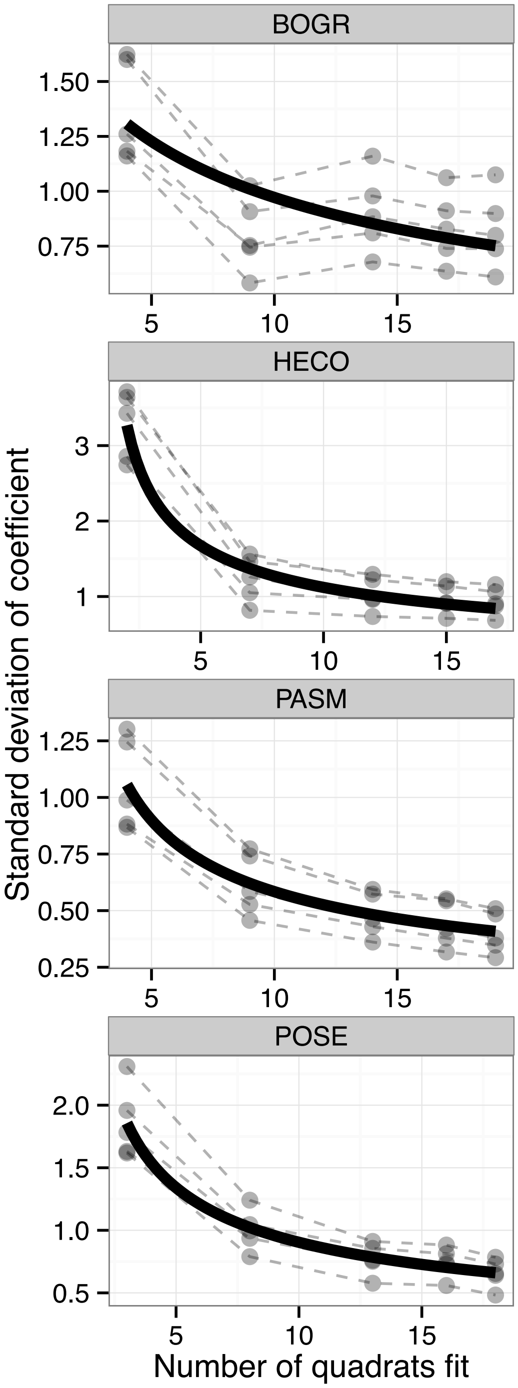

Figure 4: Effect of quadrat sample size on the precision (standard deviation) of main climate effect estimates in the QBM. Increasing the number of quadrats results in diminishing returns in terms of parameter certainty. Light dashed lines show individual climate effects at five quadrat sample sizes. Thick dark lines are inverse gaussian fits showing the mean effect of increasing quadrat sample size on parameter precision.

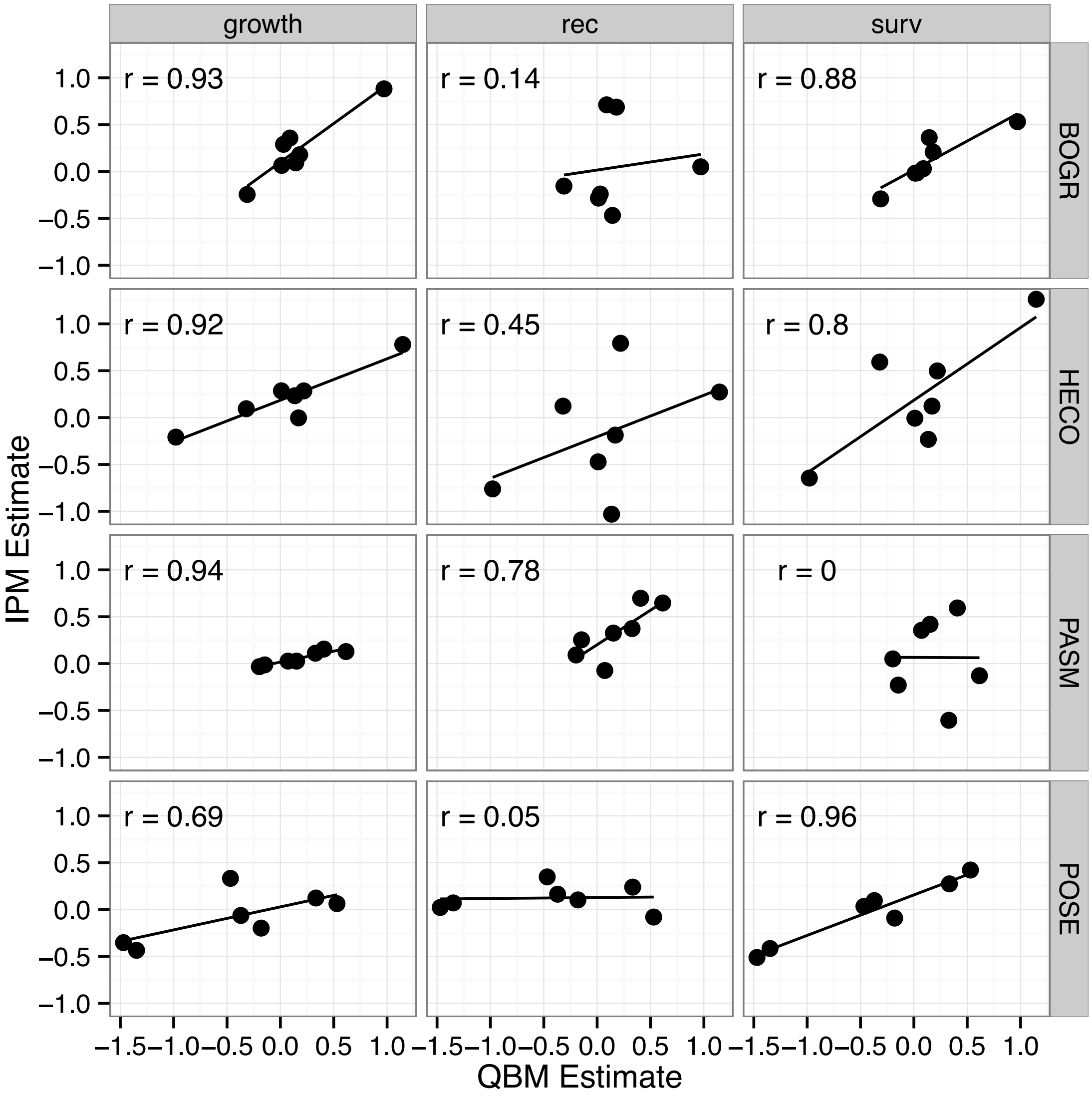

Figure 5: Correlations (r) between QBM and IPM estimates of climate effects. We ignore sizeXclimate interactions since these are not directly comparable across model types. The QBM does not have multiple vital rates, so its values are repeated across panels within each species. Across top panels, 'growth' = growth regression, 'rec' = recruitment regression, 'surv' = survival regression.

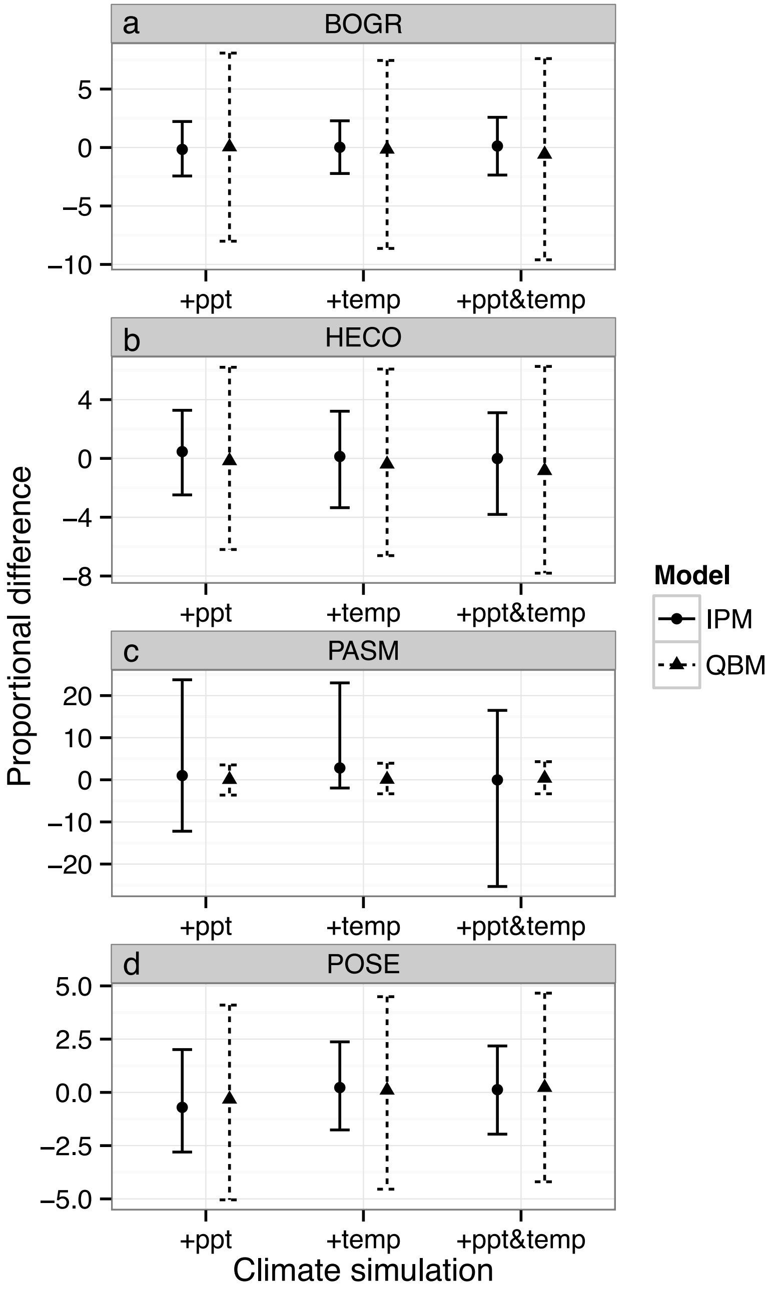

Figure 6: Mean (points) and 90% quantiles (errorbars) for the proportional difference between baseline simulations (using observed climate) and the climate pertubation simulation on the x-axis. We calculated proportional difference as log(perturbed climate cover) - log(observed climate cover), where ‘perturbed’ and ‘observed’ refer to the climate time series used to drive interannual variation in the simulations. Model error and parameter uncertainty were propagated through the simulation phase. Climate simulations are as in Figure 3.

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