Do we need detailed demographic data to forecast the impacts of climate change on plant populations?

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Abstract

Forecasting future states of populations has taken on new urgency as the rate of climate change increases. Traditional plant population models have limited utility in this regard because they are based on detailed demographic data from small, localized plots. These models are difficult to scale up to spatial scales relevant to land managers that require such forecasts to make decisions. To overcome the data limitations of traditional population models, some have proposed population models based on population level, rather than individual level, data that is much easier to collect over broad spatial scales. Using such models violates a central assumption of ecology: individuals respond to weather, not populations to climate. Here, we test whether this assumption is important when forecasting climate change impacts on four perennial grass species in a semi-arid Montana grassland. We parameterized two population models, one based on inidividual-level data with three vital rates and one on population-level data from the same dataset (percent cover of quadrats), and compared their accuracy, precision, and sensitivity to climate. The individual level model was more accurate and precise than the aggregate level model when predicting out-of-sample observations. When comparing climate effects from both models, the population-level model tends to "miss" important climate effects from at least one vital rate for each species. We also find that increasing the sample size at the population-level would not necessarily reduce forecast certainty; meaning the only way to reduce uncertainty is to capture unique climate dependence

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on individual vital rates. It appears there is no short cut to forecasting climate change impacts on plant populations — detailed demographic data is essential. However, forecasts from our individual-level model were very uncertain, so we advocate for a focus on new methods to collect demographic data more 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). To do so requires sophisticated modeling approaches that fully account for uncertainty and variability in the ecological process and associated parameters (Luo et al. 2011). This requires large amounts of data collected over large spatio-temporal extents. State-of-the-science modeling techniques cannot overcome data limitations. Such is the case for many population models.

Population models are important 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 major hurdle 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-makers 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 many 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, the scales at which many land-use decisions are made. 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, combing the extent of SDMs with information about dynamics and species abundances.

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 it might be sufficient for modeling future population states, especially since it is 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 exploit population-level data. 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) demonstrated the application of such methods in a study on arable weeds. In particular, Queenborough et al. (2011) provide empirical evidence that density-structured models are capable of reproducing population dynamics, even if some precision is lost when compared to fully continuous models. The study by Queenborough et al. (2011) included data from 500 fields (4 hectares each) in 49 farms, all collected by two people in 6 weeks. This is far more data from a far greater spatial extent than possible if measuring individual plant demography (in a world of limited time and money, at least). 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 puts us in uneasy proximity 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 an epiphenomenon of demographic processes like 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 difficult resolve in statistical models based on population-level data where demographic processes are not identifiable. If population-level data cannot detect important impacts of climate drivers on populations, then population models built with such data will make poor forecasts.

Here, we ask whether statistical and population models based on aggregated, population-level data can detect climate signals as wells as 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 then performed simulations to quantify the sensitivities of species' cover to small perturbations in

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average precipitation and temperature. We found that population models based on detailed demographic data are more accurate and precise than models based on aggregated data. Our results suggest the popuation-level model is less accurate and precise because important demographic climate signals go undetected. For these species at this location, detailed demographic data appears necessary to make accurate forecasts. A worrying caveat to our work is that forecasts from both models were very uncertain when we considered full process and parameter uncertainty. Even 14 years worth of demographic data may not be sufficient to make useful forecasts.

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

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

and extracted using a computer program (Lauenroth and Adler 2008, Chu et al. 2014). Daily climate data, which we aggregated into climate variables of interest, 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.

In this paper, we model populations 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.

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 models 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 ×

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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.

size interactions. Climate $\times$ size interactions are for climate main effects only, that is we do not include interactions among size and 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 0s and 1s 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 $t + 1$:

$$\text{logit}(S_{ijQ,t}) = \gamma_{j,t}^S + \phi_{jQ}^S + \beta_{j,t}^S x_{ij,t} + \omega_j^S w_{ij,t} + \nu_j^S w_{ij,t} x_{ij,t} + \theta_{jk}^S C_{k,t} \tag{1}$$

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

where $x_{ij,t}$ is the log of genet size, $\gamma_{j,t}^S$ is a year-specific intercept, $\beta_{j,t}^S$ is the year-specific slope parameter for size, ϕ_{jQ}^S is the random effect of quadrat group location, and θ_k^S 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$\times$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$\times$crowding interaction effect (ν^S).

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

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$$x_{ijQ,t+1} = \gamma_{j,t}^G + \phi_{jQ}^G + \beta_{j,t}^G x_{ij,t} + \omega_j^G w_{ij,t} + \nu_j^S w_{ij,t} x_{ij,t} + \theta_{jk}^G C_{k,t} \tag{3}$$

$$y_{ijQ,t}^G \sim \text{Normal}(x_{ijQ,t+1}, \sigma_j) \tag{4}$$

170   where x is log genet size and all other parameters are as described for the survival regression.

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

172   So, for recruitment, we work at the quadrat level and model the number of new individuals of

173   species j in quadrat q recruiting at time $t+1$ as a function of quadrat "effective cover" (A') in

174   the previous year (t). Effective cover is a mixture of observed cover (A) in the focal quadrat

175   (q) and the mean cover across the entire group $(\bar{A})$ of Q quadrats in which q is located:

$$A'_{jq,t} = p_j A_{jq,t} + (1 - p_j)\bar{A}_{jQ,t} \tag{5}$$

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

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

178   distribution:

$$y_{jq,t+1}^R \sim \text{NegBin}(\lambda_{jq,t+1}, \zeta) \tag{6}$$

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

$$\lambda_{jq,t+1} = A'_{jq,t} e^{(\gamma_{j,t}^R + \phi_{jQ}^R + \theta_{jk}^R C_{k,t} + \omega^R \sqrt{A'_{q,t}})} \tag{7}$$

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

181   survival and growth regressions.

₁₈₂ **Population model at the quadrat level**   The statistical approach used to model vital

₁₈₃ rates using aggregated data depends on the type of data collected. In our case, and as is

₁₈₄ often the case with census data, we have percent cover data (which can easily be transformed

₁₈₅ to proportion data). We first considered fitting three vital rate models analagous to those

₁₈₆ we fit at the individual level: one for probability of extirpation within a quadrat (analagous

₁₈₇ to survival), one for cover change within a quadrat (analagous to growth), and one for

₁₈₈ probability of colonization within a quadrat (analagous to recruitment). However, within-

₁₈₉ quadrat extirpation and colonization events were rare in our time series ($N = 9$ and $N = 10$,

₁₉₀ respectively, across all species). Given the broad spatial distribution of the quadrats we are

₁₉₁ studying, it is safe to assume that these events are in fact rare enough to be ignored for our

₁₉₂ purposes. So we constrained our statistical modeling of vital rates at the population level to

₁₉₃ change in percent cover within quadrats. For the remaining discussion of statistical modeling

₁₉₄ we refer to proportion data, which is simply percent data divided by 100.

₁₉₅ An obvious choice for fitting a linear model to proportion data is beta regression because the

₁₉₆ support of the beta distribution is [0,1], not including true zeros or ones. However, when we

₁₉₇ used fitted model parameters from a beta regression in a quadrat-based population model,

₁₉₈ the simulated population tended toward 100% cover for all species. We therefore chose a

₁₉₉ more constrained modeling approach based on a truncated log-normal likelihood. The model

₂₀₀ for quadrat cover change (G) from time t to $t + 1$ is

$$x_{jq,t+1} = \gamma_{j,t}^P + \phi_{jQ}^P + \beta_{j,t}^P x_{jq,t} + \theta_{jk}^P C_{k,t} \tag{8}$$

$$y_{jq,t+1}^P \sim \text{LogNormal}(x_{jq,t+1}, \tau j)\text{T}[0,1] \tag{9}$$

₂₀₁ where $x_{jq,t}$ is the log of species' j proportional cover in quadrat q at time t and all other

₂₀₂ parameters are as in the individual-level growth model (Eq. 3). Again, note that the climate

₂₀₃ covariate vector ($\mathbf{C}$) includes the climate×cover interaction. The log normal likelihood

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₂₀₄ includes a truncation (T[0,1]) to ensure that predicted values do not exceed 100% cover.

Model fitting

₂₀₆ Our Bayesian approach to fitting the vital rate models required choosing appropriate priors
₂₀₇ for unknown parameters and deciding which, if any, of those priors should be hierarchical. We
₂₀₈ decided to fit models where all terms were fit by species. Within a species, we fit yearly size
₂₀₉ effects and yearly intercepts hierarchically where year-specific coefficients were drawn from
₂₁₀ global distributions representing the mean size effect and intercept. We used uninformative
₂₁₁ priors (Appendix A).

₂₁₂ All of our analyses (model fitting and simulating) were conducted in R (R Core Development
₂₁₃ Team 2013). We used the 'No-U-Turn' MCMC sampler in Stan (Stan Development Team
₂₁₄ 2014a) to estimate the posterior distributions of model parameters using the package 'rstan'
₂₁₅ (Stan Development Team 2014b). We obtained posterior distributions for all model parameters
₂₁₆ from three parallel MCMC chains run for 1,000 iterations after discarding an initial 1,000
₂₁₇ iterations. We recignize such short MCMC chains may surprise those more familiar with
₂₁₈ other MCMC samplers (i.e. JAGS or WinBUGS), but the Stan sampler is exceptionally
₂₁₉ efficient, which reduces the number of iterations needed to achieve convergence. We assessed
₂₂₀ convergence visually and made sure scale reduction factors for all parameters were less than
₂₂₁ 1.01. For the purposes of including parameter uncertainty in our population models, we
₂₂₂ saved the final 1,000 iterations from each of the three MCMC chains to be used as randomly
₂₂₃ drawn values during population simulation. This step alleviates the need to reduce model
₂₂₄ parameters by model selection since sampling from the full parameter space in the MCMC
₂₂₅ ensures that if a parameter broadly overlaps zero, on average the effect in the population
₂₂₆ models will also be near zero. We report the posterior mean, standard deviation, and 95%
₂₂₇ Bayesian Credible Intervals for every parameter of each model for each species in Appendix
₂₂₈ 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 [cite Ellner and Rees 2006] and an 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 an environmentally stochastic IPM (Rees and Ellner 2009) that includes the random year effects and the climate covariates from the vital rate statistical models. However, for some simulations, we ignore the random year effects so that only the climate effects drive interannual variation. 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 $e^{u_j + du}$. So, the density function for any size v at time $t + 1$ is

$$n(v_j, t+1) = \int_{L_j}^{U_j} k_j(v_j, u_j, \bar{\mathbf{w}}_{\mathbf{j}}(u_j)) n(u_j, t) \tag{10}$$

where $k_j(v_j, u_j, \bar{\mathbf{w}}_{\mathbf{j}})$ is the population kernel that describes all possible transitions from size u to v and $\bar{\mathbf{w}}_{\mathbf{j}}$ is a vector of estimates of average crowding experienced from all other species 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 population kernel is defined as the joint contributions of survival (S), growth (G), and recruitment (R):

$$k_j(v_j, u_j, \bar{\mathbf{w}}_\mathbf{j}) = S_j(u_j, \bar{\mathbf{w}}_\mathbf{j}(u_j))G_j(v_j, u_j, \bar{\mathbf{w}}_\mathbf{j}(u_j)) + R_j(v_j, u_j, \bar{\mathbf{w}}_\mathbf{j}), \quad (11)$$

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 ($R_j(v_j, u_j, \bar{\mathbf{w}}_\mathbf{j}) = e^{u_j}R_j(v_j, \bar{\mathbf{w}}_\mathbf{j})$) to incorporate the recruitment function in the spatially-implicit IPM.

Add spatial structure mention.

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, ensures that relatively unimportant climate covariates (those that broadly overlap 0) have little effect on the simulation results. 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 Our quad-based model (QBM) perfectly mirrors its statistical description (Eqs. 8-9). 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. 8. We then make a random draw from a [0,1] truncated lognormal distribution with mean equal to x_{t+1} from Eq. 8 and the variance estimate from the fitted model. We can then iterate the model forward by drawing a new parameter set (unique to climate year and MCMC iteration) at each timestep.

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. So 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 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 model validation 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

Our main goal in this paper is to see if models based on aggregated data are as sensitive to climate covariates as models based on individual level data. So, 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.

Our expectation is that the IPM will produce more accurate and precise forecasts. This could be due to differences in sample sizes leading to larger parameter uncertainty for the QBM, or due to 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. 8-9) 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 sample size against parameter uncertainty.

To see if the QBM climate effects are correlated, or not, with climate effects for each vital

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322 rate model for the IPM, we simply regressed the QBM climate coefficients against each vital

323 rate model's climate coefficients and calculate Pearson's ρ. Strong correlations indicate the

324 QBM is capable of detecting climate effects associated with individual vital rates. A weak

325 correlation indicates the QBM "misses" the climate effect on a particular vital rate.

Results

Comparison of forecast models

328 The IPM had significantly lower overall error (MAE, mean absolute error) for three species (*B.*

329 *gracilis*, *H. comata*, *P. smithii*; Table 1). In no case did the QBM significantly outperform the

330 IPM (Table 1). The IPM was consistently more precise than the QBM, with lower distances

331 between the 90% quantiles across all species (Table 1). In general the IPM outperformed

332 the QBM because it had (1) lower MAE for three of the four species, (2) statistically similar

333 MAE for the one other species, and (3) considerably more precise forecasts for all species.

Sensitivity of models to climate

335 The response of a population to climate change is a result of the aggregate effects of climate

336 on individual vital rates. Since the IPM approach relies on vital rate regressions, we were

337 able to quantify the sensitivity of each vital rate in isolation and in pairwise combinations.

338 Across all species, climate covariates can have opposing effects on different vital rates (Fig.

339 3). Growth was the most sensitive vital rate for all species, showing a negative response

340 to increased precipitation, and stronger positive response to increased temperature, and a

341 mostly positive response when both climate factors are increased (Fig. 3). *B. gracilis* survival

342 rates were sensitive to temperature, resulting in an increase in plant cover under increased

343 temperature (Fig. 3a). In isolation, recruitment and survival were insensitive to climate

344 factors for *H. comata* (Fig. 3b). Survival and recruitment of *P. smithii* were both sensitive,

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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 precipation, but a strong positive effect on survival with increased temperature (Fig. 3d). The climate impact of recruitment on equilibrium cover was negative for precipitation and temperature increases (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 exceeded about 10 (Fig. 5). Inverse-gaussian fits show that increasing sample size beyond the number of quadrats we used will results in deminishing 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). 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. smithii* were very uncertain due to overcompensating density dependence and nonlinearities recruitment that get amplified by parameter uncertainty (Appendx C). Neither model was capable of making forecasts of proportional cover change

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distinguishable from 0 (i.e., no change in population state) when we included model error and parameter uncertainty.

Discussion

Population models built using individual-level data allow inference on demographic processes, but their ability to forecast future population states is limited by the spatial extent of the data. Population-level data, like percent cover or discrete density states, are much easier to collect of broad spatial extents, so populations built using such data offer an appealing alternative to traditional population models (Queenborough et al. 2011). However, at their core, density-structured models rely on individual level data aggregated to a population level metric. This creates a potential problem if such models are to be used in a climate change context because inidividuals respond to climate, not populations (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? These are the questions we sought to answer here.

Using individual-level and population-level forms of the same dataset, we were able to directly compare a traditional demographic modeling approach to a population model based on percent cover data. Our quad-based model (QBM) is based on percent cover data and so is in the spirit of density-structured models. In terms of each model's forecasting ability, the IPM outperformed the QBM: the IPM was more accurate and precise than the QBM (Table 1). As we suggest in the introduction, this could be due to differences in sample size or the effect of averaging over climate responses unique to individual-level vital rates.

We found no evidence that increasing sample size at the quadrat level 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 analogous to our situation, but instead of averaging over complex life histories, we are averaging over complex climate dependence.

Thus, for each species the QBM is "missing" climate signals associated with at least one vital rate. 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), statistical models of population-level data will fail. This result further confirms 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).

These results lead us to conclude that detailed demographic data is necessary to forecast climate change impacts on plant populations when vital rates have unique climate responses. This is unwelcome news since this data is difficult to collect and the models built on such data are of little use to land managers that make decisions at scales beyond that of traditional population models (Queenborough et al. 2011). While density-structured approaches may fail when climate covariates are considered, there are other alternatives. 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. Another example are distributed efforts like PlantPopNet (http://plantago.plantpopnet.com) that 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). Lastly, we foresee new approaches on the horizon that leverage photo/video of plots and advanced object recognition algorithms (e.g. Liu et al. 2014) to streamline plant mapping and digitizing efforts.

What does all this mean for model forecasts? The answer is more nuanced than one might expect. The typical approach in ecology is to use point estimates of model parameters to

420 project populations forward according to the specified model; usually allowing for some

421 variability around the determinstic process (e.g., Battin et al. (2007); Jenouvrier et al. (2009);

422 Adler et al. (2012)). If we follow tradition and calculate the mean response to climate change

423 over many iterations of the model with only model error and temporal variation included, the

424 IPM and the QBM produce opposing forecasts for three of four species (Fig. D1). However,

425 if we introduce parameter uncertainty, the forecasts are actually indistinguishable (Fig. 6).

426 IPM forecasts are generally more precise, as expected from model validation (Table 1). The

427 real story is not that the QBM produces "wrong" forecasts, but that it produces highly

428 uncertain forecasts. Our sample size analysis reveals that this uncertainty is not easily

429 overcome by including more data (Fig. 4). The only way to reduce uncertainty is to model

430 these populations based on individual-level data where climate dependence can be properly

431 identified (Fig. 5). Yet, even the IPM forecasts were highly variable (Fig. 6).

432 Our goal was not to make any explicit forecast for the future state of these populations based

433 on predicted climate change. But our results highlight the state of affairs in ecology when it

434 comes to forecasting the impacts of climate change. The analysis we conducted here could be

435 considered, with some exceptions of course, at the forefront of ecological forecasting in terms

436 of the statistical approach employed (hierarchical Bayesian), the type of population model

437 we used (stochastic IPM with parameter uncertainty), and the amount of high quality data

438 we had at our disposal (14 years of individual level data). Yet, model predictions proved so

439 uncertain that any forecast, when bounded with model and parameter uncertainty, would be

440 at best not useful and at worst meaningless. For all species, the 90% quantiles of predicted

441 changes in population size overlapped zero; we cannot even predict whether a change in

442 precipitation or temperature will cause populations to increase or decrease. How might we

443 improve on this state of affairs?

444 First, forecasts could be improved by matching the spatial scale of predictor variables with

445 the spatial scale of observations. One of the major limitations of the models we fit here is

446 that the climate data are at a much larger scale than the individual level observations of

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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 like LASSO, functional linear models (splines), and Random Forest models require 20-25 year time series (Teller et al., in review). Alternatively, as we suggest above, Teller et al. (in review) also find that matching the scale of the response and predictors improves estimate precision.

Third, ecologists as a community need to get serious about reporting uncertainty. There is a strong culture around explicitly considering model uncertainty, but parameter uncertainty is often ignored. In some cases this is because the easiest statistical methods do no make propogating parameter uncertainty a straighforward task. 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. In many cases, ignoring parameter error is justifiable when investigating basic demographic mechanisms, but it is never justifiable if forecasts are being made.

Conclusions

This work is not a critique of density-structured population models. In some cases and for certain species where climate dependence is weak or concentrated within a single vital rate, population models based on aggregated data may prove useful and unbiased. However, our work here is 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 to predicting species' responses to climate change. Thus, forecasts from population-level models should be viewed with caution and should never be unaccompianed by uncertainty. Given the importance of demographic data and its current difficulty to collect, we advocate for research on modern methods to collect demographic data more efficiently across environmental gradients in space and time.

Our results also offer a cautionary tale because uncertainty around forecasts was large for both model types. Which leads us to our most pessimistic conclusion: even with 14 years of detailed demographic data and sophisticated modeling techniques we failed to produce forecasts with any level of acceptable uncertainty. In our view, uncertainty of climate change related forecasts can be reduced by (1) longer time series and (2) climate covariates that match the scale of inference (e.g., plot rather than landscape level climate/weather metrics). Still, given the poor performance of the quad-based model, it seems there is no short cut to producing accurate and precise population forecasts. Do we need detailed demographic data to forecast the impacts of climate change on populations? Probably.

Acknowledgments

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

NOTES: 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 statisticially 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.

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.

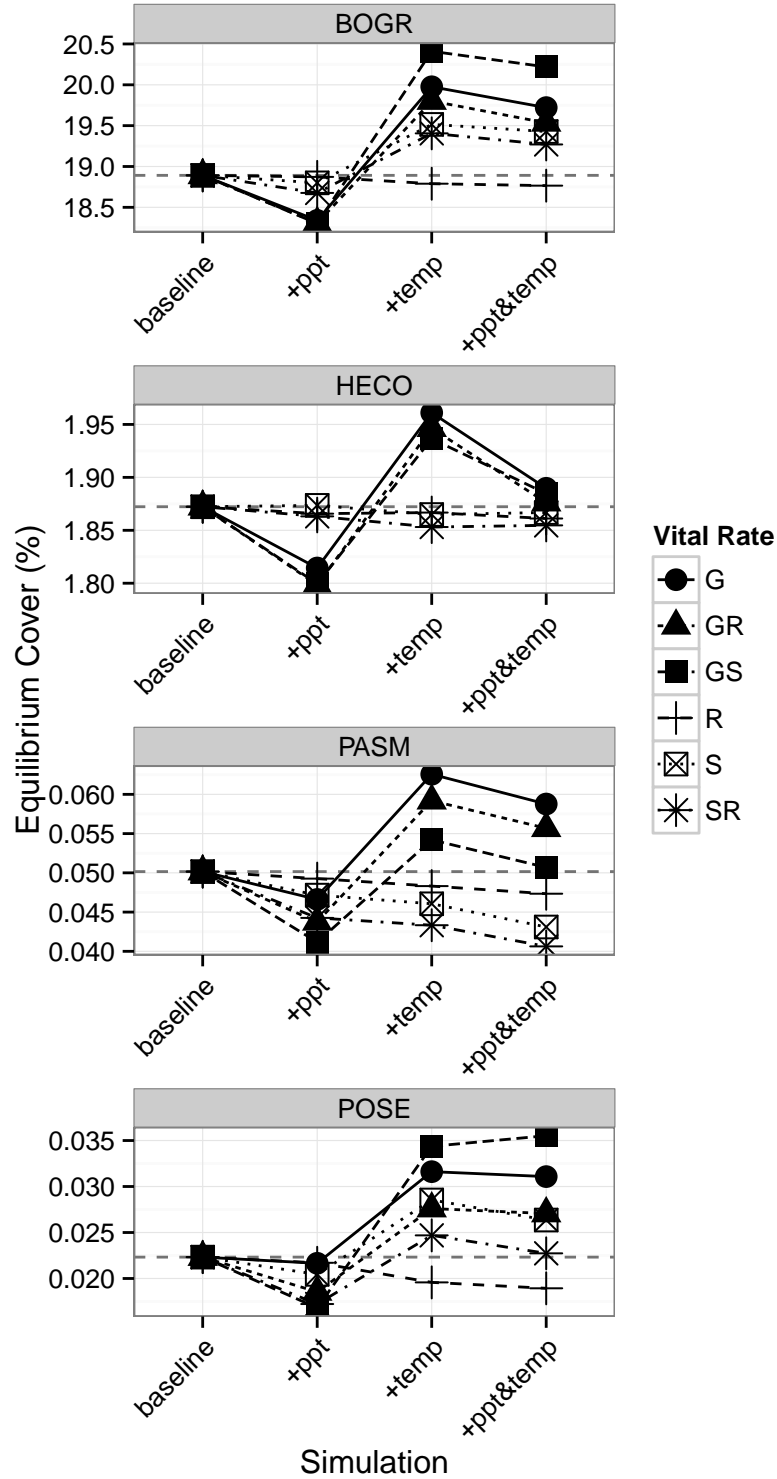Figure 2: Work flow of the data aggregation, model fitting, and population simulating.

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.
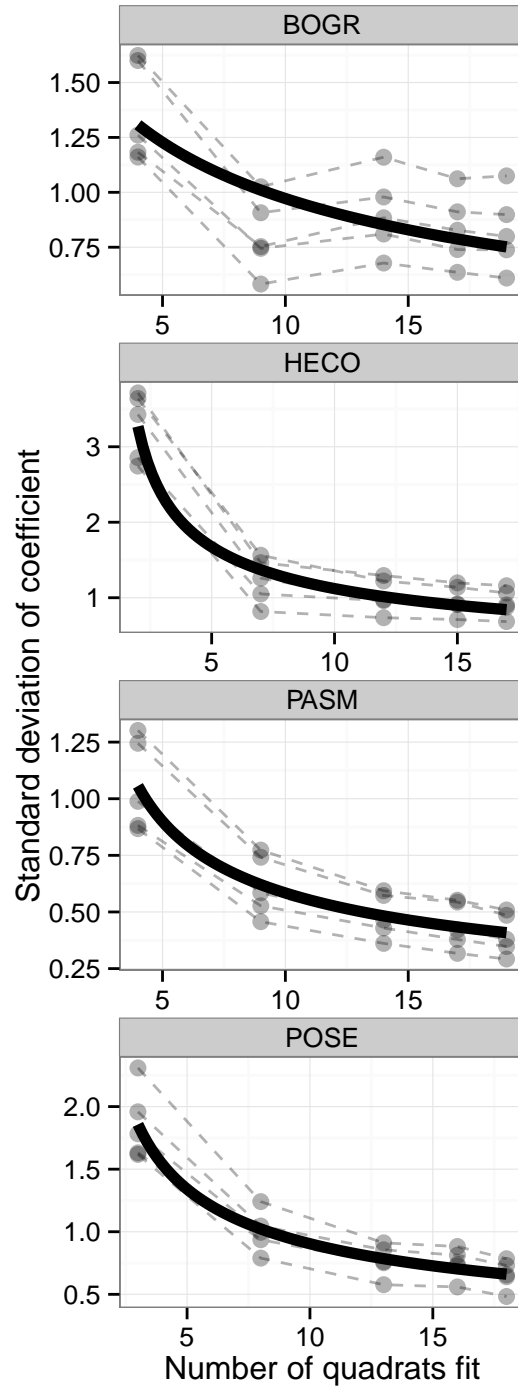
Figure 4: Effect of quadrat sample size on the precision (standard deviation) of main climate effect estimates in the QBM. Increasing the number of quadrats results in diminishing returns in terms of parameter certainty. Light dashed lines show individual climate effects at five quadrat sample sizes. Thick dark lines are inverse gaussian fits showing the mean effect of increasing quadrat sample size on parameter precision.
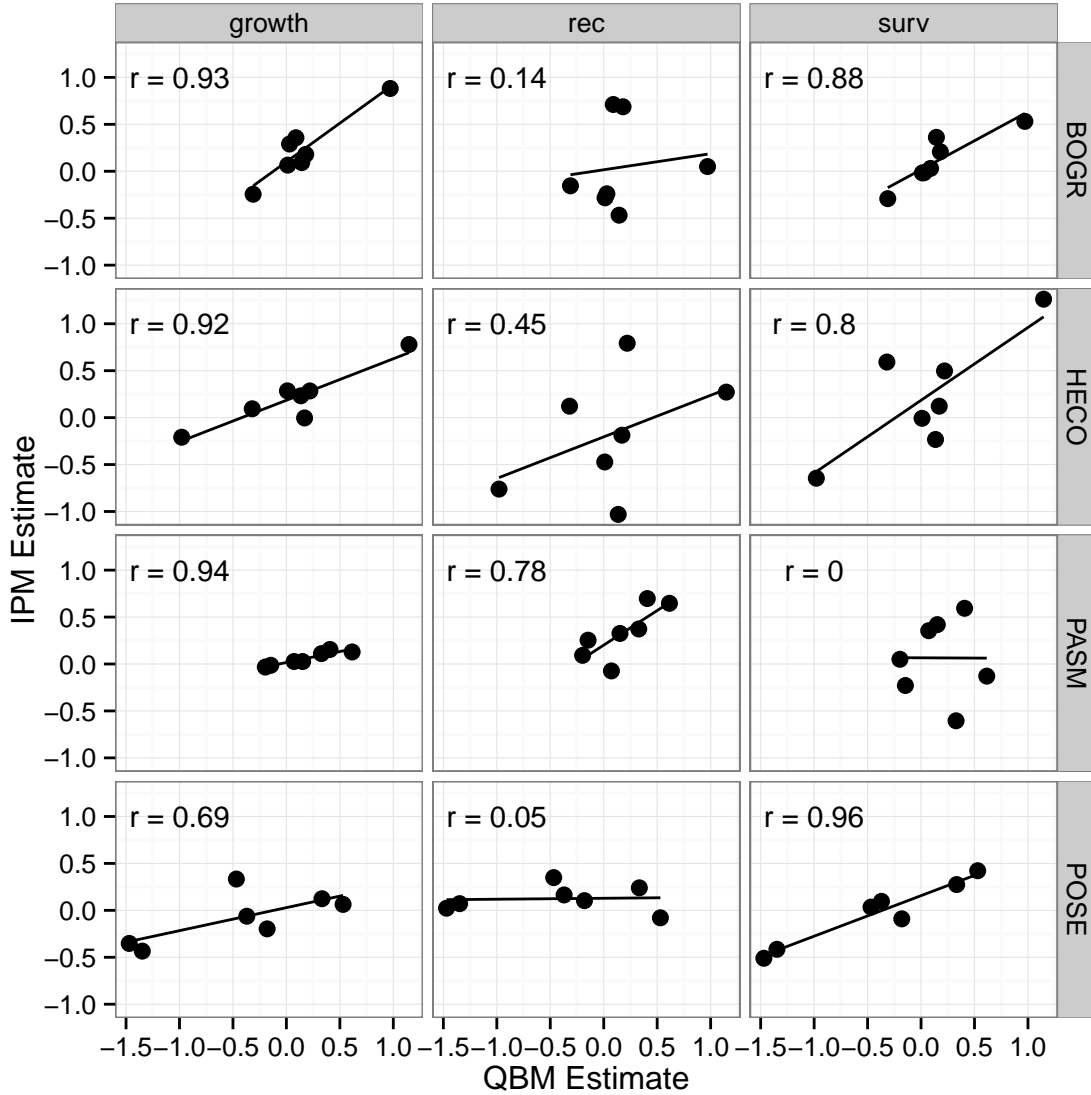
Figure 5: Correlations (r) between QBM and IPM estimates of climate effects. We ignore sizeXclimate interactions since these are not directly comparable across model types. The QBM does not have multiple vital rates, so its values are repeated across panels within each species. Across top panels, 'growth' = growth regression, 'rec' = recruitment regression, 'surv' = survival regression.
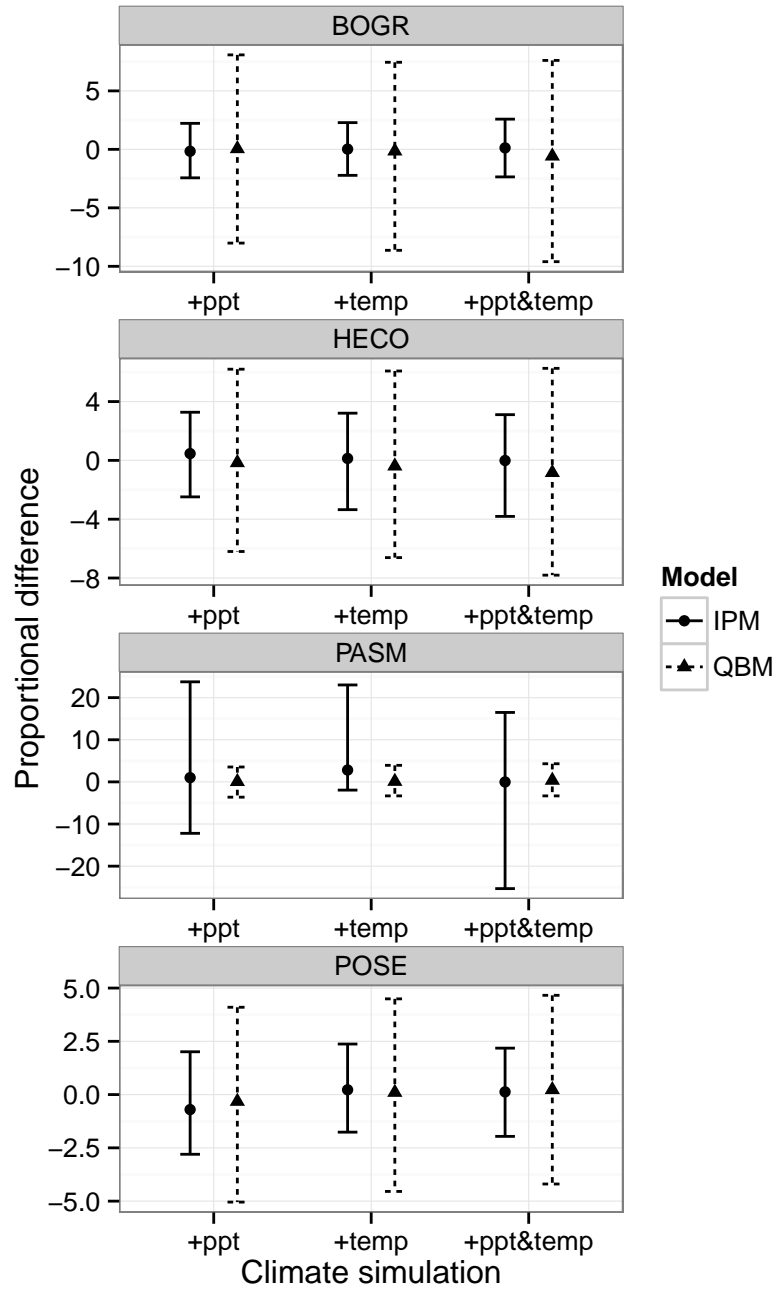
Figure 6: Equilibrium cover and 90% quantiles around the mean prediction when model error and parameter uncertainty are propogated through the simulation phase. Climate simulations are as in Figure 3.

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