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

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Abstract

The ability of population models to skillfully forecast future states under climate change is constrained by the limited spatial and temporal extent of demographic data. This data is often limited because it is difficult and costly to collect. An alternative is to rely on aggregate, population-level data that is easier and less costly to collect. Doing so requires assuming that population-level data accurately represents the aggregate response of the individuals that actually respond to weather. We tested this assumption using population models of four Montana grassland species fit using individual and aggregated forms of the same data. We fit population models with interannual variation in vital rates explained, in part, by climate covariates and then perturbed observed climate to compare model forecasts. Population models based on individual-level demographic data outperformed the models based on aggregate-level data in terms of accuracy and precision. The two model types produced inconsistent forecasts when we perturbed climate. Thus, it seems that, at least for the species in this location, demographic data is necessary to pick up key climate drivers of vital rates like survival that are not well resolved in aggregated data. On a pessimistic note, our work shows that even with detailed demographic data, model forecasts are extremely

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uncertain. It is becoming clear the long time series (over two decades) are necessary to produce meaningful forecasts.

Keywords: forecasting, climate change, grassland, integral projection model, population model

Introduction

Population models are important tools for predicting the impacts of environmental change on species. 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, at least for plant species, are built using data from small, localized plots because parameterizing traditional population models requires tracking the fates of individuals. These models are difficult to scale up from the micro to meso-scales because the fitted parameters do not fully represent the spatial variation present at scales beyond that at which the data are collected (Sæther et al. 2007). At the same time, most demographic data is collected over short time spans. For example, the most common study duration in the COMPADRE matrix population model database is 4 years and only a few exceed 10 years (Salguero-Gómez et al. 2015). The constrained spatio-temporal extent of most demographic datasets reflects the difficulty of collecting such data, but those constraints limit our ability to extrapolate population models. Thus, our ability to use population models to predict the consequences of climate change is limited when we rely on individual-level data.

Aggregate measures of individual plant performance, such as those typically collected as part of large-scale census efforts, offer an alternative to detailed demographic data for modeling populations (Clark and Bjørnstad 2004, Freckleton et al. 2011). Such population-level data will never match the precision of individual-level data, but it is more feasible to attain a broad coverage sample when collecting coarse-scale data. This presents a difficult

trade-off: on the one hand, individual-level data leads to more reliable models; on the other hand, population-level data leads to models that will produce less precise predictions but can be applied over greater spatial and temporal extents. An open question is how well models based on population-level data compare to models based on individual-level data.

To date, relatively few studies have tried to model populations based on data other than detailed individual-level data. An important exception is an effort by Taylor and Hastings (2004) to model the population growth rate of an invasive species to investigate 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. Building on this work, Freckleton et al. (2011) showed that density-structured models compare well to continuous models in theory, and Queenborough et al. (2011) showed 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. Thus, population models based on coarse, population-level data show promise for producing ecological forecasts at landscape and regional scales (Queenborough et al. 2011). However, none of these models included environmental covariates.

Basing population models on aggregated individual-level data in a climate change context is hampered by the fact that it is individuals that respond to climate, not populations (Clark et al. 2012). This fact puts us in uneasy proximity to an "ecological fallacy" where one deduces inference on the individual from statistical inference on the group (Piantadosi et al. 1988). For example, individual plants may respond positively to precipitation but a negative trend is observed at the population level due to increased competition among plants as they grow larger and consume more resources. Thus, it is important to ask the question: Can aggregated data be used to detect climate signals of the same sign and magnitude as individual-level data? If not, then building population models with climate covariates on aggregated data will lead to incorrect forecasts.

Here, we test the assumption that statistical and population models based on aggregated data can detect climate signals as wells as models based on individual-level data. We use a unique demographic dataset that tracks the fates of individual plants from four species over 14 years to build single-species population models, since those are often used tools for ecological forecasts and climate vulnerability assessments. We first fit population models with interannual variation in vital rates explained, in part, by climate covariates. We then perturb the climate covariates to test the sensitivities of species to climate change. By doing these analyses using both individual and aggregated forms of the same data we can directly compare the two types of models.

In general, we find that population models based on detailed demographic data are more accurate and precise than models based on aggregated data. Both types of models are able to detect climate signals, as evidenced by the sensitivity of simulated equilbrium plant cover under a perturbed climate scenario. But the two types of models produce inconsistent forecasts, in some cases producing completely opposing predictions. This leads us to conclude that, at least for these species at this location, detailed demographic data is necessary to detect the "right" climate signal. A worrying caveat to our work is that forecasts from both models were very uncertain. It seems that even 14 years worth of demographic data is not enough to produce meaningful forecasts when model uncertainty is explicitly considered.

Materials and Methods

Study site and data

Our demographic data comes 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 therein for a complete description. The site is

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

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 site is grass dominated and, for the purposes of our study, we focus on the four most abundant graminoid species: *Bouteloua gracilis* (BOGR), *Hesperostipa comata* (HECO), *Pascopyrum smithii* (PASM), and *Poa secunda* (POSE).

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. 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 (Figure 1). The individual data is the "raw" data. For the quadrat level we data we simply sum individual areal cover for each quadrat by species. This is equivalent to a perfect census of quadrat percent cover, so we do not need to consider measurement error. 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 replicate our analysis is archived on GitHub as release 1.0 (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.

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 of new individuals 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 covariate that we chose *a priori*: "water year" precipitation at t-1 (lagppt); fall through spring precipitation at t-1 and t-2 (ppt1 and ppt2, respectively) and mean spring 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 $\times$ TmeansSpr1) and climate $\times$ size interactions.

We fit all models using a hierarchical Bayesian approach, which we describe in more detail below. However, for each vital rate statistical model we also define the likelihood model we use. For the likelihood models, $\mathbf{Y}$ is always the relevant vector of observations (e.g., whether a genet survived [1] or not [0] from year t to $t+1$).

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 $t+1$:

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

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

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 ($C_{k,t}$). 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 modeled growth as Gaussian process describing genet size at time $t+1$ as a function of size at t and climate covariates:

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

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

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

Our data allows us to track new recruits, but we cannot assign a specific parent to new genets. So, for recruitment, we work at the quadrat level and model 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:

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

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:

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

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

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

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 vital rates using aggregated data depends on the type of data collected. In our case, and as is often the case with census data, we have percent cover data (which can easily be transformed to proportion data, of course). 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 data 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 (G) from time t to $t + 1$ is

$$x_{jq,t+1} = \gamma^G_{j,t} + \phi^G_{jQ} + \beta^G_{j,t} x_{jq,t} + \theta^S_{jk} C_{k,t} \quad (8)$$

$$Y^G_{jq,t+1} \sim \text{LogNormal}(x_{jq,t+1}, \tau j)\text{T}[0,1] \quad (9)$$

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. #). 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. We used flat, uninformative priors for all unknown parameters (Appendix X).

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. We recignize such short MCMC chains may surprise those 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 for all

parameters 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.

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 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. But note that we can, and do for some simulations, ignore the random year effects so that only the climate effects can 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 kernal 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 kernal is defined as the joint contributions of survival (S), growth (G), and recruitment (R):

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

which, said plainly, 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.

We used random draws from the final 1,000 iterations from each of three MCMC chains to introduce stochasticity into our population models. We thinned these chains by 10 to reduce potential autocorrelation, leaving us with 300 samples for each parameter. 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 (Eq. #). We use the same approach for drawing parameter values as described for the IPM.

Model validation

To test each model's ability to forecast the population state we used 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. We repeated this procedure for all 13 observation years. This model validation allowed us to compare accuracy and precision of the two modeling approaches (individual-level versus population-level).

Results

Comparison of Forecast Models

We performed one-step-ahead forecasts to compare the two models (IPM vs. QBM). We did not use the random year effects for these forecasts. Thus, beyond the effect of genet size or quadrat cover, only the climate covariates could affect expect plant cover. The IPM had significantly lower overall error (MAE, mean absolute error) for two species (*H. comata* and *P. smithii*; Table 1). In no case did the QBM significantly outperform the IPM (Table 1). As a metric of model uncertainty, we calculated the euclidean distance between the upper and lower 90% quantiles for each model's forecasts. The IPM always outperformed the QBM in this respect (Table 1), with consistently lower distances between the 90% quantiles. In general the IPM outperformed the QBM because it had (i) lower MAE for two species, (ii) statistically similar MAE for the other two species, and (iii) considerably more precise forecasts for all species.

Forecasting Climate Change Impacts

Simulated equilibrium cover simulated from the models was sensitive to climate perturbations, but the IPM and QBM produced inconsistent results (Table 2). For the IPM, proportional changes range from about 1-25% for *B. gracilis*, 7-25% for *H. comata*, 8% for *P. smithii*, and 2-20% for *P. secunda*. For the QBM, proportional changes due to climate perturbation ranged from 20-100% for *B. gracilis*, 10-14% for *H. comata*, 0.25-8% for *P. smithii*, and 4-17% for *P. secunda*. However, the forecasts were extremely uncertain (Figure 1). The IPM produced more certain forecasts than the QBM, as expected based on the validation results (Table 1). But even for the IPM forecasts, predicted percent changes in median equilibrium cover ranged from -200% to 200% (Figure 1). Forecast uncertainty did not vary appreciably among species.

The population responses of species as forecast by the IPM is a function of the combined effects of individual vital rate sensitivities to climate and the contribution of each vital to population dynamics. For *B. gracilis*, all vital rates (survival, growth, and rectruitment) were positively affected by increases in precipitation and temperature (Figure 2). Intuitively, this leads to an overall increase in *B. gracilis* cover (Table 2).

Precipitation increase resulted in all vital rates contributing to an increase in simulated cover for *H. comata*. But there is a small negative effect of temperature on recruitment. THIS IS WEIRD!!! CHECK SIMULATIONS.

P smithii responded negatively to an increase in precipitation, temperature, or both regardless of the vital rate through which perturbed climate was acting. The effects were small, however, leading to relatively minor population consequences under climate change that did not vary much across scenarios (Table 2).

For *B. gracilis*, the IPM predicted a modest increase in cover with a 1% increase in the mean of precipitation or a 1% increase in the mean of temperature, the compounding effect of both being a 20% increase in cover. This reflects the relatively strong effects of precipitation

and climate on *B. gracilis* genet growth and recruitment (Figure 1). The QBM also predicted increased *B. gracilis* cover with a precipitation increase, but increasing temperature decreased equilibrium cover (Figure 3).

The IPM and QBM produced consistent predictions for *H. comata* under increased precipitation and when both precipitation and temperature were increased (Figure 3). However, the IPM predicted more modest changes than the QBM, and for a temperature increase the two models differed: the IPM predicted an increase in cover while the QBM predicted the opposite.

Discussion

We sought to test the assumption that the sensitivities of plant populations to climate variables can be detected equally well using either individual level data or population level data. This is an important question to answer because population models are key tools for predicting the consequences of global climate change. However, they can be of limited use when built on data from a small subset of a population in space or time. If population level data (i.e., some aggregated form of individual level data) can be used to detect climate effects on population dynamics, then we would have a cheaper and easier option for data collection over relatively large temporal and spatial extents (*e.g.* Freckleton et al. 2011).

Forecasting the future, and the future of forecasting

Our goal was not make any explicit forecast for the future state of these populations based on predicted climate change. But 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, with some exceptions of course, at the forefront of ecological forecasting in terms of the statistical approach employed (hierarchical Bayesian), the type of population model we used (stochastic IPM with parameter uncertainty), and the amount of data we had at

our disposal (14 years of individual-level data). Yet, model predictions proved so uncertain that any forecast, when bounded with uncertainty, would be at best not useful and at worst meaningless.

Something about fitting the models. . . then cite Britta's paper: 20-25 years needed!

Tables

Table 1: Mean absolute error (MAE) and accuracy (Pearson's ρ) for one-step-ahead forecast from both model types. 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 90 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

The IPM MAE is significantly lower for HECO ($p = 3.3 \times 10^{-10}$) and POSE ($p = 0.00013$). MAEs are statisticially similar between models for BOGR and PASM.

Figures

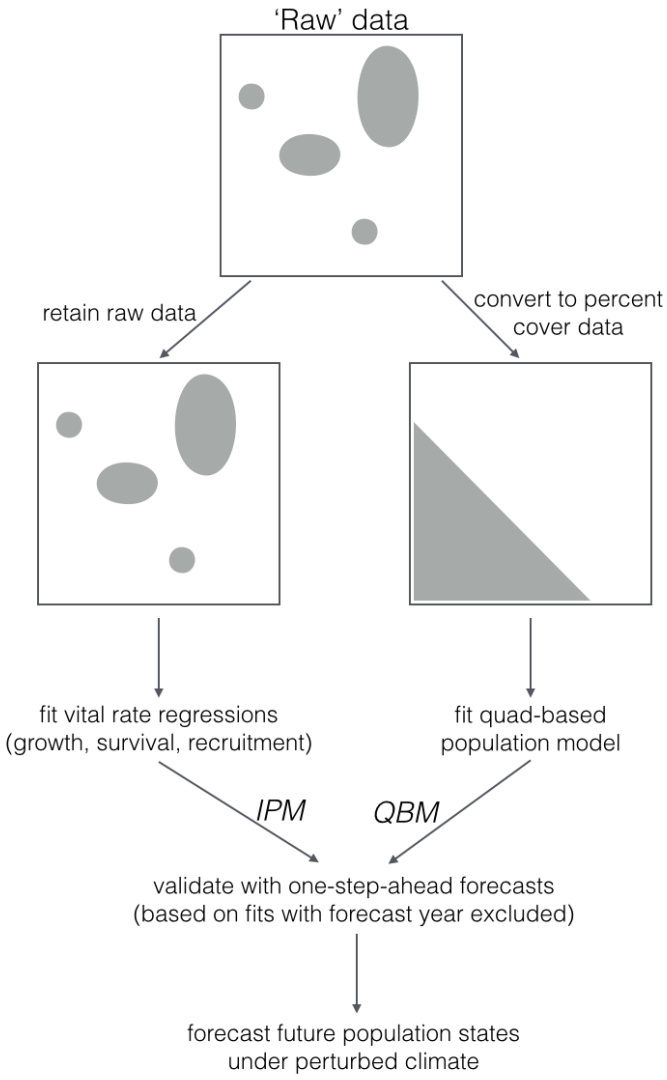

Figure 1: Work flow of the data aggregation, model fitting, and population simulating.

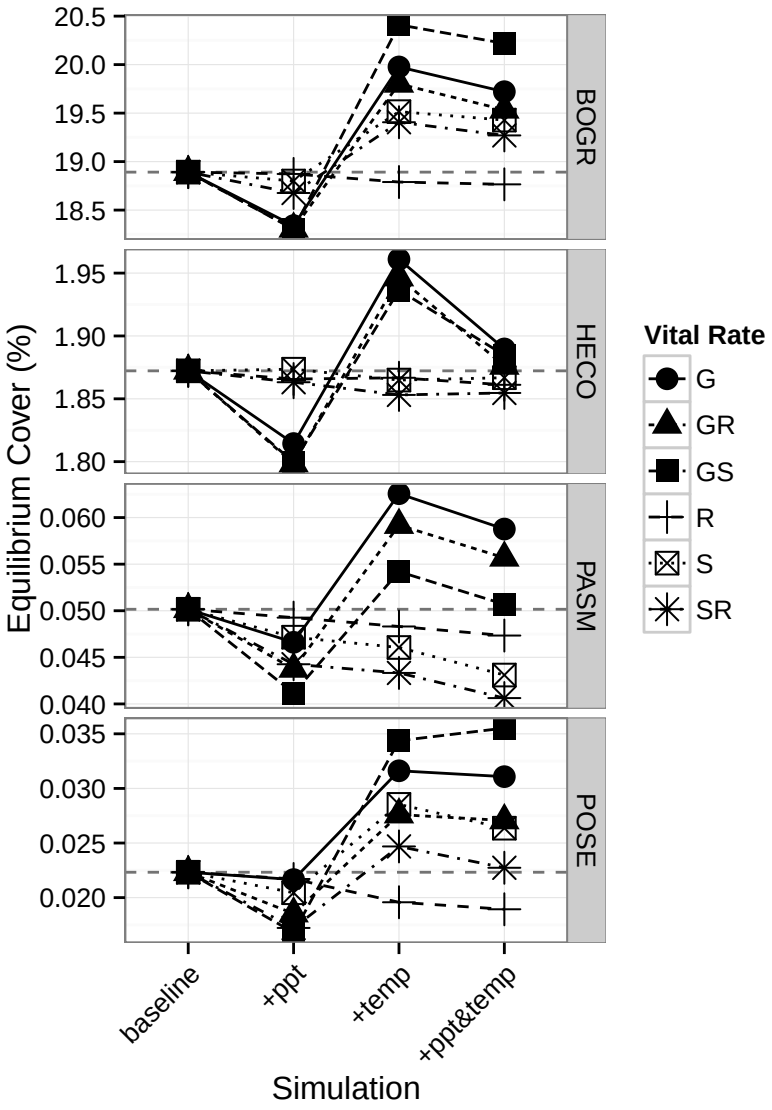

Figure 2: Sensitivity of equilibrium cover to a 1% increase in precipitation (+ppt), temperature (+temp), or both (+ppt&temp) applied to individual and combined vital rates. For example, the points associated with G show the median cover from IPM simulations where a climate perturbation is applied only to the growth regression climate covariates.

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