

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

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Abstract

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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). 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. If the goal of the model is to predict the consequences of climate change, then we argue that in the face of limited time and money population-level data are the best option. However, the performance of models based on population-level data have rarely been compared to that of 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 hypothesis (idea?) that statistical and population models based on aggregated data can detect climate signals as well as models based on individual-level data. We use a unique demographic dataset that tracks the fates of individual plants from four species 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 provide a rigorous test of our hypothesis. We find that...

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 (Anderson et al. 2011), and interested readers should refer to the metadata therein 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 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-m² 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. 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.

Statistical 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 analogous models of extinction probability, percent cover increase/decrease, and quadrat colonization for each species. We describe the statistical models separately since fitting the models required different approaches at the individual and quadrat levels. All models contain four climate covariate that we chose *a priori*: 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,

100 respectively), where t is the observation year.

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

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

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

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

107 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
 108 parameter for size, ϕ_{jQ}^S is the random effect of quadrat group location, and θ_k^S is the fixed
 109 parameter for the effect of the k th climate covariate at time t ($C_{k,t}$). We include density-
 110 dependence by estimating the effect of crowding on the focal individual by other individuals
 111 of the same species. ω is the effect of crowding and $w_{t,Q}$ is the crowding experienced by the
 112 focal individual at time t in quadrat group Q .

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

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

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

115 where x is log genet size and all other paramters are as described for the survival regression.
 116 Our data allows us to track new recruits, but we cannot assign a specific parent to new genets.
 117 So, for recruitment, we work at the quadrat level and model the number of new individuals of
 118 species j in quadrat q recruiting at time $t + 1$ as a function of quadrat “effective cover” (A') in
 119 the previous year (t). Effective cover is a mixture of observed cover (A) in the focal quadrat
 120 (q) and the mean cover across the entire group (\bar{A}) of Q quadrats in which q is located:

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

121 where p is a mixing fraction between 0 and 1 that is estimated within the model.
 122 We assume the number of individuals, Y^R , recruiting at time $t + 1$ follows a negative binomial
 123 distribution:

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

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

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

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

127 **Vital rate models: quadrat level** At the quadrat level we defined three vital rates:

- 128 1. Probability of extirpation (S): the probability that, for a given species, a particular
 129 quadrat will go from non-zero cover at time t to zero cover at time $t + 1$.
- 130 2. Cover change (G): the change in percent cover from time t to $t + 1$ for a given species
 131 within a particular quadrat.

3. Probability of colonization (R): the probability that, for a give species, a particular quadrat will go from zero cover at time t to non-zero cover at time $t + 1$.

We retain the abbreviations S , G , and R from the analagous processes at the individual level. The vital rate models at the quadrat level are all based on quadrat proportional cover. Also, at the quadrat level we do not need to explicitly include a density dependent term. Since we are modeling proportional cover, we essentially get density-dependence for “free” when proportional cover is included as a covariate. That is, density-dependence emerges because quadrats with low cover gerenally increase in cover whereas quadrats with high cover generally decrease in cover.

We modeled the probability of extirpation of species j in quadrat q from time t to $t + 1$ as:

$$\text{logit}(S_{jq,t}) = \gamma_j^S + \phi_{jQ}^S + \beta_j^S x_{jq,t} + \theta_{jk}^S C_{k,t} \quad (8)$$

$$Y_{jq,t}^S \sim \text{Bernoulli}(S_{jq,t}) \quad (9)$$

where all parameters are as in Eq. 1 except that x is now quadrat proportional cover. Note, however, that we do not include year random effects on the intercept γ or the slope term β for quadrat proportional cover. The quadrat data is inherently more sparse than the individual data from which it is aggregated, and this is especially evident when modeling rare events like extirpation and colonization. Thus, when we tried to fit random year effects, those terms did not converge.

We modeled quadrat cover change (G) from time t to $t + 1$ as:

$$\text{logit}(x_{jq,t+1}) = \gamma_{j,t}^G + \phi_{jQ}^G + \beta_{j,t}^G x_{jq,t} + \theta_{jk}^S C_{k,t} \quad (10)$$

149 where, in this case, we do include random year effects on the intercept γ and the slope term
 150 β . For cover change we had enough data for those terms to converge. Note that our model
 151 for quadrat cover change uses a logit transformation to link the expected cover at $t + 1$ ($x_{jq,t}$)
 152 to the linear predictors. We do so because during model fitting we use a beta likelihood since
 153 the data, proportional cover, is beta distributed. The beta likelihood requires shape (ρ) and
 154 rate (η) parameters that can be calculated using moment-matching:

$$\rho_{jq,t+1} = x_{jq,t+1}\tau_j \quad (11)$$

$$\eta_{jq,t+1} = (1 - x_{jq,t+1})\tau_j \quad (12)$$

155 with likelihood:

$$Y_{jq,t+1}^G \sim \text{Beta}(\rho_{jq,t+1}, \eta_{jq,t+1}). \quad (13)$$

156 Finally, we modeled probability of colonization in quadrat q by species j from time t to $t + 1$
 157 as:

$$\text{logit}(R_{jq,t}) = \gamma_j^R + \phi_{jQ}^R + \theta_{jk}^R C_{k,t} \quad (14)$$

$$Y_{jq,t}^R \sim \text{Bernoulli}(R_{jq,t}). \quad (15)$$

158 **Model fitting**

159 Our Bayesian approach to fitting the vital rate models required choosing appropriate priors
 160 for unknown parameters and deciding which, if any, of those prior should be hierarchical. We
 161 decided to fit models where all terms except climate covariates were fit by species, while the

162 climate covariates were fit hierarchically where species-specific coefficients were drawn from
 163 a shared ‘global’ coefficient distribution. We did so for two reasons: (1) the four focal species
 164 are all perennial grasses that we expect to respond similarly to climate covariates, and
 165 (2) convergence of climate effects at the quadrat level was much easier to achieve when we
 166 modeled these terms hierarchically, allowing them to “share” statistical strength via partial
 167 pooling (Gelman and Hill 2007). So, climate effects were modeled as:

$$\theta_{jk} \sim \text{Normal}(\bar{\theta}_k, \sigma_k) \quad (16)$$

168 where $\bar{\theta}_k$ is the interspecific effect of the k th climate covariate.

169 We used uninformative priors for all unknown parameters, specifically:

$$\gamma, \beta, \bar{\theta} \sim \text{Normal}(0, 1e^{-6}) \quad (17)$$

$$\phi \sim \text{Normal}(0, \sigma_\phi) \quad (18)$$

$$\sigma_\phi \sim e^{(\text{Gamma}(2, 0.5))} \quad (19)$$

$$\sigma_\theta, \sigma_\gamma, \sigma_\beta, \tau, \zeta \sim \text{Gamma}(0.001, 0.001) \quad (20)$$

170 All of our analyses (model fitting and simulating) were conducted in R (R Development
 171 Core Team 2013). We used the MCMC sampler in JAGS (Plummer 2003) to estimate the
 172 posterior distributions of model parameters and the package ‘r2jags’ (Su and Yajima 2012) to
 173 connect R to JAGS. We obtained posterior distributions for all model parameters from three
 174 parallel MCMC chains run for 50,000 iterations, after discarding an initial 50,000 iterations.
 175 We assessed convergence visually and using the Gelman and Rubin (1992) diagnostic in the
 176 R package ‘coda’ (Plummer et al. 2006). Scale reduction factors for all parameters were

less than 1.02, indicating convergence. For the purposes of introducing stochasticity in our population models, we saved the final 1,000 iterations from each chain for all parameters to be used as randomly drawn values during population simulation.

We assessed the statistical importance of the climate covariates included the final vital rate regressions by comparing the residual deviance of models with climate covariates and temporal random effects, climate covariates only, and temporal random effects only. When a model includes climate covariates, this comparison shows the relative contribution of the climate covariates in explaining the total interannual variability (Adler et al. 2012).

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. Both models take the general form:

$$N_{t+1} = S \times G + R. \quad (21)$$

So, at each time step in a simulation, we use the survival regression to determine if each genet lives or not (if each quadrat remains occupied or not), the growth regression to determine size changes of surviving individuals (cover change of occupied quadrats), and the recruitment regression to determine the number of new recruits (if a quadrat is colonized or not). We first use one-step-ahead forecasts to assess each model's ability to reproduce observed cover changes. Then we use the models to analyze the effect of potential climate changes on population size over long time scales.

We used random draws from the final 1,000 iterations from each of 3 MCMC chains to

introduce stochasticity into our population models. At each time step, we first randomly selected climate covariates from one of the 14 observed years and also randomly drew one set of random year effects for each vital rate regression. Then, we drew the full parameter set (specific random year effects, climate effects, fixed effects) from a randomly selected MCMC iteration. We selected random year effects and the climate year independently.

Results

Climate effects on vital rates

At the individual level we fit vital rate models that included climate covariates and random year effects (full model), just climate covariates (climate model), and no climate or random year effects (constant model). We used the metric from Adler et al. (2012) to quantify the contribution of climate covariates to explaining interannual variability in vital rates based on comparisons of model deviance: $(\text{Climate model} - \text{Constant Model}) / (\text{Full model} - \text{Constant model})$. At the quadrat level, we could only fit random year effects for the growth regression. This is, in fact, one of the limitation of census-based data: local extirpation and colonization events are likely to be rare, making it difficult to fit complex statistical models. So, in this section we focus on growth only.

Climate covariates improved the growth regressions at both levels, with a slightly greater contribution at the individual level (Figure 1). Parameter estimates were generally consistent in terms of sign and magnitude between the individual level and the quadrat level for each species and climate covariate (Figure 2). There is no clear pattern suggesting that parameters estimated using individual level data are more certain, as evidenced by credible interval widths, than estimates based on quadrat data.

Climate effects on population dynamics

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).

1. Climate detections

2. Limitations:

- Sample size at quadrat level
- are these species inherently sensitive to climate (compare to Chu and Adler in review – say why we chose Montana site – most sensitive to climate variables)
- we know recruitment is important, and this is something that may be easily missed at quad level

3. Implications

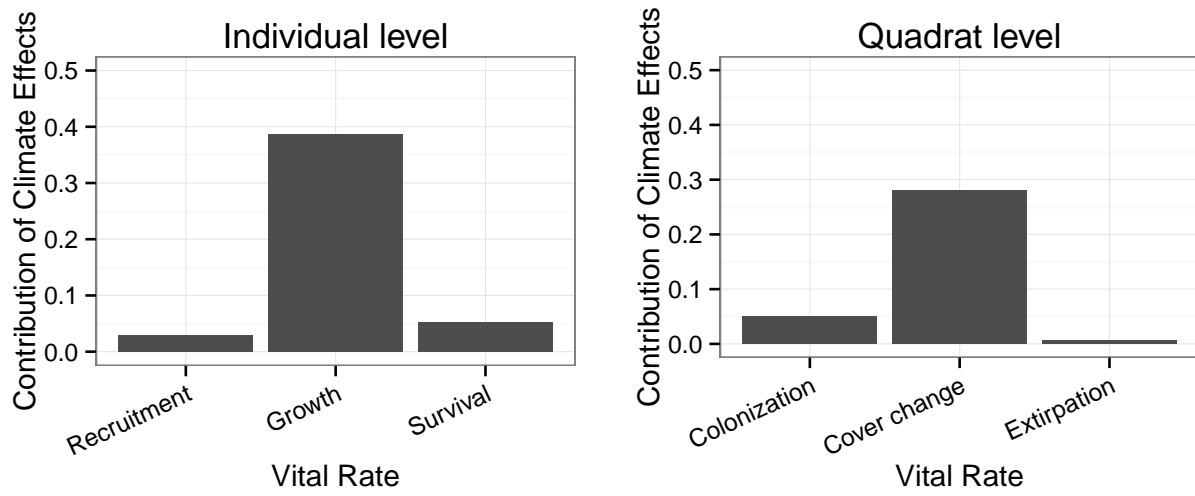


Figure 1: The proportion of interannual variability in vital rates explained by the climate covariates. The contribution for growth is defined as: $(\text{Climate model} - \text{Constant Model}) / (\text{Full model} - \text{Constant model})$. The contribution for survival and colonization, where we could not estimate a full model with year random effects at the quadrat level, is defined as: $(\text{Constant Model} - \text{Climate Model}) / \text{Constant Model}$.

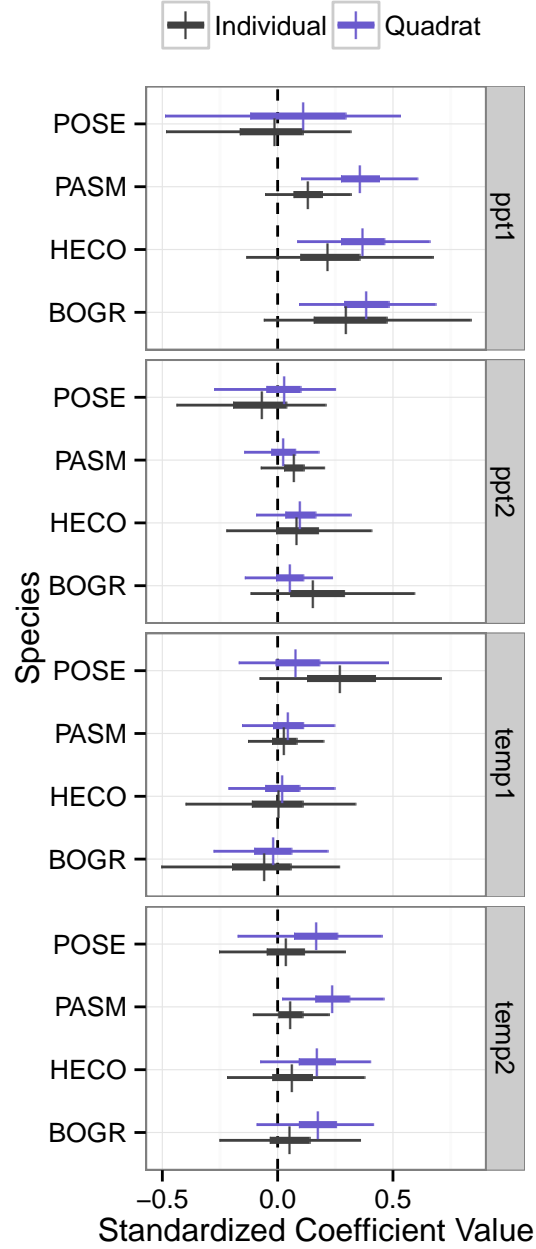


Figure 2: Posterior means (vertical ticks), 75% credible intervals (heavy lines), and 95% credible intervals (light lines) of climate effects on growth at both levels of inferences. The dashed vertical line is at 0, indicating no effect. Horizontal line at 0 indicates perfect agreement between mean observed cover in that year and the model predictions.

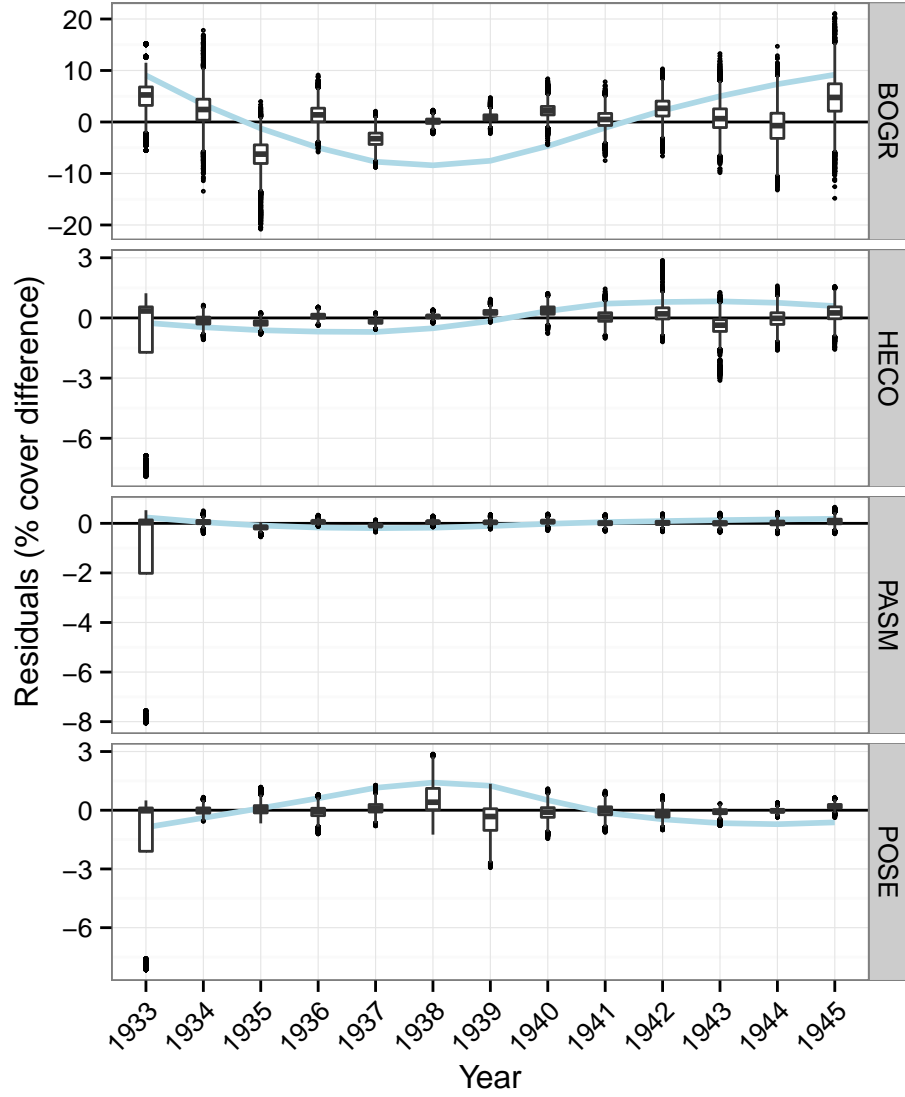


Figure 3: Boxplots of model residuals for one-step-ahead forecasts at each observation year. Each one-step forecast was simulated r nSims times. Note that the y-axes vary across panels. The light blue line shows the difference between the observed-year percent cover and the average cover observed across all years. The models tend to underpredict and perform poorly when observed cover in a given year is a large deviant from the mean.

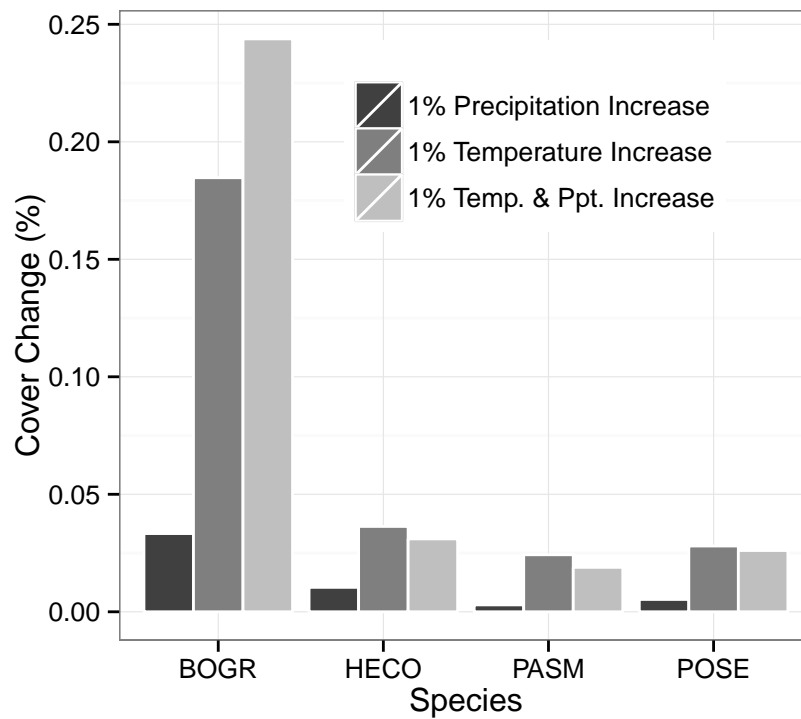


Figure 4: Simulated changes species' median cover caused by a 1% increase in observed precipitation or temperature. We used the median of simulated results because the average was highly influence by some extreme outliers.

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