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

Andrew T. Tredennick and Peter B. Adler

Andrew T. Tredennick (atredenn@gmail.com), Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT

Peter B. Adler, Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT

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). 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

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₂₃ the difficulty of collecting such data, but those constraints limit our ability to extrapolate

₂₄ population models. Thus, our ability to use population models to predict the consequences

₂₅ of climate change is limited when we rely on individual-level data.

₂₆ Aggregate measures of individual plant performance, such as those typically collected as part

₂₇ of large-scale census efforts, offer an alternative to detailed demographic data for modeling

₂₈ populations (Clark and Bjørnstad 2004, Freckleton et al. 2011). Such population-level data

₂₉ will never match the precision of individual-level data, but it is more feasible to attain a

₃₀ broad coverage sample when collecting coarse-scale data. This presents a difficult trade-off:

₃₁ on the one hand, individual-level data leads to more reliable models; on the other hand,

₃₂ population-level data leads to models that will produce less precise predictions but can be

₃₃ applied over greater spatial and temporal extents. An open question is how well models

₃₄ based on population-level data compare to models based on individual-level data.

₃₅ To date, relatively few studies have tried to model populations based on data other than

₃₆ detailed individual-level data. An important exception is an effort by Taylor and Hastings

₃₇ (2004) to model the population growth rate of an invasive species to investigate the best

₃₈ strategies for invasion control. They used a "density-structured" model where the state variable

₃₉ is a discrete density state rather than a continuous density measure. Building on this work,

₄₀ Freckleton et al. (2011) showed that density-structured models compare well to continuous

₄₁ models in theory, and Queenborough et al. (2011) showed the application of such methods

₄₂ in a study on arable weeds. In particular, Queenborough et al. (2011) provide empirical

₄₃ evidence that density-structured models are capable of reproducing population dynamics,

₄₄ even if some precision is lost when compared to fully continuous models. Thus, population

₄₅ models based on coarse, population-level data show promise for producing ecological forecasts

₄₆ at landscape and regional scales (Queenborough et al. 2011). However, none of these models

₄₇ included environmental covariates.

₄₈ Basing population models on aggregated individual-level data in a climate change context is

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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 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

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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. 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.

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 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

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⁹⁹ different approaches at the individual and quadrat levels. All models contain four climate

¹⁰⁰ covariate that we chose *a priori*: fall through spring precipitation at *t*-1 and *t*-2 (ppt1 and

¹⁰¹ ppt2, respectively) and mean spring temperature at *t*-1 and *t*-2 (TmeanSpr1 and TmeanSpr2,

¹⁰² respectively), where t is the observation year.

¹⁰³ We fit all models using a hierarchical Bayesian approach, which we describe in more detail

¹⁰⁴ below. However, for each vital rate statistical model we also define the likelihood model we

¹⁰⁵ use. For the likelihood models, **Y** is always the relevant vector of observations (e.g., whether

¹⁰⁶ a genet survived [1] or not [0] from year t to $t + 1$).

Vital rate models: individual level ¹⁰⁷ We used logistic regression to model survival

¹⁰⁸ probability (S) of genet i from species j in quadrat group Q from time t to $t + 1$:

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

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

¹⁰⁹ 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

¹¹⁰ parameter for size, ϕ_{jQ}^{S} is the random effect of quadrat group location, and θ_{k}^{S} is the fixed

¹¹¹ parameter for the effect of the kth climate covariate at time t ($C_{k,t}$). We include density-

¹¹² dependence by estimating the effect of crowding on the focal individual by other individuals

¹¹³ of the same species. ω is the effect of crowding and $w_{t,Q}$ is the crowding experienced by the

¹¹⁴ focal individual at time t in quadrat group Q.

¹¹⁵ We modeled growth as Gaussian process describing genet size at time $t + 1$ as a function of

¹¹⁶ size at t and climate covariates:

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

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

$_{117}$ where x is log genet size and all other parameters are as described for the survival regression.

$_{118}$ Our data allows us to track new recruits, but we cannot assign a specific parent to new genets.

$_{119}$ So, for recruitment, we work at the quadrat level and model the number of new individuals of

$_{120}$ species j in quadrat q recruiting at time $t+1$ as a function of quadrat "effective cover" (A') in

$_{121}$ the previous year (t). Effective cover is a mixture of observed cover (A) in the focal quadrat

$_{122}$ (q) and the mean cover across the entire group $(\bar{A})$ of Q quadrats in which q is located:

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

$_{123}$ where p is a mixing fraction between 0 and 1 that is estimated within the model.

$_{124}$ We assume the number of individuals, Y^R, recruiting at time $t+1$ follows a negative binomial

$_{125}$ distribution:

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

$_{126}$ where λ is the mean intensity and ζ is the size parameter. We define λ as:

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

$_{127}$ where A' is effective cover (cm^2) of species j in quadrat q and all other terms are as in the

$_{128}$ survival and growth regressions.

129 **Vital rate models: quadrat level** The statistical approach used to model vital rates

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

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

132 proportion data, of course). We first considered fitting three vital rate models analagous

133 to those we fit at the individual level: one for probability of extirpation within a quadrat

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

135 one for probability of colonization within a quadrat (analagous to recruitment). However,

136 within-quadrat extirpation and colonization events were rare in our time series ($N = 9$ and

137 $N = 10$, respectively). Given the broad spatial distribution of the quadrats we are studying,

138 it is safe to assume that these events are in fact rare enough to be ignored for our purposes.

139 So we constrained our statistical modeling of vital rates at the population level to change in

140 percent cover within quadrats. For most of the remaining discussion of statistical modeling

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

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

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

144 used fitted model parameters from a beta regression in quadrat-based population model the

145 simulated population tended toward 100% cover for all species. We therefore chose a more

146 constrained modeling approach based on a truncated log-normal likelihood. The model for

147 quadrat cover change (G) from time t to $t + 1$

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

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

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

149 parameters are as in the individual-level growth model (Eq. #). The log normal likelihood

150 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 except climate covariates were fit by species, while the climate covariates were fit hierarchically with species-specific coefficients drawn from a shared 'global' coefficient distribution. We did so for two reasons: (1) the four focal species are all perennial grasses that we expect to respond similarly to climate covariates, and (2) convergence of climate effects at the quadrat level was much easier to achieve when we modeled these terms hierarchically, allowing them to "share" statistical strength via partial pooling (Gelman and Hill 2007). So, climate effects were modeled as:

$$\theta_{jk} \sim \text{Normal}(\bar{\theta}_k, \sigma_k) \tag{10}$$

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

We used uninformative priors for all unknown parameters, specifically:

$$\boldsymbol{\gamma}, \boldsymbol{\beta}, \bar{\boldsymbol{\theta}} \sim \text{Normal}(0, 1e^{-6}) \tag{11}$$

$$\boldsymbol{\phi} \sim \text{Normal}(0, \boldsymbol{\sigma}_\phi) \tag{12}$$

$$\boldsymbol{\sigma}_\phi \sim e^{(\text{Gamma}(2,0.5))} \tag{13}$$

$$\boldsymbol{\sigma}_\theta, \boldsymbol{\sigma}_\gamma, \boldsymbol{\sigma}_\beta, \boldsymbol{\tau}, \boldsymbol{\zeta} \sim \text{Gamma}(0.001, 0.001) \tag{14}$$

All of our analyses (model fitting and simulating) were conducted in R (Team 2013). We used the MCMC sampler in JAGS (Plummer 2003) to estimate the posterior distributions of model parameters and the package 'r2jags' (Su and Yajima 2012) to connect R to JAGS.

166 We obtained posterior distributions for all model parameters from three parallel MCMC

167 chains run for 50,000 iterations, after discarding an initial 50,000 iterations. We assessed

168 convergence visually and using the Gelman and Rubin (1992) diagnostic in the R package

169 'coda' (Plummer et al. 2006). Scale reduction factors for all parameters were less than

170 1.01, indicating convergence. For the purposes of introducing stochasticity in our population

171 models, we saved the final 1,000 iterations from each of the three MCMC chains for all

172 parameters to be used as randomly drawn values during population simulation.

Population models

174 With the posterior distribution of the vital rate statistical models in hand, it is straightforward

175 to simulate the population models. We used an Integral Projection Model (IPM) to model

176 populations based on individual level data and an quadrat based version of an individually-

177 based model (Quadrat-Based Model, QBM) to model populations based on quadrat level

178 data. Both models take the general form:

$$N_{t+1} = S \times G + R. \tag{15}$$

179 So, at each time step in a simulation, we use the survival regression to determine if each genet

180 lives or not (if each quadrat remains occupied or not), the growth regression to determine size

181 changes of surviving individuals (cover change of occupied quadrats), and the recruitment

182 regression to determine the number of new recruits (if a quadrat is colonized or not). We

183 first use one-step-ahead forecasts to assess each model's ability to reproduce observed cover

184 changes. Then we use the models to analyze the effect of potential climate changes on

185 population size over long time scales.

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

187 introduce stochasticity into our population models. At each time step, we first randomly

188 selected climate covariates from one of the 14 observed years and also randomly drew one set

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of random year effects for each vital rate regression. Climate years and random year effects were drawn independently because they were uncorrelated. 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

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 detection

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
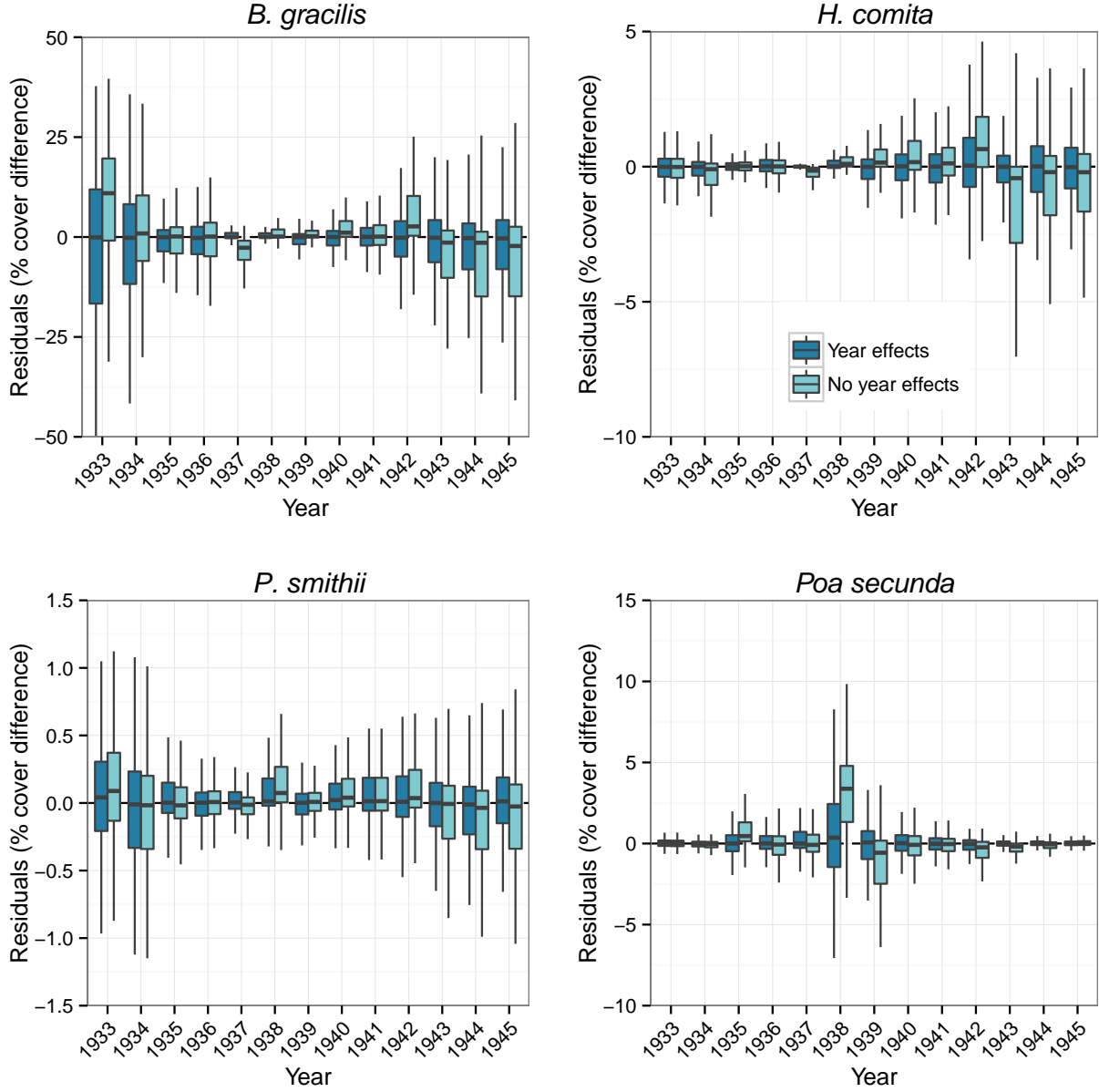
3. Implications

Figures

Figure 1: Boxplots of model residuals for one-step-ahead forecasts at each observation year for each quadrat. Residuals represent the difference in observed and predicted cover change from year $t-1$ to year t. Each one-step forecast was simulated 100 times for each quadrat. Note that the y-axes vary across panels.
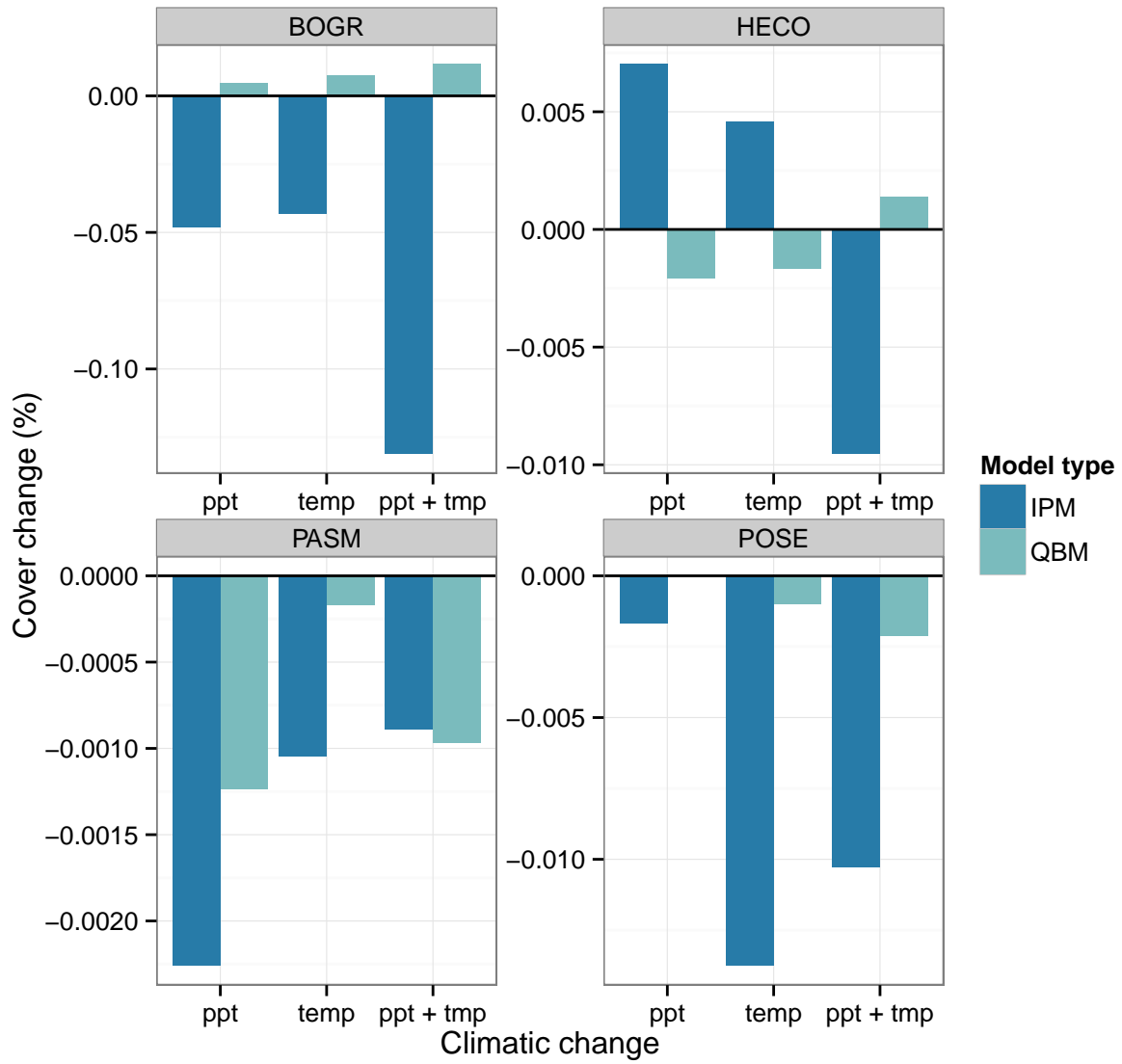
Figure 2: Changes in species' mean cover caused by a 1% increase in observed precipitation or temperature as predicted by the individual-based IPM and the aggregate-based QBM. Note that the change for POSE due to a precipitation increase predicted by the QBM is almost zero and so does not show up in the figure.

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