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

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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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²⁴ uncertain. It is becoming clear the long time series (over two decades) are necessary to ²⁵ produce meaningful forecasts.

²⁶ *Keywords*: forecasting, climate change, grassland, integral projection model, population model

Introduction

²⁸ Population models are important tools for predicting the impacts of environmental change ²⁹ on species. But reconciling the scales at which population models are parameterized and the ³⁰ scales at which environmental changes play out remains a challenge (Clark et al. 2010, 2012, ³¹ Freckleton et al. 2011, Queenborough et al. 2011). The major hurdle is that most population ³² models, at least for plant species, are built using data from small, localized plots because ³³ parameterizing traditional population models requires tracking the fates of individuals. These ³⁴ models are difficult to scale up from the micro to meso-scales because the fitted parameters ³⁵ do not fully represent the spatial variation present at scales beyond that at which the data ³⁶ are collected (Sæther et al. 2007). At the same time, most demographic data is collected ³⁷ over short time spans. For example, the most common study duration in the COMPADRE ³⁸ matrix population model database is 4 years and only a few exceed 10 years (Salguero-Gómez ³⁹ et al. 2015). The constrained spatio-temporal extent of most demographic datasets reflects ⁴⁰ the difficulty of collecting such data, but those constraints limit our ability to extrapolate ⁴¹ population models. Thus, our ability to use population models to predict the consequences ⁴² of climate change is limited when we rely on individual-level data.

⁴³ Aggregate measures of individual plant performance, such as those typically collected as part ⁴⁴ of large-scale census efforts, offer an alternative to detailed demographic data for modeling ⁴⁵ populations (Clark and Bjørnstad 2004, Freckleton et al. 2011). Such population-level data ⁴⁶ will never match the precision of individual-level data, but it is more feasible to attain a ⁴⁷ broad coverage sample when collecting coarse-scale data. This presents a difficult trade-off: ⁴⁸ 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.

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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

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[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) (Fig. 1).

From 1932 to 1945 individual plants were identified and mapped annually in 44 1-m^2 quadrats using a pantograph. The quadrats were distributed in six pastures, each assigned a grazing treatment of light (1.24 ha/animal unit month), moderate (0.92 ha/aum), and heavy (0.76 ha/aum) stocking rates (two pastures per treatment). In this analysis we account for potential differences among the grazing treatments, but do not focus on grazing×climate interactions. The annual maps of the quadrats were digitized and the fates of individual plants tracked and extracted using a computer program. 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 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 reproduce 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

124 At both levels of inference (individual and quadrat), the building blocks of our population

125 models are vital rate regressions. For individual level data we fit models for survival, growth,

126 and recruitment of new individuals for each species. At the quadrat level we fit a single

127 regression model for population growth. We describe the statistical models separately since

128 fitting the models required different approaches. All models contain five climate covariate that

129 we chose *a priori*: "water year" precipitation at *t*-1 (lagppt); fall through spring precipitation

130 at *t*-1 and *t*-2 (ppt1 and ppt2, respectively) and mean spring temperature at *t*-1 and *t*-2

131 (TmeanSpr1 and TmeanSpr2, respectively), where t is the observation year. We also include

132 interactions among same-year climate covariates (e.g., ppt1 $\times$ TmeansSpr1) and climate $\times$

133 size interactions.

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

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

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

137 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

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

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

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

140 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

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

142 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:

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

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

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:

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

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

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

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

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

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

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

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200 as randomly drawn values during population simulation. This step alleviates the need to
201 reduce model parameters by model selection since sampling from the full parameter space in
202 the MCMC ensures that if a parameter broadly overlaps zero, on average the effect in the
203 population models will also be near zero.

Population models

205 With the posterior distribution of the vital rate statistical models in hand, it is straightforward
206 to simulate the population models. We used an Integral Projection Model (IPM) to model
207 populations based on individual level data and an quadrat based version of an individually-
208 based model (Quadrat-Based Model, QBM) to model populations based on quadrat level
209 data. We describe each in turn.

210 **Integral projection model** We use an environmentally stochastic IPM (Rees and Ellner
211 2009) that includes the random year effects and the climate covariates from the vital rate
212 statistical models. But note that we can, and do for some simulations, ignore the random year
213 effects so that only the climate effects can drive interannual variation. Our IPM follows the
214 specification of Chu and Adler (2015) where the population of species j is a density function
215 $n(u_j, t)$ giving the density of sized-u genets at time t. Genet size is on the natural log scale,
216 so that $n(u_j, t)du$ is the number of genets whose area (on the arithmetic scale) is between e^{u_j}
217 and $e^{u_j + du}$. So, the density function for any size v at time $t + 1$ is

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

218 where $k_j(v_j, u_j, \bar{\mathbf{w}}_{\mathbf{j}})$ is the population kernal that describes all possible transitions from size u
219 to v and $\bar{\mathbf{w}}_{\mathbf{j}}$ is a vector of estimates of average crowding experienced from all other species
220 by a genet of size u_j and species j. The integral is evaluated over all possible sizes between
221 predefined lower (L) and upper (U) size limits that extend beyond the range of observed

₂₂₂ genet sizes.

₂₂₃ The population kernal is defined as the joint contributions of survival (S), growth (G), and
₂₂₄ recruitment (R):

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

₂₂₅ which, said plainly, means we are calculating growth (G) for individuals that survive (S)
₂₂₆ from time *t* to *t+1* and adding in newly recruited (R) individuals of an average sized
₂₂₇ one-year-old genet for the focal species. Our stastical model for recruitment (R, described
₂₂₈ above) returns the number of new recruit produced per quadrat. Following previous work
₂₂₉ (Adler et al. 2012, Chu and Adler 2015), we assume that fecundity increases linearly with
₂₃₀ 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-
₂₃₁ implicit IPM.

₂₃₂ We used random draws from the final 1,000 iterations from each of three MCMC chains to
₂₃₃ introduce stochasticity into our population models. At each time step, we randomly selected
₂₃₄ climate covariates from one of the 14 observed years. Then, we drew the full parameter
₂₃₅ set (climate effects and density-dependence fixed effects) from a randomly selected MCMC
₂₃₆ iteration. Using this approach, rather than simply using coefficient point estimates, ensures
₂₃₇ that relatively unimportant climate covariates (those that broadly overlap 0) have little effect
₂₃₈ on the simulation results. Since our focus was on the contribution of climate covariates to
₂₃₉ population states, we set the random year effects and the random group effects to zero.

₂₄₀ **Quad-based model** Our quad-based model (QBM) perfectly mirrors its statistical de-
₂₄₁ scription (Eq. #). We use the same approach for drawing parameter values as described for
₂₄₂ the IPM.

Model validation

To test each model's ability to forecast the 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 are sampled. So we made predictions for each observed quadrat in the focal year initialized with cover 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 randomdrawd 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 (individual-level versus population-level). We first calculated the median predicted cover across the 100 simulations for each quadrat-year and then calculated the absolute error as 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 aggregate level data are as sensitive to climate 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

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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 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, and recruitment vital rates individually and in pairwise combinations. This allows 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.

Results

Comparison of forecast models

The IPM had significantly lower overall error (MAE, mean absolute error) for three species (*B. gracilis*, *H. comata*, *P. smithii*; Table 1). In no case did the QBM significantly outperform the IPM (Table 1). The IPM was consistently more precise than the QBM, with lower distances between the 90% quantiles across all species (Table 1). In general the IPM outperformed the QBM because it had (1) lower MAE for three of the four species, (2) statistically similar MAE for the one other species, and (3) considerably more precise forecasts for all species.

Sensitivity of models to climate

Equilibrium cover from both models was sensitive to climate (Fig. 3a-d). The IPM projected percent changes in equilibrium cover from -3 - 8% for *B. gracilis*, -4 - 3% for *H. comata*, -15 - 9% for *P. smithii*, and -17 - 53% for *P. secunda*. The QBM projected opposite and greater percent changes in equilibrium cover for *B. gracilis* (-63 - 30%) and *H. comata* (-50 - -18%; Fig. 3a-b). For *P. smithii*, the QBM projected opposite changes in equilibrium cover than the IPM, but of similar magnitude (-5 - 6%; Fig. 3c). *P. secunda* was the only species that the IPM and QBM made projections of the same sign and somewhat similar magnitude (Fig. 3d). As expected based on model validation (Table 1), QBM projections were more uncertain than IPM projections for all species except *P. smithiii* (Fig. 3e-h).

The response of a population to climate change is a result of the aggregate effects of climate on individual vital rates. Since the IPM approach relies on vital rate regressions, we were able to quantify the sensitivity of each vital rate in isolation and in pairwise combinations. Species showed similar trends (Fig. 4). Growth was the most sensitive vital rate for all species, showing a negative response to increased precipitation, and stronger positive response to increased temperature, and a mostly positive response when both climate factors are increased (Fig. 4). *B. gracilis* survival rates were sensitive to temperature, resulting in an increase in plant cover under increased temperature (Fig. 4a). In isolation, recruitment and survival were insensitive to climate factors for *H. comata* (Fig. 4b). Survival and recruitment of *P. smithii* were both sensitive, negatively, to temperature and precipitation (Fig. 4c). *P. secunda* equilibrium cover was sensitive to the climate effects on survival and recruitment, showing a negative effect on both vital rates for increased precipition, but a strong positive effect on survival with increased temperature (Fig. 4d). The climate impact of recruitment on equilibrium cover was negative for precipitation and temperature increases (Fig. 4d).

Discussion

Perhaps the greatest challenge for ecology in the 21st century is to forecast the impacts of environmental change (Clark et al. 2001). To do so requires sophisticated modeling approaches that fully account for uncertainty and variability in the ecological process and associated parameters. 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.

As a potential remedy to the "data dearth" problem, Queenborough et al. (2011) and Freckleton et al. (2011), building on work by Taylor and Hastings (2004), advocate a "density-structured" modeling approach. Such models do not require individual level demographic data and can adequately describe population dynamics (Queenborough et al. 2011). The results from density-structured models are not as precise as those from traditional population models, but the loss in precision is traded off with a gain in data. 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, at their core, density-structured models rely on individual level data aggregated to a population level metric (e.g., density classes or percent cover). 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.

The IPM and QBM produced inconsistent forecasts

Using individual and aggregated forms of the same dataset, we were able to directly compare a traditional demographic modeling approach to a population model based on aggregated 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 (Table 1). This is unsurprising since we expected to lose some precision at the aggregated level. However, the underwhelming performance of the QBM could call in the question forecasts that differ from the IPM.

Indeed, when we perturbed climate factors the QBM made forecasts completely contradictory to those of the IPM for three of our four study species (Fig. 3a-d). In a perfect world, the QBM would have made forecasts of at least the same direction as the IPM. If that had been the case we could conclude that aggregate level models could prove useful for forecasting climate change impacts on populations. Unfortunately, this was not the case.

Given the superior ability of the IPM to predict out of sample observations (Table 1), we have no choice but to conclude it is the superior model. Following that logic, we can only assume that, at least contingent on the data in hand, the IPM is producing the correct forecasts to climate perturbations. The QBM failed to match IPM forecasts, implying that detailed demographic data may be necessary to accurately detect climate signals that are utlimately important at the population level. This result further confirms related work on the importance of individual variability on population level responses to exogenous drivers (CITATIONS).

An important caveat to the above conclusion is that our comparison of the IPM and the QBM

This result is not as dire as it seems when we consider model uncerainty. Yes, the QBM failed to match IPM forecasts under perturbed climate, but the uncertainties around those forecasts were so great (Fig. 3e-h) that we cannot say that the two model's forecasts were

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different with any level of confidence. This offers hope that with "enough" population level data one will be able to reduce parameter uncertainty and thus model forecasts. This remains an open question.

The role of vital rate climate dependence

Our intuition was that species with strong climate-dependence on vital rates not well resolved at the aggregate level would result in different forecasts from the two models. For example, survival is very size dependent: smaller individuals have a higher probability of death (Chu and Adler 2014). At the same time, a single small individual contributes relatively little to percent cover estimates at the plot scale. So, if survival of individuals was positively impacted by temperature increases, for example, we would expect to detect this signal in the individual level data but not in the aggregate level data. **PETER: do you think this is the right direction to go with this?**

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. How might we improve on this state of affairs?

First, forecasts could be improved by matching the spatial scale of predictor variables with the spatial scale of observations. One of the major limitations of the models we fit here is that

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the climate data are at a much larger scale than the plot and individual level observations of plant cover and 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. **PETER: any good citations here for decent population models fit with fine-scale climate/environmental data??**

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 and random forest require 20-25 year time series (Teller et al., in review).

Conclusions

This work is not a critique of density-structured population models. Instead, we consider our results a cautionary tale. In some cases and for certain species, population models based on aggregated data may prove useful and unbiased. But, as our work shows, that is not a foregone conclusion when considering the impact of exogenous drivers like climate on population states. Thus, forecasts from aggregate level models should be viewed with caution and should never be unaccompianed by uncertainty. As we have shown, 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). 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.
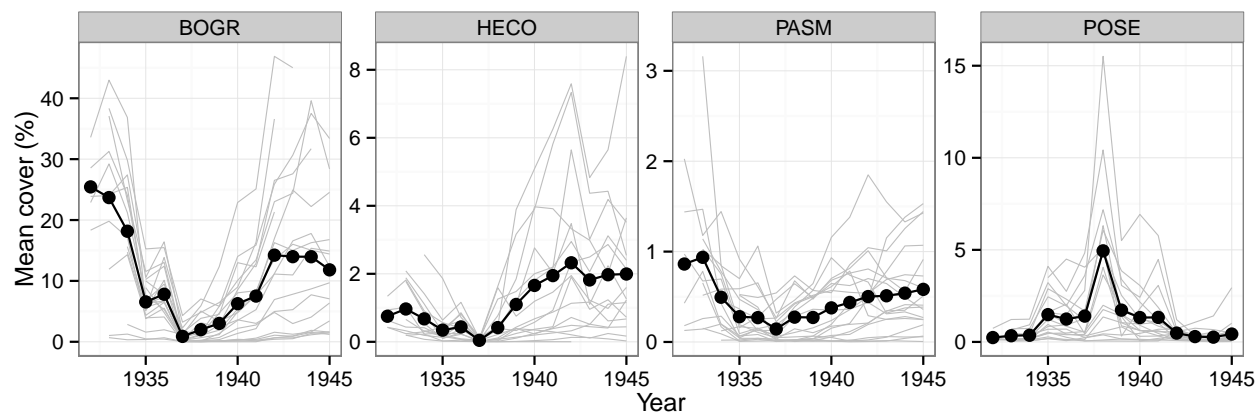
Figures

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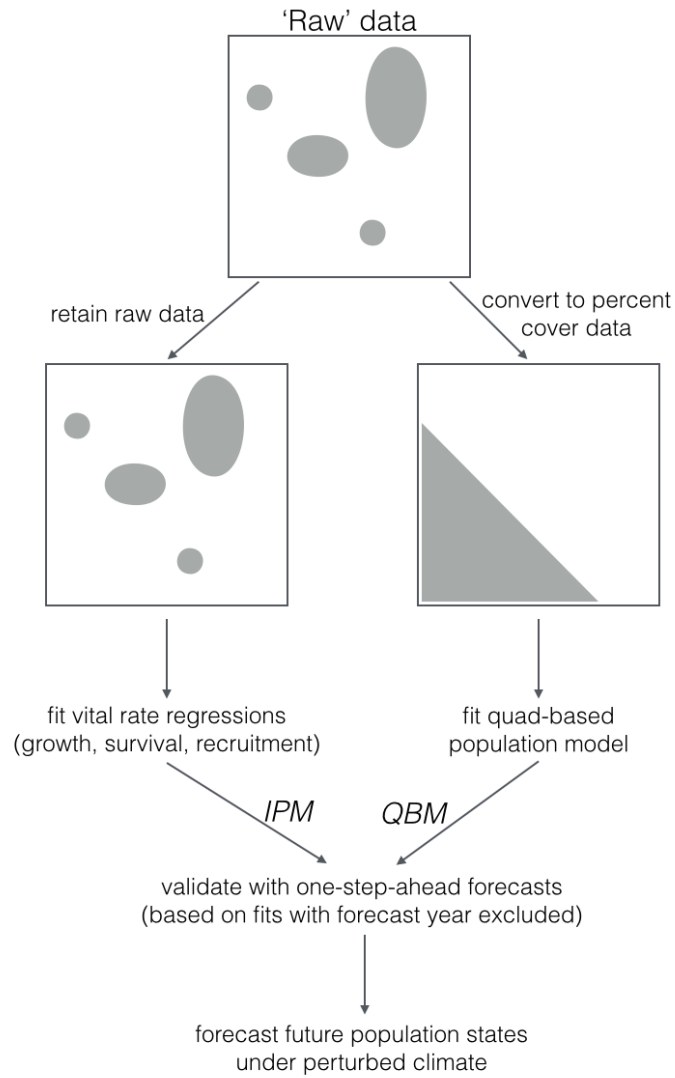
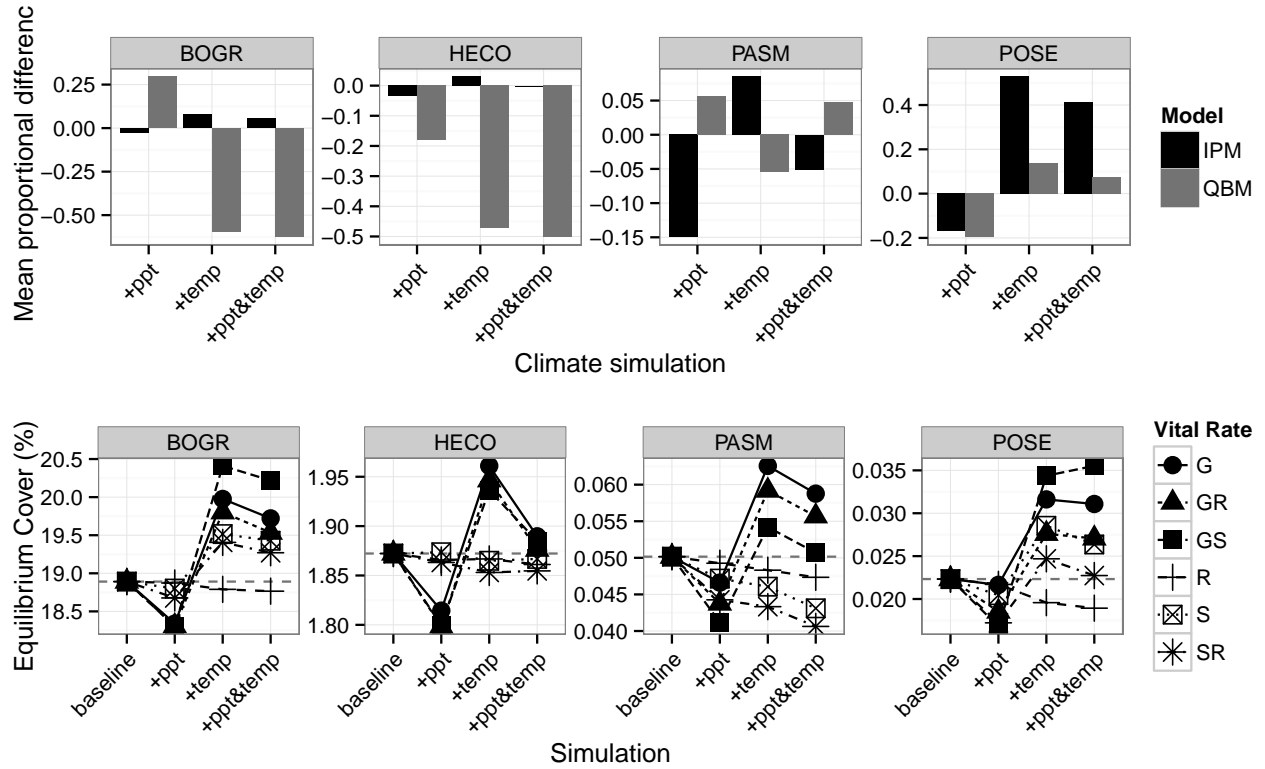Figure 2: Work flow of the data aggregation, model fitting, and population simulating.

Figure 3: Proportional change in species' mean cover caused by a 1% increase in observed precipitation (+ppt), temperature (+temp), or both (+ppt&temp) as predicted by the individual-based IPM and the aggregate-based QBM. Top panels show the mean predicted proportional change in cover. Lower panels show the 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.
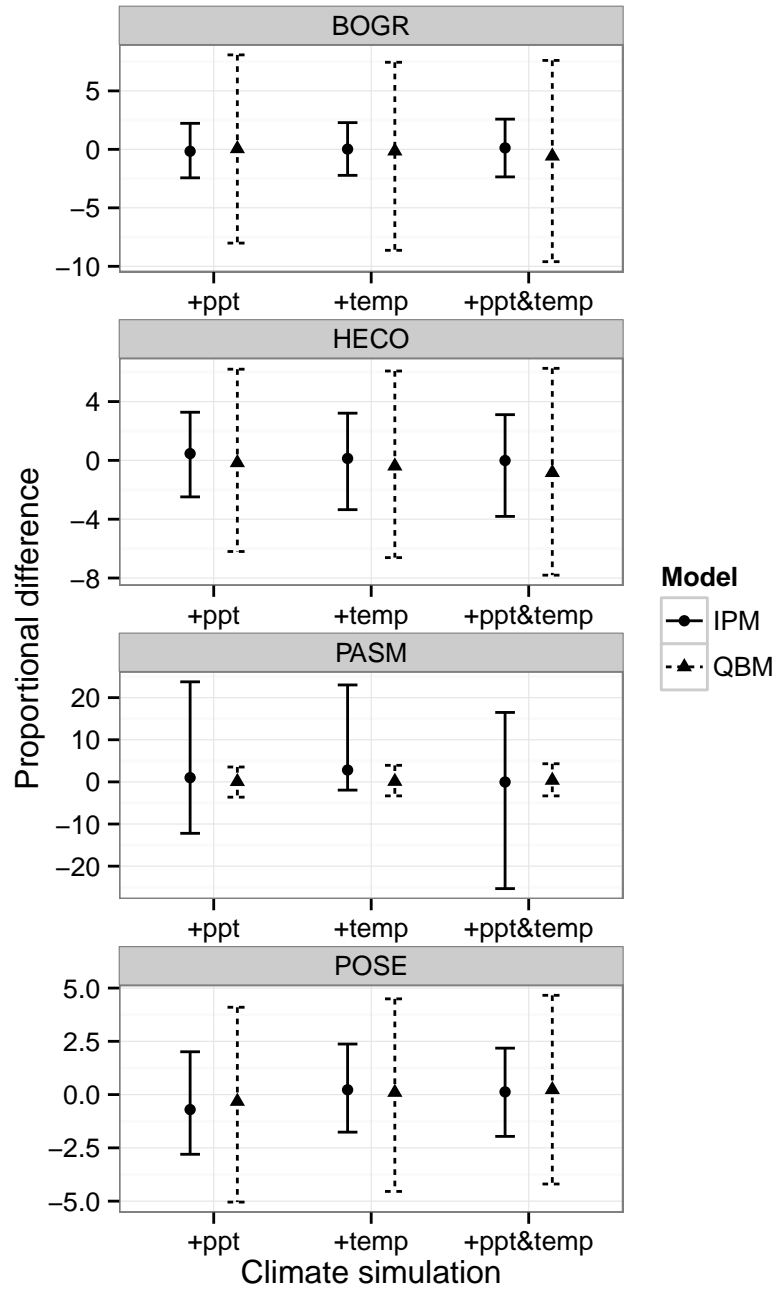
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Figure 4: Equilibrium cover and 90% quantiles around the mean prediction when model and parameter uncertainty are propogated through the simulation phase. Climate simulations are as in Figure 3.
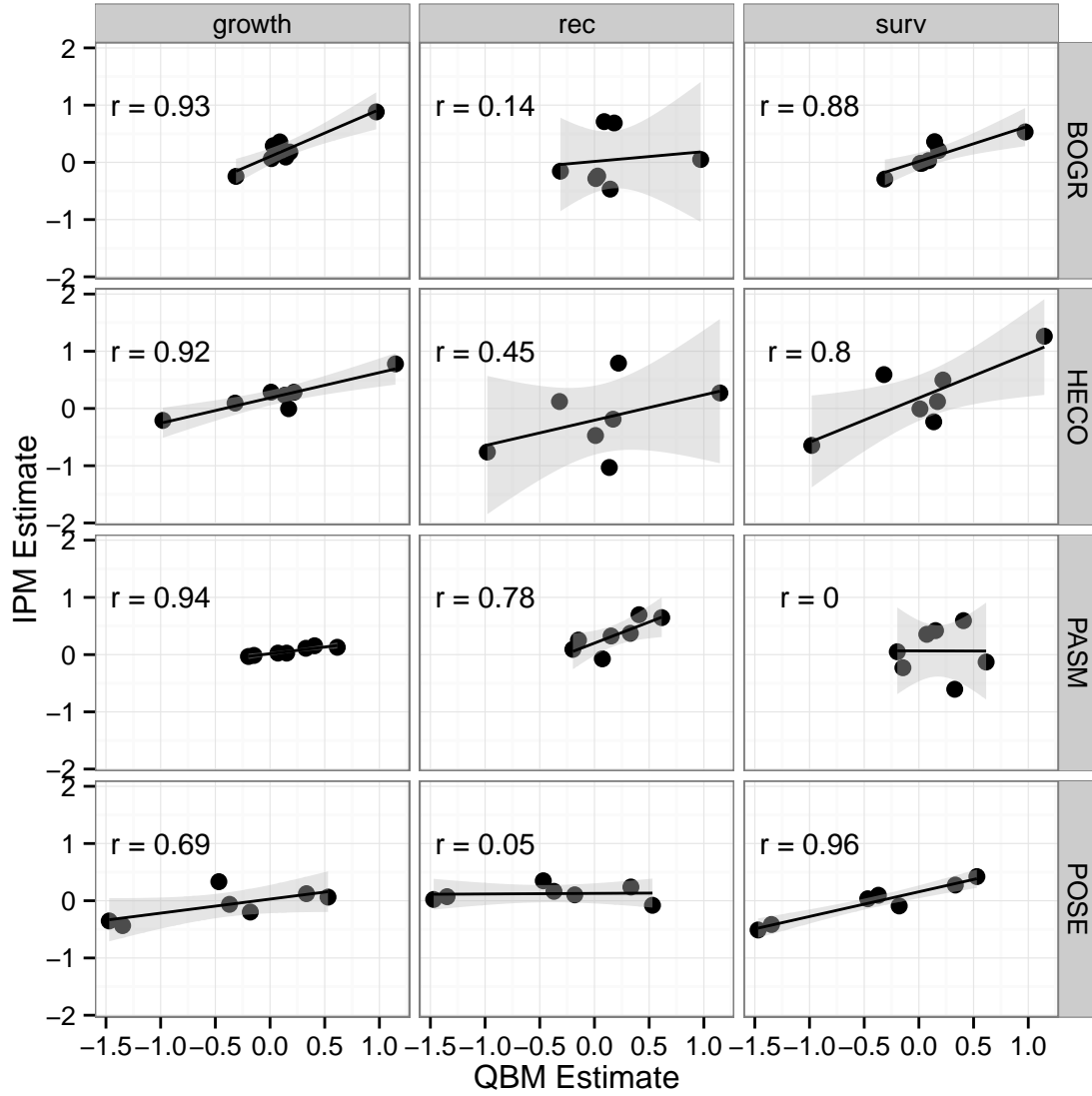
Figure 5: Correlations between QBM and IPM estimates of climate effects. We ignore sizeXclimate interactions since these are not directly comparable across model types. The QBM does not have multiple vital rates, so its values are repeated across panels within each species.
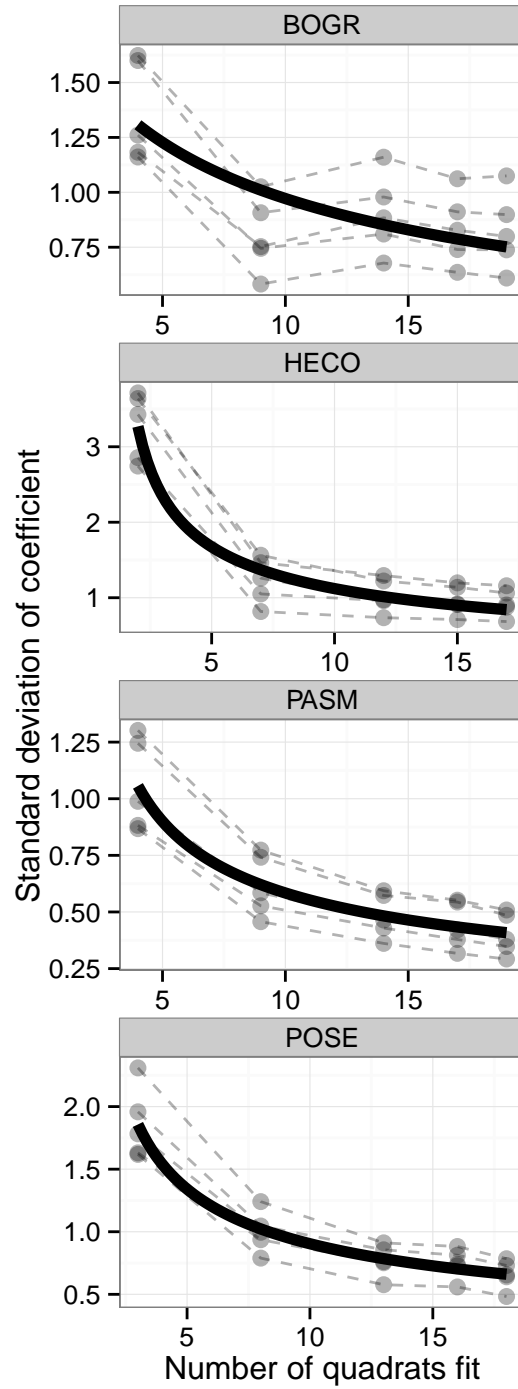
Figure 6: Effect of quadrat sample size on the precision (standard deviation) of main climate effect estimates in the QBM. Increasing the number of quadrats results in diminishing returns in terms of parameter certainty. Light dashed lines show individual climate effects at five quadrat sample sizes. Thick dark lines are inverse gaussian fits showing the mean effect of increasing quadrat sample size on parameter precision.

References

Adler, P. B., H. J. Dalgleish, and S. P. Ellner. 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? Journal of Ecology 100:478–487.

Anderson, J., L. Vermeire, and P. B. Adler. 2011. Fourteen years of mapped, permanent quadrats in a northern mixed prairie, USA. Ecology 92:1703.

Chu, C., and P. B. Adler. 2014. When should plant population models include age structure? Journal of Ecology 102:531–543.

Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs.

Clark, J. S., and O. N. Bjørnstad. 2004. Population time series: Process variability, observation errors, missing values, lags, and hidden states. Ecology 85:3140–3150.

Clark, J. S., D. M. Bell, M. Kwit, A. Stine, B. Vierra, and K. Zhu. 2012. Individual-scale inference to anticipate climate-change vulnerability of biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 367:236–246.

Clark, J. S., D. Bell, C. Chu, B. Courbaud, M. Dietze, M. Hersh, J. HilleRisLambers, I. Ibáñez, S. LaDeau, S. McMahon, J. Metcalf, J. Mohan, E. Moran, L. Pangle, S. Pearson, C. Salk, Z. Shen, D. Valle, and P. Wyckoff. 2010. High-dimensional coexistence based on individual variation: a synthesis of evidence. Ecological Monographs 80:569–608.

Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: an emerging imperative. Science (New York, N.Y.) 293:657–660.

Freckleton, R. P., W. J. Sutherland, A. R. Watkinson, and S. A. Queenborough. 2011. Density-structured models for plant population dynamics. American Naturalist 177:1–17.

Piantadosi, S., D. P. Byar, and S. B. Green. 1988. The Ecological Fallacy. American Journal of Epidemiology 127:893–904.

Queenborough, S. A., K. M. Burnet, W. J. Sutherland, A. R. Watkinson, and R. P. Freckleton. 2011. From meso- to macroscale population dynamics: A new density-structured approach. Methods in Ecology and Evolution 2:289–302.

R Core Development Team. 2013. R: A language and environment for statistical computing.

Rees, M., and S. P. Ellner. 2009. Integral projection models for populations in temporally varying environments. Ecological Monographs 79:575–594.

Salguero-Gómez, R., O. R. Jones, C. R. Archer, Y. M. Buckley, J. Che-Castaldo, H. Caswell, D. Hodgson, A. Scheuerlein, D. A. Conde, E. Brinks, H. de Buhr, C. Farack, F. Gottschalk, A. Hartmann, A. Henning, G. Hoppe, G. Römer, J. Runge, T. Ruoff, J. Wille, S. Zeh, R. Davison, D. Vieregg, A. Baudisch, R. Altwegg, F. Colchero, M. Dong, H. de Kroon, J.-D. Lebreton, C. J. E. Metcalf, M. M. Neel, I. M. Parker, T. Takada, T. Valverde, L. A. Vélez-Espino, G. M. Wardle, M. Franco, and J. W. Vaupel. 2015. The compadrePlant Matrix Database: an open online repository for plant demography. Journal of Ecology 103:202–218.

Stan Development Team. 2014a. Stan: A C++ Library for Probability and Sampling, Version 2.5.0.

Stan Development Team. 2014b. Rstan: the R interface to Stan, Version 2.5.0.

Sæther, B. E., S. Engen, V. Grøtan, W. Fiedler, E. Matthysen, M. E. Visser, J. Wright, A. P. Møller, F. Adriaensen, H. Van Balen, D. Balmer, M. C. Mainwaring, R. H. McCleery, M. Pampus, and W. Winkel. 2007. The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. Journal of Animal Ecology 76:315–325.

Taylor, C. M., and A. Hastings. 2004. Finding optimal control strategies for invasive species: a density-structured model for Spartina alterniflora. Journal of Applied Ecology 41:1049–1057.