

## DEMOGRAPHY BEYOND THE POPULATION

# Linking demography with drivers: climate and competition

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### Summary

1. In observational demographic data, the number of measured factors that could potentially drive demography (such as daily weather records between two censuses) can easily exceed the number of independent observations. Thus, identifying the important drivers requires alternatives to standard model selection and variable selection methods.
2. Spline methods that estimate smooth functions over continuous domains (such as space or time) have the potential to resolve high-dimensional problems in ecological systems. We consider two examples that are important for many plant populations: competition with neighbours that vary in size and distance from the focal individual and climate variables during a window of time before a response (growth, survival, etc.) is measured.
3. For competition covariates, we use a simulation study based on empirical data to show that a monotone spline estimate of competition kernels via approximate AIC returns very accurate estimates. We then apply the method to long-term, mapped quadrat data on the four dominant species in an Idaho (US) sagebrush steppe community.
4. For climate predictors and their temporal lags, we use simulated data sets to compare functional smoothing methods with competing linear (LASSO) or machine learning (random forests) methods. Given sufficient data, functional smoothing methods outperformed the other two methods.
5. Functional smoothing methods can advance data-driven population modelling by providing alternatives to specifying competition kernels *a priori* and to arbitrarily aggregating continuous environmental covariates. However, there are important open questions related to modelling of nonlinear climate responses and size  $\times$  climate interactions.

**Key-words:** climate, competition, demography, drivers, estimation, functional data analysis, machine learning, splines

### Introduction

Individual survival, fecundity and growth rates are highly variable over time. Multi-annual population studies have often found 10- to 100-fold (or even larger) between-year variation in per capita reproductive success of iteroparous plants and animals, for one species in one location (Hairston, Ellner & Kearns 1996). The estimated coefficient of variation (CV) in annual juvenile survival ranged from 26% to 66% in seven species of birds (Sæther & Bakke 2000). In a survey of multi-annual matrix population models for 20 plant and animal species (Pfister 1998), the majority of 660 estimated matrix entries had CVs of 20% or higher, and many had CVs above 100%.

Many classic questions in ecology and evolution concern the consequences of this variability. Are population fluctuations driven primarily by abiotic or biotic factors (Forchhammer *et al.* 1998; Bjornstad & Grenfell 2001; Coulson *et al.* 2001; Yang *et al.* 2008; Previtali *et al.* 2009; Laneri *et al.* 2010; Smallegange, van der Meer & Fiedler 2011; Crone 2016; Ehrlén *et al.* 2016)? How have life-history strategies evolved to allow persistence in variable environments (Cohen 1966; Seger & Brockman 1987; Koons, Metcalf & Tuljapurkar 2008)? Do environmental fluctuations always decrease long-term population growth rates (Lewontin & Cohen 1969) or can they sometimes accelerate population growth (Drake 2005; Koons *et al.* 2009)? Does environmental variability promote the diversity of competing species by stabilizing coexistence (Hutchinson 1961; Chesson & Warner 1981; Ellner 1987)? Despite decades of theoretical and empirical research, these questions continue to fascinate population biologists (for a review of recent manuscripts, see Griffith *et al.* 2016). Furthermore, answering these questions may be a prerequisite to predicting the impacts of environmental change (Ehrlén & Morris 2015).

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Two important drivers of demographic variability in plants are competition with neighbours, and climate (Clark *et al.* 2011). A challenge is the high-dimensional nature of both drivers. Plant performance is influenced by many neighbours, in multiple species, at different distances from the focal plant (e.g., Mack & Harper 1977; Goldberg 1987; Pacala & Silander 1987; Rees, Grubb & Kelly 1996; Turnbull *et al.* 2004; Schneider, Law & Illian 2006). That same plant will also be affected by many weather events occurring over a range of times extending from the present into the past (Dahlgren & Ehrlén 2011).

Traditional approaches for these high-dimensional problems require simplifying assumptions. Models for neighbourhood competition estimate the competitive pressure experienced by a plant as the sum of the crowding by each neighbour (possibly dependent on neighbour size and species) weighted by the *competition kernel* that downweights more distant neighbours. Current practice is to choose the kernel from a small set of *a priori* alternatives, but in our previous work (Adler, Ellner & Levine 2010), we encountered problems with that approach. We considered the exponential kernel (effect of a neighbour at distance  $d$  is proportional to  $e^{-\alpha d}$ ) and Gaussian kernel (effect proportional to  $e^{-\alpha d^2}$ ) and compared the predictive accuracy of models for individual growth and survival based on the two kernels. Exponential won by a hair. But when we used the fitted kernels in a spatially explicit individual-based model for the community, the Gaussian kernel gave a good fit to observed mean cover values and with the exponential kernel populations crashed or exploded. So we used the Gaussian kernel, with as little explanation as possible (one sentence in the online Supporting Information). We were not happy with this, but we could not do better. Even when more candidate kernels are compared (as in Schneider *et al.* 2006), there is no guarantee that the *a priori* list includes a good approximation to the actual kernel.

Similarly, to model climate effects, ecologists typically choose *a priori* a fairly small set of climate covariates that represent discrete aggregated temporal windows [e.g. precipitation or temperature aggregated by week, month or season, over several years preceding an observation; Dalglish *et al.* (2011)]. The results are only meaningful if the right variables and windows have been included. But as more climate factors and temporal windows are included, there is a rapid growth in the number of candidate models. Considering basic features of an individual's neighbours, and high-resolution data available on temperature and precipitation, the number of potential covariates for demographic models greatly exceeds the number of independent years observed in historical data sets. With so many potential covariates, we need alternatives that do not require *a priori* simplifying assumptions or *ad hoc* model selection procedures.

Recent advances in mathematical modelling and statistics have set the stage for advances in understanding and predicting the ecological consequences of environmental variation. Methods based on function approximation by splines are promising because they can use functions on continuous domains as covariates (Wood 2000; Ramsay & Silverman 2005; Ramsay, Hooker & Graves 2009). Competition and climate are func-

tions on the domains of space and time, respectively, and ecological responses may be nonlinear (Wood 2001; Dahlgren, García & Ehrlén 2011). Just as closer neighbours may have stronger effects than more distant neighbours, more recent climate events may have stronger effects than events occurring further in the past.

In this study, we developed, tested and applied spline smoothing methods that estimate the effects of competition in space and of climate drivers in time. For both cases, we began with empirical data from which we simulated data with known effects of competition or climate. We then tested the ability of smoothing methods to identify the designed effects (see Fig. 1). Despite the similarities in the case studies, the details differ, so we present each with independent Methods and Results sections. For competition kernels, we introduce spline methods in which the kernel's shape is driven by the data, rather than by the investigators' choice of functional form. For climate effects, we show that smoothing methods are superior to two currently popular methods from statistical learning, LASSO and random forests, so long as there are sufficient data. We also emphasize the importance of conducting simulation studies to confirm that a novel method can correctly identify a known signal.

## Study system and empirical data

Scientists at the U.S. Sheep Experiment Station (USSES) established 26 1-m<sup>2</sup> quadrats between 1926 and 1932. Eighteen quadrats were distributed among four ungrazed exclosures, and eight were distributed in two pastures grazed at medium intensity spring through fall. All quadrats were located on similar topography and soils. In most years until 1957, all individual plants in each quadrat were mapped using a pantograph (Blaisdell 1958). Zachmann, Moffet & Adler (2010) provide digitized versions of these maps. Our analyses here are based on data from 22 year-to-year transitions between 1926 and 1957. For the first two transitions, only four quadrats were observed; at least 16 quadrats were observed for all subsequent transitions.

The USSES is located 9.6 km north of Dubois, Idaho (44.2°N, 112.1°W), 1500 m above sea level. During the period of data collection, mean annual precipitation was 270 mm and

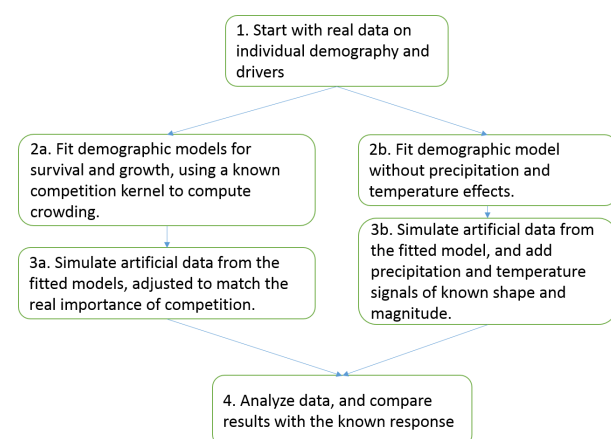


Fig. 1. Flow chart for simulation studies.

mean temperatures ranged from  $-8^{\circ}\text{C}$  (January) to  $21^{\circ}\text{C}$  (July). The vegetation is dominated by the shrub, *Artemisia tripartita* (ARTR), and the C3 perennial bunchgrasses *Pseudoroegneria spicata*, *Hesperostipa comata* and *Poa secunda* (PSSP, HECO and POSE, respectively). These four species, the focus of our analyses here, comprised over 70% of basal cover (grasses) and 60% of canopy cover (shrubs and forbs).

We extracted demographic data from the digitized plots by tracking individuals based on their spatial location (Lauenroth & Adler 2008). Our approach tracks genet, which may be composed of multiple polygons, as they fragment and/or coalesce. Each mapped polygon with a buffered area that overlaps with a genet present in previous years was classified as a survivor, inheriting the identity of the existing genet with the greatest overlap. Polygons having no overlap with any pre-existing genets were classified as new recruits. The resulting data allow us to study the factors influencing individual survival and growth. For modelling neighbourhood competition, we computed for each genet the cover (basal cover for grasses, canopy cover for the shrub) of each of the four dominants in a series of annuli bounded by the circles of radius 0, 2, 4, ..., 18, 20, 25, 30, ..., 45, 50, 60, 70, ..., 140, 150 cm, centred at the centroid of the focal genet. Cover in an annulus was treated as being at distance equal to the average of the inner and outer radii. This slight rounding of distances allowed orders of magnitude speedup in computing, which was essential for fitting the kernels.

## Neighbourhood competition: methods

For many decades, the importance of neighbours' locations has been recognized (e.g. Mack & Harper 1977) and modelled using competition kernels (e.g. Pacala & Silander 1987). Despite this, 'surprisingly little is known about competition kernels. When kernel functions are used in modelling growth of interacting plants they tend to be based more on assumptions than on observations' (Schneider *et al.* 2006; p. 311), or on a comparison between a few candidate kernels (e.g. Turnbull *et al.* 2004; Adler *et al.* 2010). Our goal here is to estimate the shape of the competition kernel from observational data such as our Idaho permanent quadrat data. The approach we propose is to model size-dependent demography using the sort of regression models usually used to build integral projection models, with the total crowding experienced by each plant as a covariate. The competition kernel is fitted by maximizing the predictive power of the regression models.

To present and test this approach, we use conventional competition and demographic models that include all of the qualitative features that are likely to be encountered in practice, as follows. Interspecific competition is far weaker than intraspecific in our focal system (Adler *et al.* 2010), as in others (Rees *et al.* 1996), so we model each species assuming only intraspecific competition. Survival probability and expected subsequent size of survivors are both functions of log genet area  $z$ , crowding  $W$  as a measure of competition, and quadrat group (a categorical variable identifying a cluster of nearby quadrats). Some models also include year as a factor. The crowding experienced by genet  $i$  is the sum of neighbour areas across a set of concentric annuli centred at the plant,

$$w_{i,k} = F(d_k)A_{i,k} \quad (\text{eqn 1})$$

where  $F$  is the competition kernel,  $d_k$  is the average of the inner and outer radii of annulus  $k$ , and  $A_{i,k}$  is the total area of conspecific genets in annulus  $k$  around genet  $i$ . The total crowding on genet  $i$  is

$$W_i = \sum_k w_{i,k}. \quad (\text{eqn 2})$$

The crowding measure in our previous papers (Adler *et al.* 2010; and refs. therein) was similar but used a sum over neighbouring genets (rather than annuli) with  $d$  the centroid-to-centroid distance between focal and neighbour genets. However, we found that centroid-to-centroid distances can be misleading for irregularly shaped genets; for example, when one genet is essentially a doughnut wrapped around another, the centroids are much closer than the minimum genet-to-genet distance.

$W_i$  is then used as a covariate in demographic models. For example, survival probability  $s$  might be modelled as

$$\text{logit}(s_i) = \alpha_0 + \alpha_1 z_i + \gamma_q + \delta W_i \quad (\text{eqn 3})$$

where  $\alpha_0$  and  $\alpha_1$  are the intercept and slope parameters for size  $z$  (log of total area), and  $\gamma$  is the coefficient for quadrat group  $q$ . Between-year variation can be incorporated by fitting  $\alpha_0$  and/or  $\alpha_1$  as fixed or random effects. The coefficient  $\delta$  gives the effect of crowding on survival; a negative value of  $\delta$  indicates competition. All genets in a quadrat are included in calculating  $W$ , but plants located within 5 cm of quadrat edges are not used in fitting or selecting demographic models.

For the tests here, we used eqns (1) and (3) because they are typical of previous spatial competition models and IPMs. More general or different models will often be needed in empirical applications. For example, nonlinear effects of plant size could be included applying a log or power transformation to  $A_{i,k}$ ,  $W_i$  or  $z$ , and terms for climate covariates and for interactions between crowding and focal plant size could be added to eqn (3). Our approach to estimating the competition kernel generalizes very straightforwardly to these more general demographic models.

We assume that the competition kernel,  $F(d)$ , is non-negative and decreasing, which means that distant plants have less effect than close plants. Otherwise, we want to let the data dictate the shape of  $F$ . To achieve this, let  $r$  and  $R$  be the minimum and maximum mid-annulus radii, respectively, and

$$F(d) = e^{-f(d)}, \quad f(d) = \int_r^d g^+(u) du, \quad r \leq d \leq R \quad (\text{eqn 4})$$

where  $g(u)$  can be any function and  $g^+ = \max(0, g)$ . This form ensures that  $g^+$  is a positive function; hence,  $f$  is increasing and  $F$  is positive and decreasing. In practice, we specify  $g$  as

$$g(d) = \sum_j b_j \phi_j(d) \quad (\text{eqn 5})$$

where the functions  $\phi_j$  are a cubic B-spline basis on  $[r, R]$  with dimension high enough to overfit any plausible distance kernel (for a basic description of B-splines see Table S1). To make  $F$  a smooth function of the spline coefficients, we do not actually use  $g^+$ , which is non-differentiable at  $g = 0$ . Instead, we use  $H(g) = (g^+)^2 / (0.02 + g^+)$ , which is very close to  $g^+$  except that it slightly rounds off the corner at  $g = 0$  (see Figure AppS1.1).

The demographic models such as eqn (3) have  $\alpha_0, \alpha_1, \gamma_q, \delta$  and the vector of spline coefficients  $\vec{b}$  as parameters to be fitted. This can be done in the statistical computing environment, R, by making  $\vec{b}$  the argument of an objective function that computes  $W$  using the input value of  $\vec{b}$ , calls a model-fitting function such as `lm`, `lmer` and/or `glm` to fit the

other model parameters and returns the negative log-likelihood. In all examples below, models for both survival and growth were fitted, and the sum of the two log-likelihoods was used. This assumes that one measure of crowding affects survival and growth but in principle two different competition kernels could be fitted.

With a high-dimensional spline basis, the fitted kernel can have spurious wiggles driven by noise in the data. We therefore use a penalized likelihood approach, which is standard for spline regression models. The spline and other model parameters are chosen to minimize

$$-(\log \mathcal{L}_g + \log \mathcal{L}_s) + \lambda \int_r^R (g''(x))^2 dx \quad (\text{eqn 6})$$

where  $\log \mathcal{L}_g$  and  $\log \mathcal{L}_s$  are the log-likelihoods of the fitted growth and survival regressions, and the rightmost term is the standard roughness penalty on cubic splines. The *smoothing parameter*  $\lambda$  controls how much wiggleness in the  $g$  curve is penalized, with larger  $\lambda$  producing a less wiggly curve.

The remaining step is finding an objective way of choosing  $\lambda$ . In Appendix S1, we show how an approximate AIC value can be computed for a model fitted with a given value of  $\lambda$ , and we propose to choose  $\lambda$  by minimizing  $\text{AIC}(\lambda)$ . Source code for these methods is provided in the online Supplementary Information.

#### SIMULATION STUDY DESIGN

The goal of the simulation study was to see how accurately we can recover the shape of the competition kernel, from artificial data that were generated with a known kernel.

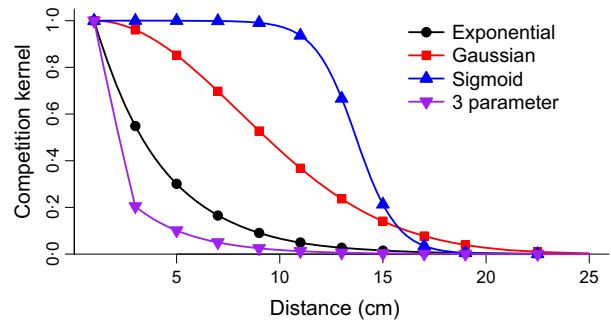
The artificial data were based on the real data for two of the dominants in our study system, the shrub *Artemisia tripartita* (ARTR) and perennial bunchgrass *Pseudoroegneria spicata* (PSSP). These species were chosen because they had the lowest and highest importance of competition (see below for how this was estimated). ARTR also has the fewest observations. We generated simulated data using four test kernels: exponential  $e^{-\alpha d}$ , Gaussian  $e^{-\alpha \max(d-1,0)^2}$ , sigmoid  $1/(1 + e^{0.5(d-d_c)})$  and the exponential-linear kernel  $f e^{-\alpha d} + (1-f) \max(0, 1-bd)$ , where  $d$  in all cases is the distance from the focal individual (see Fig. 2). The  $\max(d-1,0)$  in the Gaussian is because the smallest annulus radius is  $d = 1$ , and putting the kernel peak at  $d = 1$  makes the Gaussian qualitatively different from the exponential at small distances.

For each assumed kernel and each species, we used the actual data and our assumed kernel to compute crowding  $W$  for each genet, which represents what competition would be like if our assumed kernel were reality. We then fitted regression models using the real data with the calculated  $W$ ,

```
fitG = lm(logarea.t1 ~ Group + logarea.t0 + W)
fitS = glm(survives ~ Group + logarea.t0 + W)
```

Next, we generated artificial data sets by simulating new responses based on the fitted models: survival or death by a 'coin toss' using the fitted survival probability for each individual in each year and growth by adding a randomly chosen residual to the fitted value from the growth model.

An important step (glossed over in the preceding paragraph) is that before generating artificial data, the fitted models were modified to match the importance of competition in the real data. This adjustment is needed because fitting a deliberately wrong kernel underestimates the impact of competition. The importance of com-



**Fig. 2.** The four competition kernels used to generate artificial data for the simulation study on fitting the competition kernel; three parameter refers to the exponential-linear kernel with three parameters. The filled circles show the kernel values at the mid-radius of each annulus; only the values of the kernel at those distances are used to compute the crowding experienced by a focal genet.

petition for growth and survival was estimated by first fitting the regression models above, in which  $W$  was calculated using the 3-parameter exponential-linear kernel with kernel parameters chosen to maximize the combined log-likelihoods for survival and growth. This is done by the script *ImportanceOfCompetition.R* in Data S1. The final results on our real data suggest that the exponential-linear kernel is a good approximation to the best-fitting kernel, so using it here should give a good approximation to the true importance of competition. The importance of competition was measured by refitting the models without  $W$  as a covariate, and computing the fractional reduction in residual variance (for growth) or residual deviance (for survival) that results from having  $W$  as a covariate (i.e.  $(R0-R1)/R0$  where  $R1$  and  $R0$  are the residual deviance or variance for models with and without  $W$ ). The importance of competition for growth in all species was under 0.02; the importance of survival was 0.10 for ARTR, 0.165 for PSSP and 0.12 for the two other bunchgrasses (results were very similar when this analysis was repeated with *factor(year)* as an additional covariate). Getting back (finally) to our artificial data: the coefficient on  $W$  in the fitted survival models was magnified so that the importance of competition for survival in the artificial data, averaged over 25 replicate artificial data sets, equalled the estimated actual importance for the species.

We generated 40 test data sets (5 replicates  $\times$  4 kernels  $\times$  2 species). For each data set, we fitted the kernel by using the NEWUOA algorithm in the *minqa* package (Bates *et al.* 2014) to minimize the penalized likelihood at a grid of  $\lambda$  values ( $\log \lambda = -6, -5, \dots, 5, 6$ ); we also recorded the estimated model degrees of freedom (DoF) for each  $\lambda$  (we explain in Appendix S1 how DoF is calculated). We used multistart optimization, described in Appendix S1. Graphs of AIC vs.  $\lambda$  or DoF had a sigmoid shape, with high AIC at large  $\lambda$ /low DoF, a steep decrease over a few orders of magnitude decrease in  $\lambda$ , and a shelf of much lower AIC values at smaller  $\lambda$ /higher DoF (see Figure S1.1 for an example). The approximations justifying AIC break down at high DoF, which can result in AIC being minimized at  $\lambda \approx 0$ . To avoid this kind of overfitting, we used the smoothest (lowest DoF) local minimum of AIC as a function of DoF within the lower shelf.

#### Neighbourhood competition: results

For all four test kernels and both species, fitting by approximate AIC produced good estimates of the competition



kernel shape used to generate the data (Fig. 3). The fits are far from perfect and somewhat variable across replicate data sets. However, the baseline for evaluating the fits is that the spline model has the flexibility to produce essentially any non-increasing function of distance. Despite competition only explaining a relatively small fraction of the observed responses (10% of the residual deviance in survival for ARTR, 16.5% of the residual deviance in survival for PSSP, and under 2% of the growth variance for both), the spatial scale of interaction was estimated well in all cases. The shape was generally estimated well in most cases for both ARTR and PSSP. The fits for artificial data sets based on ARTR (red curves) are generally more variable than those based on PSSP, probably because competition was less important and the sample size is smaller.

We used only five replicate data sets for each kernel-species pair, because fitting by nonlinear optimization could not be automated. Getting trapped in local optima was common, even with repeated restarts as part of each optimization. It was necessary to inspect results, and repeat unsuccessful optimization runs, to obtain fairly smooth curves of AIC as a function of  $\lambda$  and of model degrees of freedom.

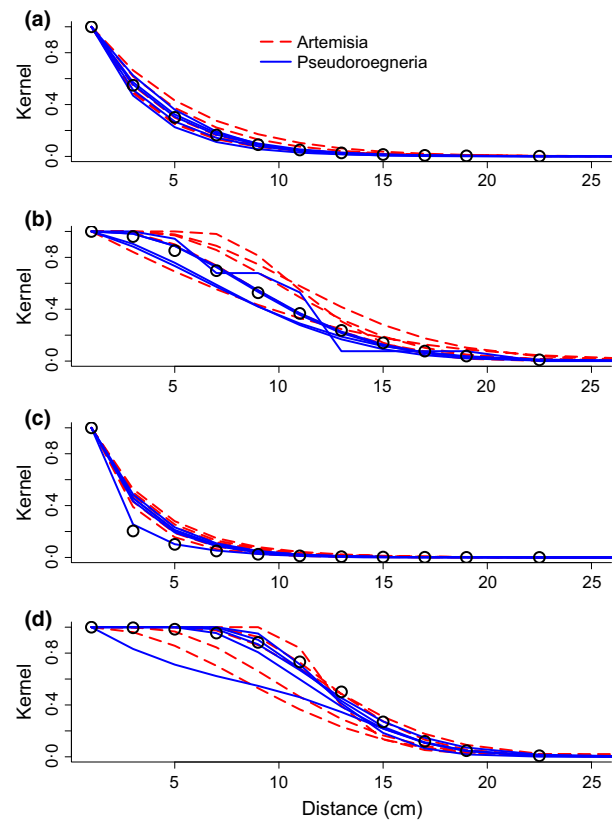
The kernels estimated for the sagebrush steppe real data (Fig. 4) are very similar for the four dominant species. The fitted kernels suggest a zone of intense competition with close neighbours, a slightly wider zone of weaker competition, and no competition at all with neighbours separated by 10 cm or more. Very similar kernels were estimated when the demographic models account for temporal variability by including year as an unordered covariate (Figure S1.2).

### Climate covariates: methods

The traditional approach to high-dimensional problems is to combine *a priori* assumptions with forward model selection routines [that choose the model with the lowest AIC; for example, Dalglish *et al.* (2011)]. Recently, ecologists have also begun applying a wider range of data-driven methods, such as least absolute shrinkage and selection operator (LASSO) which underlies maxEnt (Elith *et al.* 2011) and machine learning methods such as random forests (RF) (Cutler *et al.* 2007; Dahlgren 2010). Here, we compare the performance of functional linear models (FLM) with LASSO and RF.

#### FUNCTIONAL LINEAR MODELS USING SPLINES

Functional linear models are linear regression models in which the covariate is a function on a continuous domain (Ramsay & Silverman 2005; Ramsay *et al.* 2009). The critical feature of FLM is that it uses the temporal relationships among climate covariates. Precipitation and temperature values at discrete times (e.g., monthly rainfall) are typically entered into regressions as independent covariates. FLM assumes that the effects of such variables are smooth functions of time. For example, the coefficients relating monthly precipitation to survival should be similar for February and March, but the coefficients for March and September could be quite different. We estimate the response as the convolution over time lags between a coefficient function  $\beta(l)$  and the climate covariates:



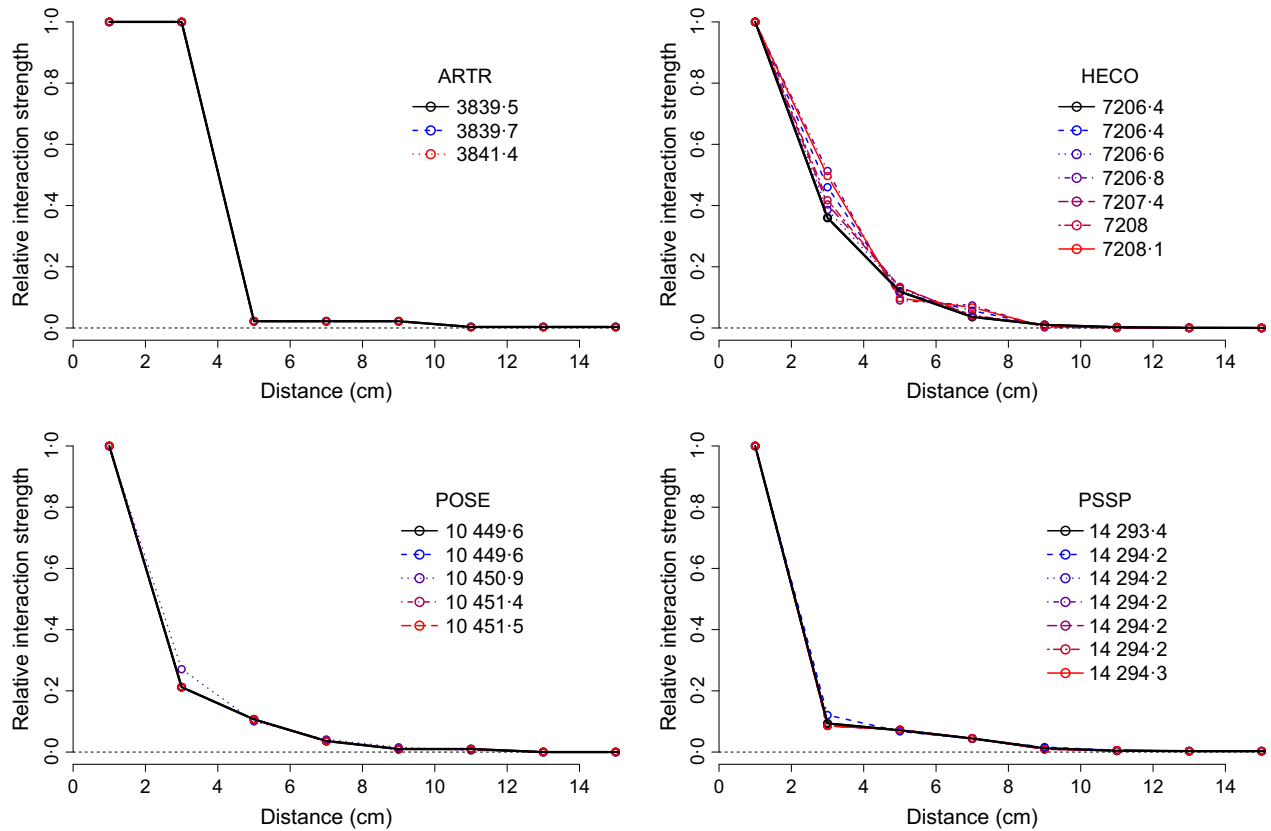
**Fig. 3.** Results of fitting artificial data with known competition kernels. (a) Exponential, (b) Gaussian, (c) Exponential-linear three-parameter kernel and (d) Sigmoid. In each panel, the lines (red: *Artemisia*; blue: *Psuedoroegneria*) show the optimized kernels, at the value of the smoothing parameter  $\lambda$  that minimized the approximate AIC, evaluated at the mid-radius of each of the annuli used to crowding. Each line corresponds to one of the five artificial data sets for that kernel  $\times$  species combination. The black open circles are the kernels used to generate the data, evaluated at the same points.

$$y_i = \alpha_0 + \sum \alpha_j x_{ij} + \int_0^L \beta(l) X(t_i - l) dl + \epsilon_i. \quad (\text{eqn } 7)$$

Here,  $X(t)$  represents the climate process, the integral is over time lags  $l$  from the current time  $t_i$  back to  $t_i - L$ . The  $x_{ij}$  are scalar covariates such as competition and current plant size. The smooth function  $\beta(l)$  is parameterized by a spline basis expansion  $\beta(l) = \sum_k d_k \phi_k(l)$ , just like eqn (5) for the competition kernel. The parameters  $\alpha_j$  and  $d_k$  are again fit by penalized least squares with roughness penalty

$$\lambda \int_0^L (\beta''(l))^2 dl. \quad (\text{eqn } 8)$$

This is a standard spline regression problem (unlike our spline model for competition kernels). We fit the FLM model using the *mgcv* package in R (see Wood, 2006, 2011). For a complete example script, see Data S1: ...Rcode/Climate/AuthenticAnalysis/AuthenticAnalysis.R. We used the *cs* spline basis which adds a small ridge penalty to eqn (8) and so favours setting the coefficient to 0 for a covariate that has no real effect. We chose  $\lambda$  by the GCV criterion with model degrees of freedom inflated by 20% to avoid overfitting. Thanks to Wood (2011), one call of *gam* fits the model and returns estimated coefficients and standard errors similar to traditional methods. See van de Pol & Cockburn (2011) and Bailey & van de Pol (2015) for a similar



**Fig. 4.** The competition kernels fitted to the four dominant species in the Idaho sagebrush steppe data set. The curves are the best-fit kernel (black line: the smoothest local minimum of AIC as a function of model complexity) and all other fits (coloured lines), at other values of the smoothing parameter  $\lambda$ , with AIC values larger than the fitted kernel by 0 to 2 AIC units. The circles show the kernels evaluated at the mid-radius of each of the annuli used to compute competition pressure. Legends give the species code for each panel, and the AIC values, for the plotted kernels.

approach that fits a parametric curve to describe a single time window of climate impacts.

#### LASSO

The LASSO, introduced by Tibshirani (1996) as a variant on ridge regression for linear models, can handle a high number of covariates by ensuring that covariates with little effect on the response have little effect on predictions. The parameter vector  $(\beta_0, \beta_1, \dots, \beta_p)$  is estimated by minimizing the penalized squared error

$$\sum_{i=1}^n \left( y_i - \beta_0 - \sum_{k=1}^p \beta_k x_{ik} \right)^2 + \lambda \sum_{k=1}^p |\beta_k|. \quad (\text{eqn 9})$$

The  $\beta_k$  returned from LASSO have the same meaning as the  $\beta$  coefficients in an FLM. Tibshirani (1996) demonstrated that as  $\lambda$  is increased from 0, more and more of the estimated  $\beta_k$  are exactly 0. This gives us a natural sequence of models to consider, with fewer and fewer covariates and coefficients. We obtained the  $\beta_k$  that minimize eqn (9) using the coordinate descent algorithm implemented in the `glmnet` package in R (Friedman, Hastie & Tibshirani 2010), and we used cross-validated mean square prediction error (leaving out one year of data at a time) to choose the value of  $\lambda$ .

#### RANDOM FORESTS

Machine learning algorithms built for ‘big data’ have also received increasing attention in recent years. Random forests (RF - Breiman

2001) constructs a large number of decision trees using bootstrap samples of the data and averages their predictions. This simple idea works remarkably well: in applications with abundant but very high-dimensional data (i.e. many possible covariates), RF has been found to have exceptional ‘off-the-shelf’ predictive accuracy (that is, without requiring specialized knowledge of either the data or the fitting algorithm; Hastie, Tibshirani & Friedman 2009).

Random forests is not explicitly designed to identify coefficients – the predictive ability of machine learning methods usually comes at the cost of interpretability. For the analyses here that compare the performance of all three methods, we use local sensitivity to identify which covariates are important in a fitted model. With a set of potential covariates  $X = (x_1, \dots, x_p)$ , each model framework (FLM, LASSO and RF) produces a function  $\hat{F}(X)$  that predicts an outcome  $y$ . To evaluate the importance of a covariate  $x_1$ , we perturb the values of (for example)  $x_1$  in the predictor set by  $\epsilon$  equal to 5% of the covariates standard deviation and evaluate sensitivity as follows:

$$s(x_1) = \sum_{i=1}^b \frac{\hat{F}(x_{i1} + \epsilon, x_{i2}, \dots, x_{ip}) - \hat{F}(x_i)}{\epsilon} \quad (\text{eqn 10})$$

If the sensitivity of the model to perturbation of covariate  $i$  is large when the assigned coefficient for that covariate is large (and *vice versa*), the correlation between the two will be positive; here, we use this correlation to measure how well the truly important covariates have been identified.

We use our sensitivity and correlation measures of concordance with the generating model because the variable importance measures

originally proposed in Breiman (2001) perform poorly on correlated covariates (see Hooker 2007; Strobl *et al.* 2007). However, because RF estimates a nonlinear relationship between covariates and response, sensitivity measures may not correlate with the true coefficients as well as LASSO and FLM, which exactly mimic the linear relationship in our generated data.

#### SIMULATION STUDY DESIGN

To assess how well FLM, LASSO and RF can recover a known climate signal, we generated artificial data sets with known effects of climate, based on the real data from our study system. The simulated data sets include a daily sequence of temperature and precipitation values that can be modified by changing the temporal autocorrelation within each predictor,  $\theta_s$ , the amount of cross-correlation between temperature and precipitation,  $\theta_c$ , and the number of years of data. These daily data can be aggregated in any number of ways, but here, we have limited the aggregation to monthly or weekly means.

To simulate artificial temperature data (see Appendix S2 for a full description), we estimated the seasonal trend by fitting a spline to 70 years of historical data from Dubois, ID, USA, (average of daily maximum and minimum temperatures as a function of day of year) and added to this an AR1 (first-order autoregressive) process to represent deviations from the trend. For precipitation, splines were fit to the probability of precipitation. We generated a log precipitation amount for each day by adding a first-order autoregressive process to the seasonal trend in log precipitation. We then did a 'coin toss' to decide whether or not precipitation actually occurred on each day, based on the fitted seasonal trend in the probability.

We also generated a demographic data set based on the real data that gives individual size  $z(t+1)$  as a function of  $z(t)$  and climate covariates for a specified number of individuals ( $z = \log$  genet area). As shown in Fig. 1 2b., the first step is to fit a regression model for  $z(t+1)$  as a function of  $z(t)$ , using the real data on the dominant shrub, *Artemisia tripartita*. Note that, this regression did not include climate covariates. Then, in Fig. 1. step 3b., we create an artificial  $z(t+1)$  for each  $z(t)$  in the data set by doing a residual bootstrap from the fitted model. We then add a known response to climate at specified lags based on designed regression coefficients. The analyses begin at lag time 0 (the time at which a demographic transition,  $z(t+1)$  is recorded), and proceed back in time to cover the previous three years of climate data. Coefficients include a positive effect of spring precipitation and a negative effect of winter temperature over the previous two years; climate signals more than 2 years prior have no effect. In simulations where we compared aggregation by month and by week, coefficients were assigned the same way (that is, coefficients for the month are distributed over four weeks). We chose these coefficients with the intent to make it difficult for the models to detect the true signal, especially when cross-correlation in climate covariates ( $\theta_c$ ) is high. The artificial climate response is scaled to have a known fraction ( $f_\sigma$ ) of the true variance in growth in the data,  $\sigma^2 = f_\sigma * \text{Var}[z(t+1) - z(t)]$  (for exact methods and code, see Appendix 2 and Data S1).

We generated 10 artificial climate and demography data sets for each set of user-specified parameters (Table AppS2.1). with lagged climate covariates (monthly or weekly) and  $z(t)$  as potential predictors of  $z(t+1)$ . Finally (step 4 in Fig. 1), we applied each statistical method to the same data set. Model success is judged based on sensitivity analysis (described above) and (for FLM and LASSO) by comparing estimated to

true coefficients. We only examined growth, but our methods are readily adapted to data on survival.

#### Climate covariates: results

Figure 5 shows that in the most favourable trial case, with 50 years of data and 60 individuals per year, both FLM and LASSO perform well, identifying the correct climate drivers and their relative importance. With fewer years of data, but more individuals per year (keeping the total number of observations constant), model performance is poorer (Fig. 6). All three methods appear to require at least 20–25 independent observations of a climate signal and the response (here, 20–25 years of demographic data). More observations within each year does not substantially improve the performance with <20–25 years of demographic data, because each individual within a year shares the same climate history. Figures S1.3 and S1.4 show very similar results for a scenario with constant sample size per year, rather than constant total sample size.

Over a range of relative variances ( $f_\sigma$ ), given sufficient years (>25–30), linear methods (FLM and LASSO) can generally detect artificial climate signals that are small relative to the demographic response (Fig. 6). This remains true for FLM, but not LASSO, when the resolution of the lagged climate data is increased from monthly to weekly (Figs 7 and 8).

At a fixed half-life of autocorrelation ( $\theta_s$ ; covariates are correlated with themselves over time), the degree to which climate variables are cross-correlated ( $\theta_c$ ) does not strongly affect performance for any of the fitting methods, despite our best efforts to sow 'confusion' by adding correlations among the covariates (Fig. 9).

#### Discussion

Over the past two decades, new statistical methods have allowed ecologists to fit dynamic population and community models to field data, bridging the gap between theory and empirical research in ecology (e.g., Kendall *et al.* 2005; Cao, Fussmann & Ramsay 2008; New *et al.* 2009; Karban & de Valpine 2010; Mantilla-Beniers *et al.* 2010; Meisner, Harmon & Ives 2014; and the many examples of data-driven matrix projection and integral projection models). Our results represent a further step in this progression. Currently, models of local competition assume some parametric competition kernel *a priori* (Adler *et al.* 2010), and models incorporating climate drivers typically aggregate continuous data to specific time periods based on assumptions about when organisms are most active or most sensitive to the environment. The functional smoothing approaches we developed and evaluated greatly reduce the need for such assumptions: given sufficient data, the form of the competition kernel and the effects of climate covariates at different times of the year can emerge from the data themselves.

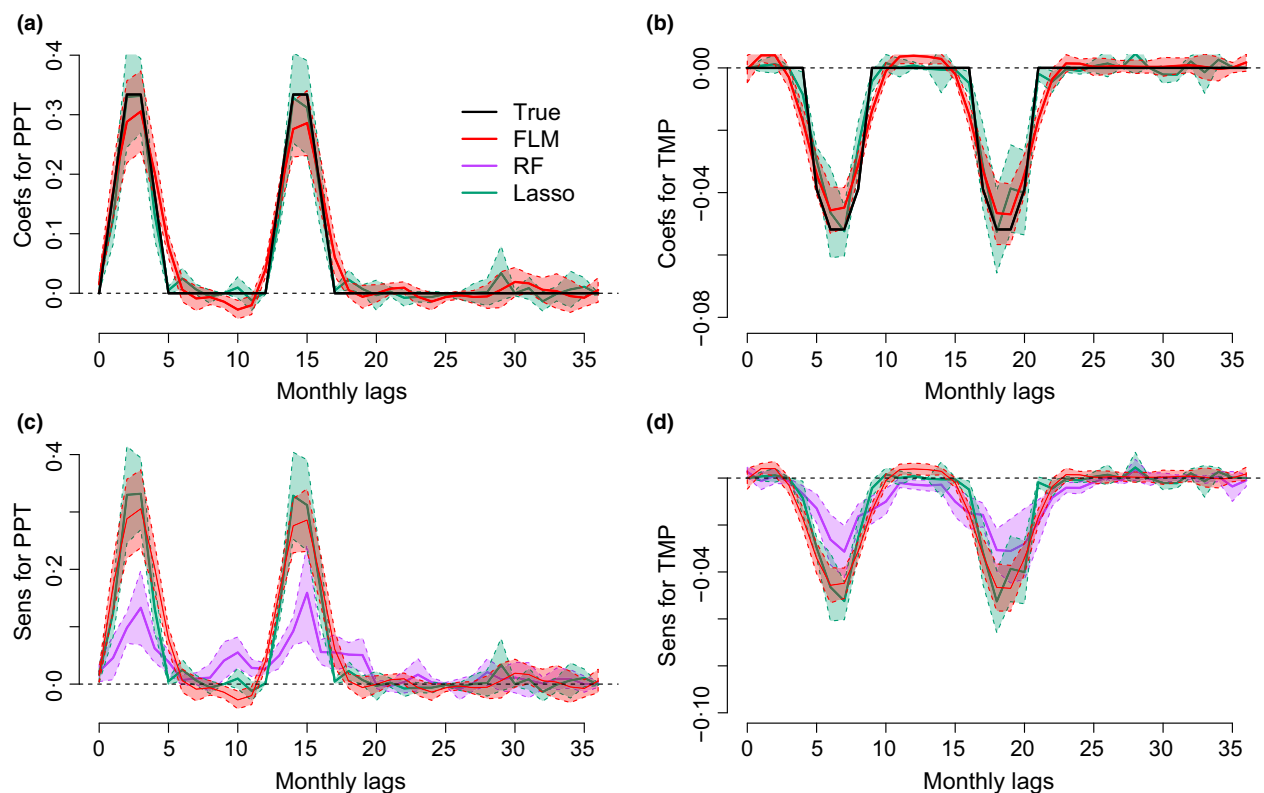
For our four study species, the effect of competition on growth and survival was very weak relative to other sources of variation. Nonetheless, in artificial data generated to have the same low importance of competition, our method for

estimating the competition kernel identified the scale of the competitive neighbourhood very accurately and was mostly successful at estimating the shape of the competition kernel (Fig. 3). The kernels estimated for the real data (Figs 4 and S1.2) are unlike any typically used in theoretical or data-driven models (e.g. exponential or Gaussian kernels). However, our estimates align with the findings of Schneider *et al.* (2006). They found that competitive effects in their data were well described by a simple kernel in which the intensity of competition is proportional to the spatial overlap between two genets. This gives a narrow zone of intense competition, falling off quickly to no competition at all, even between fairly close neighbours. Our estimated kernels also have an outer zone of weak competition, but omitting this feature may not have much effect on the predicted fates of individuals. Our approach could easily be extended to study interspecific interactions.

Our climate driver simulations showed that functional smoothing methods (FLM) successfully detected the drivers of the demographic response, given sufficient independent observations of climate history (20–25 years or more). This generalization holds true across many different kinds of simulated data sets including different temporal resolutions of the climate data, relatively high and low relative variance ( $f_\sigma$ ) of the climate response and cross-correlations of the climate covariates (see Fig. 8). FLMs have a notable advantage over

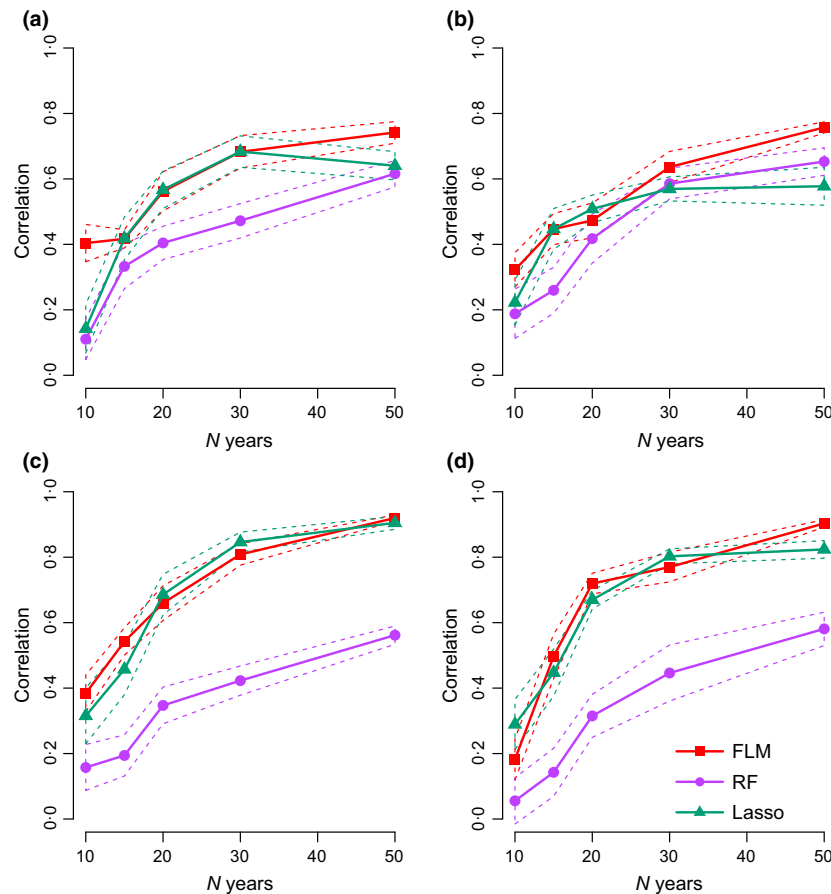
the other methods because they assume that the response is a smooth function of the predictors as a function of time lag. Rainfall 100 days ago should have about the same effect on the demographic response as rainfall 99 or 101 days ago. FLM turns an overabundance of temporal data into an opportunity, rather than an obstacle. Furthermore, applications of FLM need not be limited to climate covariates. Other continuously monitored biotic and abiotic drivers, such as soil moisture, nutrient availability or physiological performance, could be handled the same way. For high-dimensional problems in which the effects of covariates are not likely to be smooth functions of distance or time, LASSO would be more appropriate. Of course in observational data, collinear predictors may obscure the true driver of a demographic signal, and so practitioners ought to take care to identify unobserved correlated covariates that may contribute to the trends that they identify using these methods.

Our studies of climate drivers relied on ‘off-the-shelf’ statistical tools that can be used in traditional ways for inference and prediction (similar to `lm` or `glm` in R). Ongoing development, most notably in LASSO and RF, may further improve model performance. Recent research on LASSO includes alternative selection methods (Belloni, Chernozhukov & Wang 2011; G’Sell *et al.* 2013; Lederer & Müller 2015) as well as penalties designed for other



**Fig. 5.** Functional linear models (FLM), random forests (RF) and LASSO models with 50 years of artificial data, when the climate covariates for each observation of size  $z(t+1)$  are monthly averages of temperature and precipitation over the three years preceding the observation ( $t_0 = 0$ ). These artificial data sets had no climate cross-correlation ( $\rho = 0.0$ ) and a strong climate signal in growth ( $f_\sigma = 0.5$ ). Upper panels show true coefficients (black lines) and the estimated coefficients from FLM and LASSO, and the lower panels show the relative importance of each covariate as measured by local sensitivity analysis, eqn (10) (mean and SE of 10 replicates).



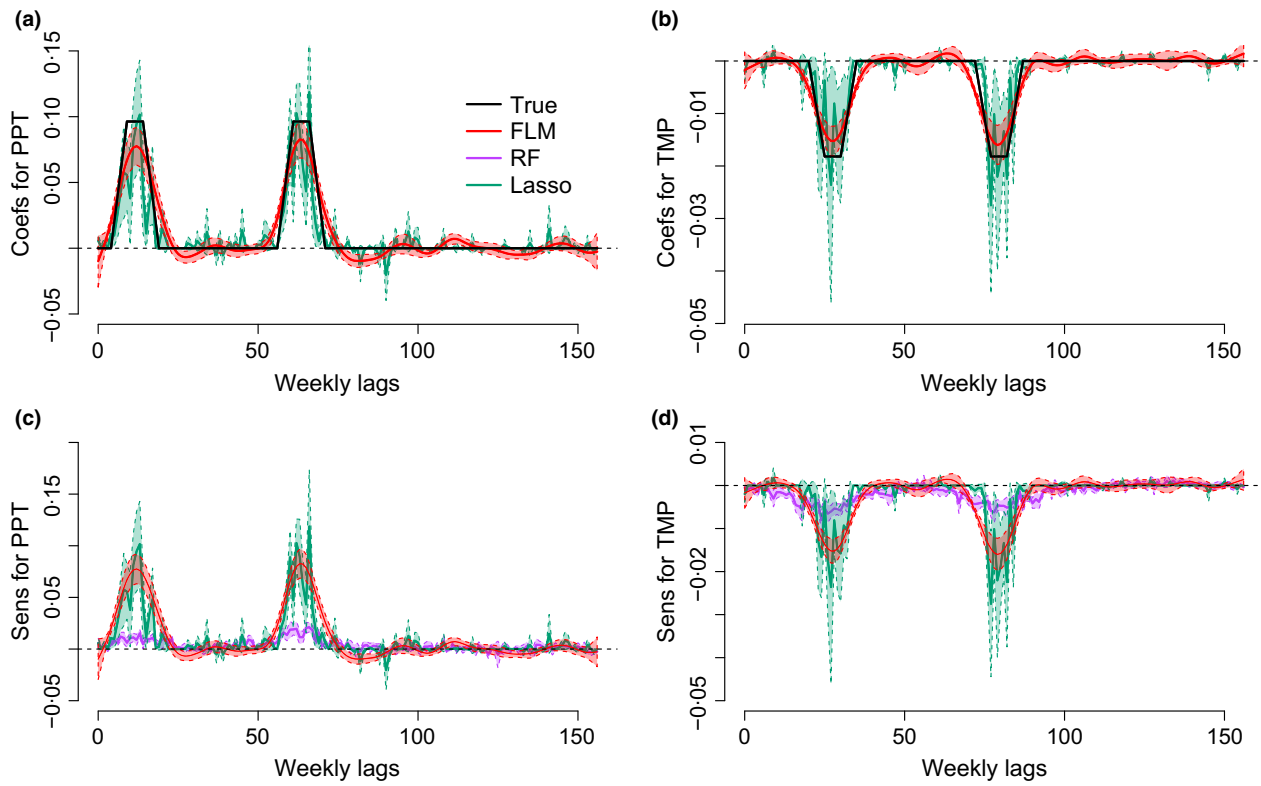


**Fig. 6.** Summarized model performance (correlation with true coefficients) vs. the number of independent observations of growth (years) when climate data is lagged by month. In the top panels (a and b), relative variance of the climate response is low ( $f_{\sigma} = 0.05$ ); model performance with regard to precipitation coefficients is plotted on the left, and temperature coefficients on the right. In the lower panels (c and d), the relative variance of the climate response is high ( $f_{\sigma} = 0.5$ ).

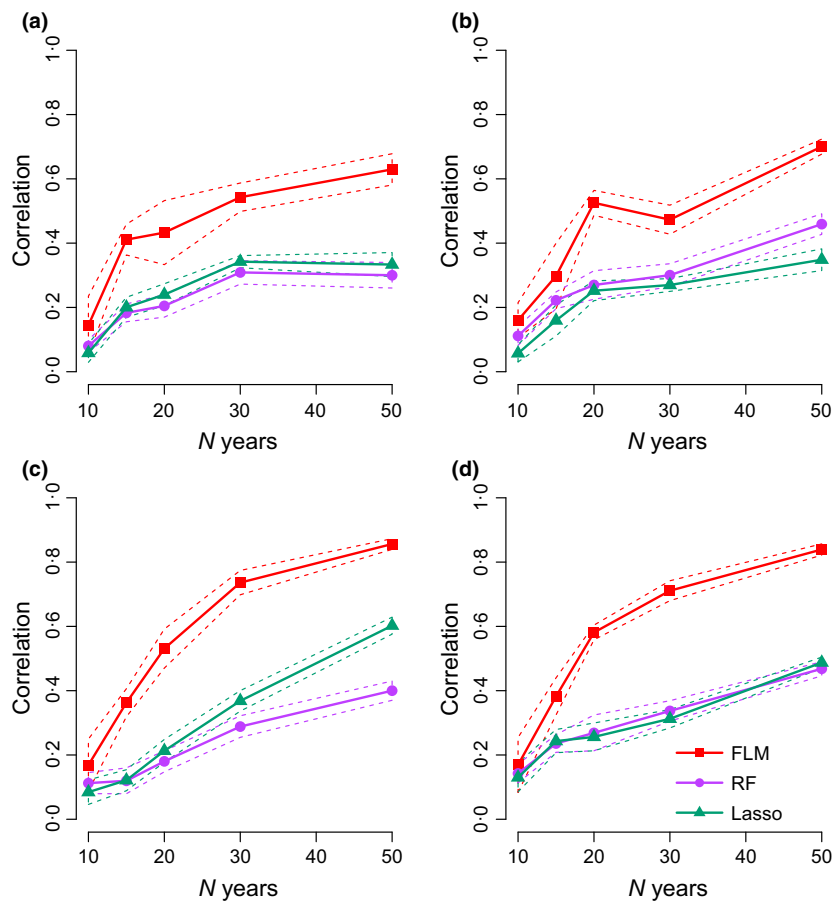
forms of sparsity, such as giving adjacent coefficients the same value (Tibshirani *et al.* 2005; Wang & Leng 2008). Functional linear models have been extended to allow non-linear responses (McLean *et al.* 2014), to include sparsity-type penalties (James, Wang & Zhu 2009) and to allow data-driven selection of how much past history to use (Hall & Hooker 2014). Machine learning methods rarely come with statistical measures of uncertainty, but confidence intervals and hypothesis tests for RF have very recently been developed (Mentch & Hooker 2014a, 2014b; Wager 2014). Better ways of assessing variable importance in RF are still needed. The standard methods work poorly on correlated data, and our sensitivity measure is not well-suited to strongly nonlinear responses and may have underestimated the performance of RF. In addition, moving window approaches that use flexible functions to directly test hypotheses about the importance of specific lags or time periods are also available (van de Pol & Cockburn 2011; Bailey & van de Pol 2015).

Despite our general optimism about smoothing methods, we did find some important limitations. First, our ability to identify climate drivers is limited by the number of independent observations of climate history. Our data sets contain observations on thousands of individual plants, but only 22

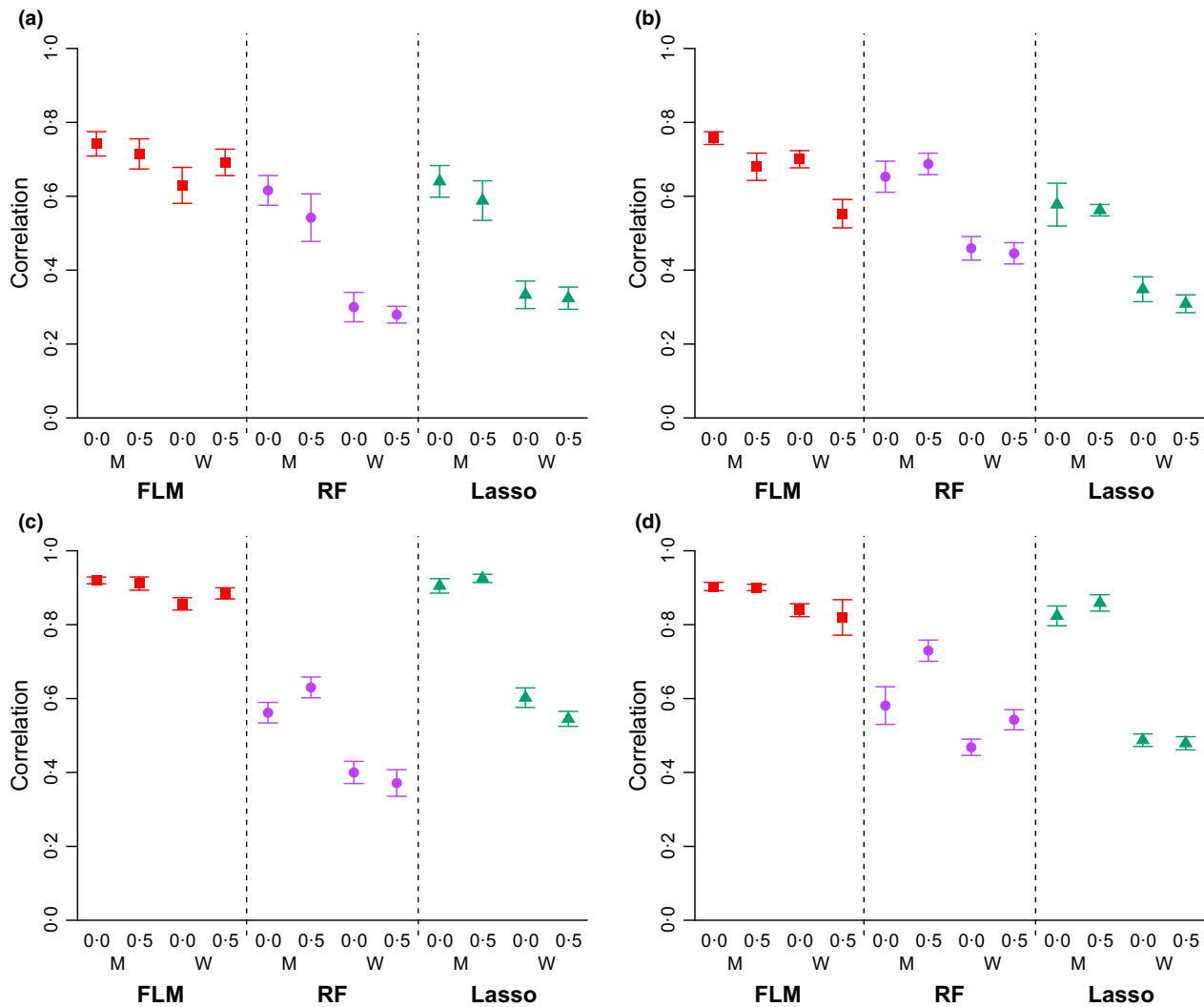
different year-to-year transitions. All observations at one census have a common climate history. Given that few demographic data sets are much longer, to learn more about climate drivers we need creative ways to increase the effective sample size. A possible solution is to take advantage of spatial variation in climate (e.g. Doak & Morris 2010), however, spatial variation in climate is likely to be accompanied by variation in other abiotic and biotic variables. Second, our simulations of climate effects on demography did not include several significant biological processes that may complicate the analysis of real data. For example, our simulated demographic data sets considered only linear growth responses to climate conditions, and these responses may be better characterized by nonlinear reaction norms (Schlichting & Pigliucci 1998). We did not consider interactions between individual size and climate. In fact, exploratory analyses of the Idaho data set suggest that size by climate interactions are important, with small plants responding more strongly and in different ways than large plants. While these analyses are possible, they are beyond the scope of the current analysis, and we decided that it would not yet be appropriate to present empirical analyses of climate responses in the Idaho data set. Ecologists should consider these limitations before applying our methods to their data.



**Fig. 7.** As in Fig. 5, except that the climate covariates are weekly rather than monthly averages over the three years preceding each observation.



**Fig. 8.** As in Fig. 6, except that the climate covariates are weekly rather than monthly averages over the 3 years preceding each observation.



**Fig. 9.** Summarized model performance with 50 years of data at different levels of cross-correlation between climate covariates ( $\rho$  is 0.0 or 0.5) and at different aggregations of climate data: by month ('M') or by week ('W'). The performance measure is the correlation coefficient between the true regression coefficients for each lag and the variable importance estimated by sensitivity analysis, eqn (10). Panels show model performance for precipitation and temperature coefficients (left and right, respectively) when the relative variance of the climate response is low (panels a and b;  $f_\sigma = 0.05$ ), and when relative variance is high (c and d;  $f_\sigma = 0.5$ ).

The best way to determine whether our methods, or others, are appropriate for a given data set is to follow our example and standard practice in the statistical literature: simulate artificial data with a known response and confirm that the method can recover the signal. The code and discussion (Appendix 3) that we provide illustrate how to perform that exercise. It may be important to add other ecological sources of variation in simulations (in addition to the climate and competition signals we describe here). If simulations show that the data set does not contain enough independent observations, or if exploratory analysis reveals important interactions, then traditional approaches for simplifying models based on *a priori* information may be necessary.

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### Data accessibility

Data and R scripts to replicate the analyses are available as online Supporting Information for this article, Data S1 (see below).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.1.** Basic descriptions of statistical methods: functional linear methods (splines), LASSO, and random forests.

**Figure S1.1.** Plot of approximate AIC vs. estimated model degrees of freedom (see Appendix S2) for one of the artificial data sets with a sigmoid competition kernel based on the PSSP real data.

**Figure S1.2.** The competition kernels fitted to the four dominant species in the Idaho sagebrush steppe data set, plotted as in Fig. 4, when year is included as a factor covariate in the demographic regression models.

**Figure S1.3.** Model performance with constant effort (100 individuals per year) vs. the number of independent observations of growth (years) when climate data is lagged by month.

**Figure S1.4.** Summarized model performance with constant effort (100 individuals per year) and 50 years of data at differing levels of cross-correlation between climate covariates ( $\rho$  is 0.0 or 0.5), and at differing levels of lag aggregation: month ('M') or week ('W').

**Appendix S1.** Detailed methods on fitting the spatial interaction kernel.

**Appendix S2.** Detailed methods on climate simulation and user's guide.

**Data S1.** Data, R scripts and user's guide (zip file) for the analyses in this paper.