



# Should Species Distribution Models Account for Spatial Autocorrelation? A Test of Model Projections Across Eight Millennia of Climate Change

## Citation

Record, Sydne, Matthew C. Fitzpatrick, Andrew O. Finley, Sam Veloz, and Aaron Ellison. Forthcoming. Should species distribution models account for spatial autocorrelation? A test of model projections across eight millennia of climate change. *Global Ecology and Biogeography*:12017.

## Published Version

doi:10.1111/geb.12017

## Permanent link

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1 Running title: Projecting spatial species distribution models

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4 Should species distribution models account for spatial autocorrelation? A test of model

5 projections across eight millennia of climate change

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15 Key words: Bayesian, historical validation, spatial random effect, paleoecology

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18 Article type: Research Paper

19 **ABSTRACT**

20 **Aim** The distributions of many organisms are spatially autocorrelated, but it is unclear whether  
21 including spatial terms in species distribution models (SDMs) improves projections of species  
22 distributions under climate change. We provide one of the first comparative evaluations of the  
23 ability of a purely spatial SDM, a purely non-spatial SDM, and a SDM that combines spatial and  
24 environmental information to project species distributions across eight millennia of climate  
25 change.

26 **Location** Eastern North America.

27 **Methods** To distinguish between the importance of climatic versus spatial explanatory variables,  
28 we fit three Bayesian SDMs to modern occurrence data for *Fagus* and *Tsuga*, two tree genera  
29 whose distributions can be reliably inferred from fossil pollen: a spatially-varying intercept  
30 model, a non-spatial model with climatic variables, and a spatially varying intercept plus climate  
31 model. Using high temporal resolution paleoclimate data, we hindcasted the SDMs in 1,000 year  
32 time steps for 8000 years, and compared model projections with palynological data for the same  
33 periods.

34 **Results** For both genera, spatial SDMs provided better fits to the calibration data, more accurate  
35 predictions of a hold-out validation dataset of modern trees, and higher variance in current  
36 predictions and hindcasted projections than non-spatial SDMs. Performance of non-spatial and  
37 spatial SDMs according to the Area Under the Curve of the Receive Operating Curve varied by  
38 genus. For both genera, false negative rates between non-spatial and spatial models were similar,  
39 but spatial models had lower false positive rates than non-spatial models.

40 **Main conclusions** The inclusion of computationally demanding spatial random effects in SDMs  
41 may be warranted when ecological or evolutionary processes prevent taxa from shifting their  
42 distributions or when the cost of false positives is high.

## 43 INTRODUCTION

44 The last decade has witnessed a marked increase in the application of models that project the  
45 potential geographic distributions of species by linking observations of species occurrences to  
46 environmental predictor variables. These models, commonly called bioclimatic envelope,  
47 ecological niche, or species distribution models (hereafter SDMs), are important tools for  
48 forecasting impacts of climatic change on biological diversity and for generating conservation  
49 plans and climate-change policy (Guisan & Thuiller, 2005). To project future distributions under  
50 different, plausible scenarios of climatic change, SDMs use statistical relationships between  
51 present-day distributions of species and climate (Elith *et al.*, 2010). Although generally  
52 successful at explaining and predicting current distributions of species (Franklin & Miller, 2009),  
53 impact assessments derived from SDMs have been criticized for their reliance on a number of  
54 largely untested ecological assumptions, methodological issues, and statistical concerns (e.g.,  
55 Pearson & Dawson, 2003; Dormann, 2007).

56 Chief among these issues is the failure of most SDMs to account for spatial dependence  
57 of occurrence data (Gelfand *et al.*, 2006; Bahn and McGill, 2007; Dormann, 2007; Elith *et al.*,  
58 2010). Spatial autocorrelation arises in ecological data because nearby points tend to be more  
59 similar, in physical characteristics and/or species occurrences or abundances, than are pairs of  
60 locations that are farther apart (Legendre, 1993). When model assumptions about independent  
61 and identically distributed residuals are violated, there could be a bias in the regression  
62 parameter estimates, potentially leading to poor inference. Studies illustrate that failure to  
63 account for spatial autocorrelation can lead to misidentification of important driving variables  
64 and overly optimistic error rates (e.g., Lichstein, *et al.*, 2002; Segurado *et al.*, 2006; Diez &  
65 Pulliam, 2007; Dormann, 2007), especially when small-scale patterns of explanatory variables

66 create instability in broad-scale regression parameter estimates (Hawkins *et al.*, 2007). Further,  
67 models based solely on spatial interpolation can provide better fits to species range data than  
68 models based on explanatory environmental variables (Bahn & McGill, 2007), suggesting that  
69 spatial autocorrelation in unmeasured factors (e.g., population processes such as dispersal or  
70 underlying resources such as soil moisture) may account for most of the observed distributional  
71 patterns.

72         Analysis of spatial SDMs primarily has focused on predicting current or simulated  
73 species' distributions using a hold-out dataset for model validation (Gelfand *et al.*, 2006; Wilson  
74 *et al.*, 2010), but projections of spatial SDMs in changing climates over long time scales remain  
75 largely untested. Observed changes in species distributions as a result of past climatic dynamics  
76 provide a unique opportunity to compare projections of spatial and non-spatial SDMs  
77 parameterized with current conditions (Pearman, *et al.*, 2008a; Nogués-Bravo, 2009; Dobrowski  
78 *et al.*, 2011, Veloz *et al.*, 2012).

79         Projections to environmental conditions different from those used to calibrate SDMs are  
80 subject to error (Heikkinen *et al.*, 2006) and may not be ecologically meaningful or statistically  
81 valid if there are changes in correlations between variables across time and space (Elith *et al.*,  
82 2010) or if species-environment relationships are not conserved (e.g., Fitzpatrick *et al.*, 2007,  
83 Veloz *et al.*, 2012). It also is not known whether it is desirable to project models with spatial  
84 random effects based on the partially observed spatial distribution of a species at one time point  
85 into a new temporal domain.

86         In this study, we developed non-spatial and spatial SDMs for two genera of trees in  
87 eastern North America. We calibrated the models with current climate data and Forest Inventory  
88 and Analysis (FIA) data collected by the United States Forest Service. We then projected the

89 models back in time using paleoclimate simulations and extensive pollen records as independent  
90 validation data. Our approach is similar to that of Pearman *et al.* (2008a), who used fossil pollen  
91 to validate SDMs of European trees projected back to a single time in the mid-Holocene (6,000  
92 years before present). However, the availability of new paleoclimate reconstructions, which  
93 provide millennial snapshots of historic climate for the last 21,000 years before present, allowed  
94 us to validate the models at a much finer temporal resolution.

95       To assess the usefulness of adding a spatial term to SDMs we consider the following: 1) a  
96 spatially-varying intercept model with no climate variables; 2) a non-spatial model with climate  
97 variables; and 3) a spatially-varying intercept model with climate variables. As detailed in the  
98 Methods Section and Appendix S3, the spatially-varying intercept was introduced via spatial  
99 random effects. The rationale for choosing these candidate models is as follows. If climate  
100 variables describe a significant portion of the variability in the observed distribution and if these  
101 variables change over time, then projections from models with climatic variables will show a  
102 conservative shift away from the observed distribution. For the spatially varying intercept model  
103 with climate variables, any projected shifts in distributions are tempered by the spatial random  
104 effects. Depending on the amount of spatial autocorrelation, spatial random effects act to draw  
105 the projected distribution back toward the observed distribution used to calibrate the model. If  
106 climate variables do not describe a significant portion of the variability in the observed  
107 distribution, then the spatial random effects will keep projected distributions close to the  
108 observed distribution, i.e., the only learning for prediction will come from the observed  
109 distribution and hence projected probability of species occurrence will be similar to the observed  
110 probability of occurrence. With these three candidate models, we were able to tease apart  
111 differences due to the spatial random effects alone, the climate variables alone, and their additive

112 effects. We parameterized and estimated model parameters following a Bayesian framework,  
113 which provided full posterior distributions for model parameters and allowed us to estimate the  
114 uncertainty in our statistical inferences. We focus on two tree genera, *Fagus* and *Tsuga*, whose  
115 distributions can be readily inferred from fossil pollen and which possess contrasting life  
116 histories.

117 We address three questions. (1) Do non-spatial SDMs of current distributions of *Fagus*  
118 and *Tsuga* based on climate variables exhibit residual spatial autocorrelation? (2) Do SDMs with  
119 spatial random effects that include or exclude climate variables provide better fits to the observed  
120 distributions than non-spatial SDMs with climate variables only? (3) Do hindcasted spatial  
121 SDMs better predict historic distributions than non-spatial SDMs?

## 122 **Methods**

### 123 *Study genera*

124 We studied two tree genera, *Fagus* and *Tsuga*. In eastern North America, *Fagus* is represented by  
125 only one species, *F. grandifolia* (Ehrh.) (American Beech), and *Tsuga* by only two, the  
126 widespread *T. canadensis* (L.) Carr. (Eastern Hemlock), and the narrow endemic *T. caroliniana*  
127 Engelm.) (Carolina Hemlock). For both *Fagus* and *Tsuga*, the relationship between local  
128 abundance of trees and relative abundance of pollen in sediment cores has already been derived  
129 (Davis, 1981). *Tsuga* is a conifer with passively-dispersed cones, whereas *Fagus* is deciduous  
130 with animal-dispersed seeds.

### 131 *Occurrence data*

132 We used FIA data to describe the current distribution of *Fagus* and *Tsuga*. In every 2428 ha of  
133 land in the United States classified “forested”, there is one permanent FIA plot, each containing  
134 four 7.2 m fixed-radius subplots (Woudenberg *et al.*, 2010). In each subplot, all trees >12.7 cm



135 diameter at breast height have been measured periodically since the 1940s; consistent nationwide  
136 annual inventories were initiated in 2001. We used data from the most recent full plot inventory  
137 (2003 – 2008) to calibrate our models.

138 Historic distributions of *Fagus* and *Tsuga* were derived from fossil pollen data in the  
139 Neotoma Paleoecology Database (<[www.neotomadb.org](http://www.neotomadb.org)>). Paleoclimate data (described below)  
140 were available at 1 kiloannum before present (kaBP) intervals from 0–21 kaBP, so we focused on  
141 millennial historic distributions of *Fagus* and *Tsuga*. Given the variation in temporal scale and  
142 spatial resolution across study sites and uncertainties associated with radiocarbon aging of pollen  
143 from sediment cores (Blauw *et al.*, 2007), we compiled pollen datasets in which *Fagus* and  
144 *Tsuga* were counted as present at a site if their pollen percentages reached threshold levels at any  
145 time within 500 years centered on each historic millennium (Appendix S1). We chose a 500 year  
146 window because cross-validation analyses of biostratigraphic ages from recently revised age  
147 models for all pollen sites suggested that 500 years is a conservative estimate of temporal  
148 uncertainty for sites in the Neotoma database (Blois *et al.*, 2011). To determine the sensitivity of  
149 historic tree distributions to the pollen percentage thresholds used to define a genera's presence  
150 or absence at a site, we specified low and high thresholds for each genus (Pearman *et al.*, 2008a):  
151 0.5% or 1% for *Fagus* and 1% or 2% for *Tsuga* (Davis, 1981).

### 152 ***Extent and resolution***

153 The extent of the study area was the portion of eastern North America with the highest density of  
154 pollen data (Fig. 1). This region contained 75,251 FIA sites and up to 379 Neotoma locations,  
155 depending on time period considered. Paciorek & McLachlan (2009) found that spatial patterns  
156 relating current and past climates to abundances of pollen and trees were unreliable at resolutions  
157 below ~50 km, so the climatic predictors for our model (see below) were downscaled to a

158 resolution of 0.5-degrees (~50-80 km depending on latitude). We upscaled the current tree  
159 occurrence data for each grid cell in the climate spatial data layers, keeping track of the number  
160 of FIA sites per 0.5-degree cell to be used as weights in the models (Appendix S2). Following  
161 this aggregation there were a total of 1,419 FIA observations with presence/absence ratios for  
162 *Fagus* and *Tsuga* of 706/713 and 380/1,039, respectively. The number of aggregated pollen  
163 observations varied for each 1 kaBP time period (Fig. 2). Although both paleoclimatic and pollen  
164 data extended back 21 kaBP, the total sample size and the number of pollen grains of each genus  
165 declined rapidly beyond 8 kaBP (Fig. 2). Thus, our hindcast projections extend only from 1 to 8  
166 kaBP, which allowed us to validate the models using a minimum of 200 grid cells containing  
167 observations, and at least 50 of which contain presences for each genus.

#### 168 *Climate data*

169 Modern climate data came from the observed dataset of the Climate Research Unit (CRU),  
170 University of East Anglia (Brohan *et al.*, 2006). Paleoclimate data for this study came from a  
171 recent transient simulation of the CCSM3 global circulation model (GCM) (Liu *et al.*, 2009).  
172 The standard change-factor approach was employed to statistically downscale and reduce bias in  
173 the climate data (Wilby *et al.*, 2004). For each climate variable at each millennial interval, the  
174 difference between modeled paleoclimate and modeled modern climate was calculated and then  
175 resampled to a  $0.5 \times 0.5$ -degrees grid to match the resolution of the CRU observed climate  
176 dataset (Mitchell & Jones, 2005).

177 Decadal averages of seasonal variables were the highest temporal resolution data  
178 available from the archived CCSM3 simulations. To get a 'snapshot' of climatic conditions at  
179 each millennial time point, decadal averages of seasonal climate variables from the CRU or  
180 CCSM3 simulations were calculated for the first 100 years of each millennium (e.g., 8.0 to 7.9

181 kaBP). Because summaries of modern observed climate are available at centennial scales, these  
182 same centennial summaries of paleoclimate were derived to aid comparisons between paleo and  
183 modern SDMs. Bioclimatic variables that captured precipitation and temperature averages and  
184 seasonalities were used because response surface analyses for *Fagus* and *Tsuga* have shown that  
185 climatic annual averages, annual ranges, and seasonality were important factors controlling the  
186 Holocene migrations of these genera (Bartlein *et al.*, 1986). Specifically, we calculated six  
187 bioclimatic variables (Hijmans *et al.*, 2005): annual mean temperature (BIO1), mean diurnal  
188 range (BIO2), temperature seasonality (BIO4), temperature annual range (BIO7), annual  
189 precipitation (BIO12), and precipitation seasonality (BIO15).

190       Two of the six calculated bioclimatic variables, temperature seasonality and temperature  
191 annual range, had within-time correlations with the other bioclimatic variables  $\geq 0.7$ , so they were  
192 not included as explanatory variables in the models that included environmental predictors (see  
193 Appendix S3). The correlations between mean diurnal range and annual precipitation varied  
194 between modern and historic times (see Appendix S3), and such changing correlation structures  
195 between times could be problematic when projecting models beyond the present (Elith *et al.*,  
196 2010). To determine if sufficient variance in the current distribution was explained by the two  
197 remaining variables with stable correlation structures over time (i.e., annual mean temperature  
198 and precipitation seasonality), we compared a model with annual mean temperature,  
199 precipitation seasonality, mean diurnal range, and annual precipitation with another that included  
200 only annual mean temperature and precipitation seasonality.

### 201 ***Model calibration***

202 We used Bayesian generalized linear models (GLMs) to model genera occurrence. While  
203 approaches such as neural networks and genetic algorithms have been used for SDMs and

204 although model projections can be sensitive to the type of statistical model employed (Elith *et*  
205 *al.*, 2010), classical approaches do not provide the statistical inferences we sought. Even though  
206 GLMs describe a central tendency and not a limiting effect (e.g., of temperature or precipitation  
207 extremes), Bayesian spatial GLMs provide exact inference for the random model parameters,  
208 including spatial random effects, by estimating entire posterior distributions at both observed and  
209 unobserved geographic locations (Gelfand *et al.*, 2006). Because our goal was to compare  
210 consistently SDMs with three different specifications (i.e., spatially-varying intercept only  
211 (SVI), climate only, and spatially-varying intercept plus climate), we adopted a Bayesian  
212 approach in fitting all of the models. Model structure is detailed in Appendix S2; model code is  
213 provided in Appendix S4.

214 Including the SVI has a potential for overfitting as it allows variable intercepts for every  
215 location and thus a very flexible spatial fit to the FIA data. As a null model, we also fit a  
216 multilevel B-Spline to the FIA data (Lee *et al.*, 1997) using the 'MBA' package of 'R' statistical  
217 software to determine whether our hindcasting test for the inclusion of a SVI in the Bayesian  
218 models was sufficient. As an exploratory analysis into the strength of the residual spatial  
219 dependence in the FIA data, we calculated Moran's I from the residuals of the non-spatial GLMs.  
220 This latter analysis was conducted using the Spatial Analyst Tool in ArcMap10 (ESRI, 2011).

#### 221 ***Model fit to calibration data***

222 We fit the Bayesian models to 90% of the FIA data ( $N = 1,277$ ) and randomly selected a  
223 10% holdout dataset ( $N = 142$ ) to assess predictive performance. We also used DIC to rank the  
224 Bayesian models fit to the calibration data (Spiegelhalter *et al.*, 2002). DIC is the sum of the  
225 Bayesian deviance (a measure of model fit) and the effective number of parameters (a penalty for

226 model complexity). Lower DIC values indicate better model fit. Models are compared using  
227  $\Delta$ DIC:

$$228 \quad \Delta\text{DIC}_i = \text{DIC}_i - \min(\text{DIC}), \quad (3)$$

229 where  $\min(\text{DIC})$  is the DIC value for the model with the best fit (i.e., lowest DIC value). In  
230 general,  $\Delta\text{DIC} < 2$  indicates weak evidence;  $5 < \Delta\text{DIC} < 10$  indicates strong evidence, and  $\Delta\text{DIC}$   
231  $> 10$  indicates very strong evidence that one model is preferred over another (Spiegelhalter *et al.*,  
232 2002).

### 233 ***FIA hold-out dataset and pollen validations***

234 When projecting the spatial models back in time for the pollen validation, the random effects  
235 serve to draw the projected distributions for each genus back toward that of the observed  
236 distribution used for model calibration (i.e., the FIA data) in the new time period (Appendix S2).  
237 To compare the performance of the models in predicting current and projecting past distributions,  
238 three measures were calculated using the 'ROCR' package of 'R' statistical software: the Area  
239 Under the Curve (AUC) of a Receiver Operating Curve (ROC), false negative rates (FNR), and  
240 false positive rates (FPR). The calculation of FNRs and FPRs requires converting the continuous  
241 outputs to a binary form using a threshold, in this case the value that maximizes the sum of  
242 sensitivity and specificity (Liu *et al.*, 2005; Lobo *et al.*, 2008).

243 Differences in AUC, FNR, and FPR between models, genera, pollen percentage  
244 thresholds, time, and the model  $\times$  genus interaction were tested with three GLMs. To normalize  
245 residuals and reduce heteroskedasticity, AUC, FNR, and FPR were all arcsin transformed.  
246 Model, genera, pollen percentage threshold, and the model  $\times$  genus interaction entered the GLM  
247 as fixed factors, and time entered as a covariate. The model  $\times$  genus interaction was of particular  
248 interest as it tested whether or not different models performed better or worse in hindcasting the

249 presence-absence of the two genera. The data were analyzed with separate GLMs for AUC, FNR,  
250 and FPR to facilitate the interpretation of Tukey's Honest Significant Differences post-hoc  
251 comparisons at the expense of increasing Type II error rates. Bonferroni corrections of the *P*-  
252 values from the tests did not alter the significance of any of the effects.

## 253 **Results**

### 254 *Parameter estimates and model fit to calibration data*

255 In non-spatial models with two climatic variables (i.e., annual mean temperature and  
256 precipitation seasonality) or four climatic variables (i.e., annual mean temperature, mean diurnal  
257 range, annual precipitation, and precipitation seasonality), all climatic variables were significant  
258 predictors of presence/absence: none of the 95% credible intervals of the parameter estimates  
259 included zero (Tables 1, 2). In contrast, in the spatial models some of the climatic explanatory  
260 variables were not significant predictors of presence/absence (e.g., annual mean temperature in  
261 the *Tsuga* models with two climatic variables and mean diurnal range in the *Fagus* model with  
262 four climatic variables; Tables 1 & 2). Changes in the magnitude and sign of parameter estimates  
263 between non-spatial and spatial models suggested that non-spatial models violated the  
264 assumption of independent identically distributed residuals. The residuals of the non-spatial  
265 models for both *Fagus* and *Tsuga* also exhibited significant positive spatial autocorrelation  
266 (Moran's  $I = 0.604$ ,  $P < 1 \times 10^{-7}$  for *Fagus*; Moran's  $I = 0.761$ ,  $P < 1 \times 10^{-7}$  for *Tsuga*),  
267 supporting the conclusion that non-spatial models were inappropriate for these data.

268 For *Fagus*, the SVI plus climate model with annual mean temperature and precipitation  
269 seasonality had the lowest DIC value and  $\Delta\text{DIC} > 10$  relative to all other *Fagus* models (Table 3,  
270 Fig. 3). In contrast, for *Tsuga*, the SVI model with no bioclimatic predictors had the lowest DIC  
271 value and  $\Delta\text{DIC} > 10$  relative to all other *Tsuga* models (Table 3, Fig. 4).

272 The non-spatial SDMs for both *Fagus* and *Tsuga* that included only annual mean  
273 temperature and precipitation seasonality had  $\Delta$ DIC values  $>10$  relative to the non-spatial models  
274 that included annual mean temperature, precipitation seasonality, mean diurnal range, and annual  
275 precipitation (Table 3). Given that the correlative relationship between mean diurnal range and  
276 annual precipitation was unstable between modern and historic times (see Appendix S3) and that  
277 the inclusion of them did not provide a large decrease in the  $\Delta$ DIC, these two climatic variables  
278 were excluded from the models used for prediction that were validated with the 10% holdout FIA  
279 dataset and fossil pollen record.

#### 280 ***FIA hold-out dataset and pollen validations***

281 For the contemporary 10% hold-out FIA dataset for both genera, the non-spatial model  
282 performed worse than the SVI, SVI plus climate, or multilevel B-Spline models in terms of  
283 AUC, FNR, and FPR (Table 4; Appendix S5). However, the same was not true when models  
284 were hindcasted. Based on AUC, there were significant main effects of model type (non-spatial,  
285 SVI, SVI plus climate, FIA B-Spline;  $F_{3,118} = 32.4$ ,  $P = 2.4 \times 10^{-15}$ ), and a significant genus  $\times$   
286 model interaction ( $F_{3,118} = 13.8$ ,  $P = 8.8 \times 10^{-8}$ ) (Table 4, Appendix S5) on model performance.  
287 For the *Fagus* hindcasts, on average the non-spatial model had higher AUC values than the  
288 spatial models (i.e., SVI and SVI plus climate) and FIA multilevel B-spline models, but the  
289 opposite was true for *Tsuga*. The FNRs in the hindcasting validation varied by model ( $F_{3,118} =$   
290  $8.1$ ,  $P = 6.2 \times 10^{-5}$ ). The FIA data multilevel B-spline model had the highest FNR and post-hoc  
291 comparisons showed that there were no significant differences between the non-spatial and  
292 spatial models in FNRs (Table 4, Appendix S5). Similar to the FNRs, the FPRs also varied by  
293 model ( $F_{3,118} = 9.0$ ,  $P = 1.95 \times 10^{-5}$ ) (Table 4, Appendix S5). The FIA data multilevel B-spline  
294 and the non-spatial models had higher FPRs than the spatial models. There were no significant

295 genus  $\times$  model interactions for FNRs ( $F_{3,118} = 2.3, P = 0.08$ ) and FPRs ( $F_{3,118} = 1.7, P = 0.18$ ).  
296 Overall for the three measures, model performance worsened as models were projected further  
297 back in time (AUC:  $F_{1,118} = 118, P = 2.0 \times 10^{-6}$ ; FNR:  $F_{1,118} = 98.7, P = 2.0 \times 10^{-16}$ ; FPR:  $F_{1,118} =$   
298  $109, P = 2.0 \times 10^{-16}$ ). Also, model performance was better (i.e., higher AUC and lower FNR and  
299 FPR) for *Tsuga* than for *Fagus* (AUC:  $F_{1,118} = 10.0, P = 0.002$ ; FNR:  $F_{1,118} = 65.5, P = 5.8 \times 10^{-$   
300  $13$ ; FPR:  $F_{1,118} = 88, P = 6.3 \times 10^{-16}$ ) and for the low pollen percentage thresholds than for the  
301 high pollen percentage thresholds (AUC:  $F_{1,118} = 14.0, P = 2.8 \times 10^{-4}$ ; FNR:  $F_{1,118} = 15.3, P = 1.5$   
302  $\times 10^{-4}$ ; FPR:  $F_{1,118} = 24.9, 2.13 \times 10^{-16}$ ). For all three test metrics (i.e., AUC, FNR, FPR), the  
303 multilevel B-spline fit to the FIA data, which we used as a ‘perfectly fit’ model to assess whether  
304 or not the spatial models were overfit to the calibration data, performed the worst. This assured  
305 us that the pollen validation test was stringent enough.

## 306 Discussion

307 A key question regarding the application of SDMs to predicting the response of species to  
308 climate change is whether the failure to include ecological and evolutionary processes (e.g.,  
309 dispersal, biotic interactions, readjustment lags) will prove to be problematic (reviewed by  
310 Pearson & Dawson, 2003). Depending on the species and its life history, ecological and  
311 evolutionary processes may (or may not) lead to its inability to track changes in climate. While  
312 there is evidence that vagile organisms (e.g., butterflies) can track rapid climate change (Warren  
313 *et al.*, 2001), sessile organisms (e.g., trees) may not readily disperse to newly suitable habitat  
314 resulting in limited niche space filling (Svenning & Skov, 2004; Meier *et al.*, 2012). Species  
315 undergoing climate driven range expansions coupled with enemy release are hypothesized to be  
316 more capable of realizing their potential niche (Hellman, *et al.*, 2012), whereas species limited  
317 by a particular resource (e.g., host availability) can be constrained to the spatial distribution of



318 the resource (Merrill *et al.*, 2007). There is evidence that shorter-lived taxa (e.g., insects and  
319 herbaceous plants; Woodward, 1990; Thomas *et al.*, 2001) can evolve in response to rapid  
320 climate change, but longer-lived taxa that cannot evolve as quickly may experience readjustment  
321 lags (Pearson & Dawson, 2003).

322         For those taxa whose distributions do not shift over time as a result of ecological and  
323 evolutionary processes, the inclusion of spatial random effects in SDMs could improve  
324 projections by providing a more conservative prediction of distributional shifts, especially when  
325 climatic variables do not explain much variability in their observed distributions. Alternatively,  
326 when climatic variables explain most of the variability in a taxon's observed distribution and the  
327 taxon is capable of tracking climate, then accounting for spatial autocorrelation in SDMs won't  
328 provide better projections. In other words, the spatial random effects keep the projected  
329 distribution similar to the data used for model calibration, unless the covariates (e.g., climatic  
330 variables) suggest otherwise. Further, if the climate variables do not explain much of the  
331 variability in the observed distribution and the genera's distribution shifts far from the observed  
332 distribution over time, then none of the models defined here will perform well. The predictive  
333 abilities of non-spatial and spatial SDMs have rarely been compared with temporally varying  
334 validation datasets to test these assertions (Gelfand *et al.*, 2006).

335         In this study we tested the predictive abilities of non-spatial and spatial SDMs across  
336 eight millennia using data from the pollen record (Appendix S1). We found that spatial SDMs  
337 had better fits to the calibration data, higher predictive accuracy for a modern hold-out validation  
338 dataset, and greater variance in their outputs than non-spatial SDMs (see also Gelfand *et al.*,  
339 2006; Bahn & McGill, 2007). For *Fagus*, the SVI plus climate model provided a better fit to the  
340 calibration data than the SVI model, but the opposite was true for *Tsuga*. Also for the two

341 climatic variable models, for *Fagus* there was no change in the sign of the climatic regression  
342 coefficients between the non-spatial and spatial models (Table 1), but with *Tsuga* there was a  
343 sign change in the regression coefficient for annual mean temperature between the non-spatial  
344 and SVI plus climate models (Table 2). This result suggests that for *Tsuga* the spatial random  
345 effect could be accounting for dependence in the model's residuals across space as several other  
346 studies have found that parameter estimates are affected by spatial autocorrelation (Dormann,  
347 2007; Kühn, 2007; Bini *et al.*, 2009; Hodges & Reich, 2010).

348         In the hindcasting analyses, the SVI and SVI plus climate models performed similarly.  
349 This suggests that the climatic variables do not contribute much to explaining the variability of  
350 occurrence relative to that explained by the spatial random effects. AUC values based on fossil  
351 pollen indicated that the non-spatial model performed better for *Fagus* than either of the two  
352 spatial models, but the opposite was true for *Tsuga*. However, FNR values did not differ among  
353 the models for either genus, and FPR values were greater for non-spatial models for both genera.  
354 We have more confidence in FNR and FPR values than in AUC values because the latter  
355 describe portions of the ROC curve that are rarely encountered and weights omission and  
356 commission errors equally (Lobo *et al.*, 2008). With the pollen record, equal weighting of  
357 omission and commission errors may not be ideal; we have much more confidence in the  
358 presence of pollen grains than in their absence (Blauww *et al.*, 2007; Blois *et al.* 2011) and false  
359 negatives in the pollen record are more problematic than false positives. The lack of differences  
360 in false negative rates between models shows that the non-spatial and spatial models have similar  
361 FNRs.

362         Although we have less confidence in actual absences in the pollen data, the FPRs are  
363 interesting when considering the ecological and evolutionary processes leading to conserved

364 spatial structure in the distributions of species. The greater FPRs of non-spatial models for both  
365 genera suggest that spatial effects may account for smaller-scale climatic spatial structure that is  
366 not otherwise estimated in large-scale or averaged temperature and precipitation values (Gelfand  
367 *et al.*, 2006; Hawkins *et al.*, 2007). Evidence from the fossil pollen and paleoclimate records  
368 suggests that climatic shifts can result in abrupt ecological changes in vegetation that are driven  
369 by internal dynamics, such as site-specific environmental characteristics (*e.g.*, soil moisture) or  
370 biotic interactions (*e.g.*, competition) that create geographically localized variation in vegetation  
371 composition (Williams *et al.*, 2011). Taxon-specific responses to climate forcing also could  
372 explain why the SVI model had the lowest DIC for *Tsuga* and why the two spatial models  
373 performed better in regards to both AUC and FPR for *Tsuga*, but not for *Fagus*. Approximately  
374 5.5 kaBP *Tsuga* experienced a range contraction known as the “hemlock decline” potentially due  
375 to an abrupt change in climate, a phytophagous insect infestation, or both (Bhiry & Filion, 1996;  
376 Foster *et al.*, 2006). If the hemlock decline was due to an abrupt change in climate, then localized  
377 ecological changes could have resulted in stronger spatial structure in its distribution. However,  
378 decoupling changes in distributions due to climate and spatial structure due to biotic interactions  
379 or site-specific abiotic characteristics is difficult because observed spatial structure is (or was)  
380 inherently linked to abrupt climate change.

381         Alternatively, the spatial random effects may have captured a missing covariate, such as  
382 an ecological process that generates spatial structure (Clayton *et al.*, 1993; Paciorek, 2010). Such  
383 processes could include dispersal, competitive interactions, land-use history, or underlying  
384 features of the terrain. For example, if dispersal limitation prevents distributional shifts, then we  
385 might expect that spatial SDMs would perform better for dispersal-limited taxa (*e.g.*, *Tsuga*) that  
386 cannot track changes in climate, but not necessarily for taxa with effective dispersal vectors (*e.g.*,

387 *Fagus*) that can gain dominance by migrating faster to climatically favorable sites (Pearman *et*  
388 *al.*, 2008b). These taxon-specific differences in dispersal mode and degree of dominance could  
389 explain why *Tsuga* seemed to be less responsive to climate over the past 8 millennia than *Fagus*  
390 as evidenced by the better performance over time of the two spatial models in regards to both  
391 AUC and FPR for *Tsuga*, but not for *Fagus*. Simulation experiments for European trees with  
392 spatially explicit process models accounting for changing macroclimate, competition, and habitat  
393 connectivity showed that some of the spatial autocorrelation between two time periods may be  
394 due to very slow migration rates resulting in severe time lags that are not accounted for in non-  
395 dynamic and non-spatial SDMs (Meier *et al.*, 2012). Also, Dobrowski *et al.* (2011) found that  
396 non-spatial SDMs fit to widespread plants with more effective dispersal mechanisms had higher  
397 predictive accuracy over 75 years of climate change in California than non-spatial SDMs fit to  
398 dispersal-limited plants.

399         Given the results of this study, should researchers include spatial random effects in  
400 SDMs? We found that for two long-lived eastern North American trees, spatial models provided  
401 better fits to calibration data and lower FPRs, but not necessarily improvements in AUC or the  
402 FNR. The better fits of the spatial SDMs may have resulted from the richness of the FIA data  
403 used to calibrate the models. Large samples of evenly-dispersed data likely will capture any  
404 spatial structure; consequently a spatial SDM should fit well. However, when sample sizes are  
405 small, there is less of a chance that the spatial structure will be represented adequately.  
406 Ultimately, whether to include spatial random effects in SDMs will depend on the taxon being  
407 modeled, the cost of false positives, and the quality of the data.

408

409 **Acknowledgments**

410 This research was supported by the U.S. Department of Energy's National Institute for Climate  
411 Change Research, through sub-award 3892-HU-DOE-4157 to AME and MCF, NSF grant DBI  
412 10-03938 to AME, and NSF grants DMS-1106609 and EF-1137309 to AOF. FIA data were  
413 provided by Brett Butler and Elizabeth LaPoint (both with the U.S. Forest Service) pursuant to a  
414 Memorandum of Understanding 09MU11242305123 between the USFS and Harvard University.  
415 Eliza Ledwell and Elisabete Baker-Vail assisted with initial data organization and programming.  
416 The Harvard Forest Lab Group, J. Williams, N. Zimmerman, and three anonymous reviewers  
417 provided valuable insights.

#### 418 **Supplementary material**

419 **Appendix S1** Presence-absence plots of historic pollen distributions.

420 **Appendix S2** Detailed description of the models.

421 **Appendix S3** Plots of between- and within-time correlations of paleoclimate data.

422 **Appendix S4** Code for analyses programmed in R and C++.

423 **Appendix S5** Results of the *Fagus* and *Tsuga* low pollen threshold analysis.

#### 424 **Biosketch**

425 Sydne Record is a post-doctoral research fellow at Harvard University – Harvard Forest with  
426 broad research interests in validating ecological models and Bayesian statistics.

427 Author contributions: M.C.F., S.R., and A.M.E. conceived the ideas for the study. S.R., M.C.F.,  
428 and A.O.F. conducted statistical analyses. S.R. led the writing of the manuscript with critical  
429 comments from all co-authors. S.V. provided the downscaled climate data.

430 **Literature Cited**

- 431 Bahn, V. & McGill, B.J. (2007) Can niche-based distribution models outperform spatial  
432 interpolation? *Global Ecology and Biogeography*, **16**, 733-742.
- 433 Bartlein, P.J., Prentice, I.C. & Webb, T. (1986) Climatic response surfaces from pollen data for  
434 some eastern North American taxa. *Journal of Biogeography*, **13**, 35-57.
- 435 Bhiry, N. & Fillion, L. (1996) Mid-Holocene decline in eastern North America linked with  
436 phytophagous insect activity. *Quaternary Research*, **45**, 312-320.
- 437 Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., *et al.* (2009) Coefficient shifts in  
438 geographical ecology: an empirical evaluation of spatial and non-spatial regression.  
439 *Ecography*, **32**, 193-204.
- 440 Blauw, M., Christen, J.A., Mauquoy, D., van der Plicht, J. & Bennett, K.D. (2007) Testing the  
441 timing of radiocarbon-dated events between proxy archives. *Holocene*, **17**, 283-288.
- 442 Blois, J.L., Williams, J.W., Grimm, E.C., Jackson, S.T. & Graham, R.W. (2011) A  
443 methodological framework for assessing and reducing temporal uncertainty in  
444 paleovegetation mapping from late-Quaternary pollen records. *Quaternary Science*  
445 *Reviews*, **30**, 1926-1939.
- 446 Brohan, P., Kennedy, J.J., Harris, I., Tett, S.F.B. & Jones, P.D. (2006) Uncertainty estimates in  
447 regional and global observed temperature changes: a new dataset from 1850. *Journal of*  
448 *Geophysical Research*, **111**, D12106.
- 449 Clayton, J.S., Carlin, B.P. & Montomoli, C. (1993) Spatial correlation in ecological analysis.  
450 *Journal of Epidemiology*, **22**, 1193-1201.
- 451 Davis, M.B. (1981) Quaternary history and the stability of forest communities. *Forest Succession*  
452 (ed. by D.C. West, H.H. Shugart and D.B. Botkin), pp. 132-153. Springer, New York.

453 Diez, J.M. & Pulliam, H.R. (2007) Hierarchical analysis of species distributions and abundance  
454 across environmental gradients. *Ecology*, **88**, 3144-3152.

455 Dobrowski, S.Z., Thorne, J.H., Greenberg, J.A., Safford, H.D., Mynsberge, A.R., Crimmins,  
456 S.M. & Swanson, A.K. (2011) Modeling plant distributions over 75 years of measured  
457 climate change in California, USA: relating temporal transferability to species traits.  
458 *Ecological Monographs*, **81**, 241-257.

459 Dormann, C.F. (2007) Effects of incorporating spatial autocorrelation into the analysis of species  
460 distribution data. *Global Ecology and Biogeography*, **16**, 129-138.

461 Elith, J., Kearney, M. & Phillips, S. (2010) The art of modeling range-shifting species. *Methods*  
462 *in Ecology and Evolution*, **1**, 330-342.

463 Fitzpatrick, M.C., Weltzin, J.F., Sanders, N.J. & Dunn, R.R. (2007) The biogeography of  
464 prediction error: why does the introduced range of the fire ant over-predict its native  
465 range? *Global Ecology and Biogeography*, **16**, 24-33.

466 Foster, D.R., Oswald, W.W., Faison, E.K., Doughty, E.D. & Hansen B.C.S. (2006) A climatic  
467 driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New  
468 England. *Ecology*, **87**, 2959-2966.

469 Franklin, J. & J.A. Miller. (2009) *Mapping species distributions: spatial inference and*  
470 *prediction*. Cambridge University Press, Cambridge.

471 Gelfand, A.E., Latimer, A., Wu, S. & Silander, J.A. (2006) Building statistical models to analyze  
472 species distributions. *Hierarchical Modelling for the Environmental Sciences: Statistical*  
473 *Methods and Applications*. (ed. by J.S. Clark and A.E. Gelfand), pp. 77-07. Oxford  
474 University Press, Oxford.

475 Guisan, A. & W. Thuiller. (2005) Predicting species distribution: offering more than simple  
476 habitat models. *Ecology Letters*, **8**, 993-1009.

477 Hawkins, B.A., Diniz-Filho, J.A.F., Bini, L.M., De Marco, P. & Blackburn, T.M. (2007) Red  
478 herrings revisited: spatial autocorrelation and parameter estimation in geographical  
479 ecology. *Ecography*, **30**, 375-384.

480 Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006)  
481 Methods and uncertainties in bioclimatic envelope modeling under climate change.  
482 *Progress in Physical Geography*, **30**, 751-777.

483 Hellman, J.J., Prior, K.M. & Pelini, S.L. (2012) The influence of species interactions on  
484 geographic range change under climate change. *Annals of the New York Academy of*  
485 *Sciences*, **1249**, 18-28.

486 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution  
487 interpolated climate surfaces for global land areas. *Journal of Climatology*, **25**, 1965-  
488 1978.

489 Hodges, J.S. & Reich, B.J. (2010) Adding spatially-correlated errors can mess up the fixed effect  
490 you love. *American Statistical Association*, **64**, 325-334.

491 Kühn, I. (2007) Effects of incorporating spatial autocorrelation into the analysis of species  
492 distribution data. *Global Ecology and Biogeography*, **16**, 129-138.

493 Lee, S., Wolberg, G. & Shin, S.Y. (1997) Scattered data interpolation with multilevel B-splines.  
494 *IEEE Transactions on Visualization and Computer Graphics*, **3**, 229-244.

495 Legendre, P. (1993) Spatial autocorrelation – trouble or new paradigm. *Ecology*, **74**, 1659-1673.

496 Lichstein, J.W., Simons, T.R., Shiner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and  
497 autoregressive models in ecology. *Ecological Monographs*, **72**, 445-463.



498 Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in  
499 the prediction of species distributions. *Ecography*, **28**, 385-393.

500 Liu, Z., Otto-Bleisner, B.L., He, F., *et al.* (2009) Transient simulation of last deglaciation with a  
501 new mechanism for Bolling-Allerod warming. *Science*, **325**, 310-314.

502 Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the  
503 performance of predictive distribution models. *Global Ecology and Biogeography*, **17**,  
504 145-151.

505 Meier, E.S., Lischke, H., Schmatz, D.R. & Zimmerman, N.E. (2012) Climate, competition and  
506 connectivity affect future migration and ranges of European trees. *Global Ecology and*  
507 *Biogeography*, **21**, 164-178.

508 Merrill, R.M., Gutierrez, D., Lewis, O.T., Gutierrez, J., Diez, S.B. & Wilson, R.J. (2007)  
509 Combined effects of climate and biotic interactions on the elevational range of a  
510 phytophagous insect. *Journal of Animal Ecology*, **77**, 145-155.

511 Mitchell, T.D. & Jones, P.D. (2005) An improved method of constructing a database of monthly  
512 climate observations and associated high-resolution grids. *International Journal of*  
513 *Climatology*, **25**, 305-314.

514 Nogués-Bravo, D. (2009) Predicting the past distribution of species climatic niches. *Global*  
515 *Ecology and Biogeography*, **18**, 521-531.

516 Paciorek, C.J. (2010) The importance of scale for spatial-confounding bias and precision of  
517 spatial regression estimators. *Statistical Science*, **25**, 107-125.

518 Paciorek, C.J. & McLachlan, J.S. (2009) Mapping ancient forests: Bayesian inference for spatio-  
519 temporal trends in forest composition using the fossil pollen proxy record. *Journal of the*  
520 *American Statistical Society*, **104**, 608-622.

521 Pearman, P.B., Randin, C.F., Broennimann, *et al.* (2008a) Prediction of plant species  
522 distributions across six millennia. *Ecology Letters*, **11**, 357-369.

523 Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008b) Niche dynamics in space  
524 and time. *Trends in Ecology and Evolution*, **23**, 149-158.

525 Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the  
526 distribution of species: Are bioclimate envelope models useful? *Global Ecology and*  
527 *Biogeography*, **12**, 361-371.

528 Segurado, P., Araújo, M.B. & Kunin, W.E. (2006) Consequences of spatial autocorrelation for  
529 niche-based models. *Journal of Applied Ecology*, **43**, 433-444.

530 Spiegelhalter, D.J., Best, N., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of  
531 model complexity and fit (with discussion). *Journal of the Royal Statistical Society Series*  
532 *B*, **64**, 583-639.

533 Svenning, J.-C. & Skov, F. (2004) Limited filling of the potential range in European tree species.  
534 *Ecology Letters*, **7**, 565-573.

535 Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davis, Z.G., Musche, M. &  
536 Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins.  
537 *Nature*, **411**, 577-581.

538 Veloz, S.D., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B. & Liu, Z. (2012) No-analog  
539 climates and shifting realized niches during the late Quaternary: implications for 21<sup>st</sup>-  
540 century predictions by species distribution models. *Global Change Biology*, **18**, 1698-  
541 1713.

542 Warren, M.S., Hill, J.K., Asher, T.J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S.,  
543 Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D.

544 (2001) Rapid responses of British butterflies to opposing forces of climate and habitat  
545 change. *Nature*, **414**, 65-69.

546 Wilby, R.L., Charles, S.P., Zorita, E., Timbal, B., Whetton, P. & Mearns, L.O. (2004) Guidelines  
547 for use of climate scenarios developed from statistical downscaling methods. IPCC Task  
548 Group on data and scenario support for Impact and Climate Analysis (TGICA), pp. 1-27.

549 Williams, J.W., Blois, J.L. & Shuman, B.N. (2011) Extrinsic and intrinsic forcing of abrupt  
550 ecological change: case studies from the late Quaternary. *Journal of Ecology*, **99**, 664-  
551 677.

552 Wilson, T.L., Odei, J.B., Hooten, M.B. & Edwards, T.C. (2010) Hierarchical spatial models for  
553 predicting pygmy rabbit distribution and relative abundance. *Journal of Applied Ecology*,  
554 **47**, 401-409.

555 Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical  
556 distribution of plants. *Philosophical Transactions of the Royal Society of London B*, **326**,  
557 585-593.

558 Woudenberg, S.W., Conkling, B.L., O'Connell, B.M., LaPoint, E.B., Turner, J.A. & Waddell,  
559 K.L. (2010) The Forest Inventory and Analysis Database: Database description and user's  
560 manual version 4.0 for Phase 2. Gen. Tech. Rep. RMRS-GTR- 245. Fort Collins, CO:  
561 U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 336  
562 p.

563 **Table 1.** Parameter credible intervals (2.5%, 50.0%, and 97.5% percentiles) for the *Fagus*  
564 spatially-varying intercept (SVI), non-spatial (NS2 and NS4) and SVI plus climate (SVI2 and  
565 SVI4) models. The numbers two and four in the acronyms for the non-spatial and SVI plus  
566 climate models indicate the number of bioclimatic explanatory variables included in the models.  
567 The two climatic variables models included annual mean temperature (BIO1) and precipitation  
568 seasonality (BIO15). The four climatic variables models included annual mean temperature  
569 (BIO1), mean diurnal range (BIO2), annual precipitation (BIO12), and precipitation seasonality  
570 (BIO15). For models with spatial random effects, the spatial random effect variance and spatial  
571 decay parameter are denoted  $\sigma^2$  and  $\phi$ , respectively.

572	Model	$\beta$ Parameter	2.5%	50.0%	97.5%
574	SVI	Intercept	-7.23	-5.28	-2.72
575	SVI	$\sigma^2$	8.11	12.90	20.24
576	SVI	$\phi$	1.09 $10^{-6}$	1.62 $10^{-6}$	2.63 $10^{-6}$
577	NS2	Intercept	-3.06	-3.01	-2.96
578	NS2	BIO1	-0.48	-0.46	-0.43
579	NS2	BIO15	-1.83	-1.78	-1.72
580	NS4	Intercept	-3.11	-3.06	-3.01
581	NS4	BIO1	-0.62	-0.58	-0.54
582	NS4	BIO2	0.33	0.37	0.40
583	NS4	BIO12	-0.20	-0.14	-0.09
584	NS4	BIO15	-2.03	-1.96	-1.90
585	SVI2	Intercept	-7.49	-5.77	-4.41

586	SVI2	BIO1	-1.57	-1.25	-0.89
587	SVI2	BIO15	-0.97	-0.47	-0.08
588	SVI2	$\sigma^2$	6.35	10.32	17.25
589	SVI 2	$\varphi$	$1.15 \cdot 10^{-6}$	$1.90 \cdot 10^{-6}$	$3.20 \cdot 10^{-6}$
590	SVI 4	Intercept	-8.27	-5.47	-3.13
591	SVI 4	BIO1	-1.37	-0.83	-0.25
592	SVI 4	BIO2	-0.16	-0.03	-0.11
593	SVI 4	BIO12	-0.15	-0.47	0.80
594	SVI 4	BIO15	-0.89	-0.36	-0.12
595	SVI 4	$\sigma^2$	5.53	10.50	17.78
596	SVI 4	$\varphi$	$1.14 \cdot 10^{-6}$	$1.91 \cdot 10^{-6}$	$3.69 \cdot 10^{-6}$

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597

598 **Table 2.** Parameter credible intervals (2.5%, 50%, and 97.5% percentiles) for the *Tsuga* spatially-  
 599 varying intercept (SVI), non-spatial (NS2 and NS4) and SVI plus climate (SVI 2 and SVI 4)  
 600 models. The numbers two and four in the acronyms for the non-spatial and SVI plus climate  
 601 models indicate the number of bioclimatic explanatory variables included in the models. The two  
 602 climatic variables models included annual mean temperature (BIO1) and precipitation  
 603 seasonality (BIO15). The four climatic variables models included annual mean temperature  
 604 (BIO1), mean diurnal range (BIO2), annual precipitation (BIO12), and precipitation seasonality  
 605 (BIO15). For models with spatial random effects, the spatial random effect variance and spatial  
 606 decay parameter are denoted  $\sigma^2$  and  $\phi$ , respectively.

607	Model	$\beta$ Parameter	2.5%	50%	97.5%
608					
609	SVI	Intercept	-9.10	-7.68	-4.15
610	SVI	$\sigma^2$	12.6	22.3	36.4
611	SVI	$\phi$	1.09 $10^{-6}$	2.23 $10^{-6}$	2.74 $10^{-6}$
612	NS2	Intercept	-3.50	-3.45	-3.40
613	NS2	BIO1	-1.14	-1.11	-1.07
614	NS2	BIO15	-1.20	-1.16	-1.12
615	NS4	Intercept	-3.55	-3.50	-3.45
616	NS4	BIO1	-1.34	-1.30	-1.25
617	NS4	BIO2	0.31	0.35	0.40
618	NS4	BIO12	0.07	0.14	0.21
619	NS4	BIO15	-1.25	-1.21	-1.12
620	SVI2	Intercept	-10.18	-8.38	-3.45

621	SVI 2	BIO1	0.07	0.48	0.89
622	SVI 2	BIO15	-1.09	-0.55	-0.05
623	SVI 2	$\sigma^2$	10.86	18.57	32.11
624	SVI 2	$\varphi$	$1.09 \cdot 10^{-6}$	$1.68 \cdot 10^{-6}$	$2.96 \cdot 10^{-6}$
625	SVI 4	Intercept	-8.28	-5.73	-4.00
626	SVI 4	BIO1	-1.28	-0.85	-0.26
627	SVI 4	BIO2	-0.16	-0.03	0.11
628	SVI 4	BIO12	-0.15	0.47	0.80
629	SVI 4	BIO15	-0.81	-0.36	0.12
630	SVI 4	$\sigma^2$	5.94	10.58	17.86
631	SVI 4	$\varphi$	$1.14 \cdot 10^{-6}$	$1.89 \cdot 10^{-6}$	$3.43 \cdot 10^{-6}$

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632

633 **Table 3.** Fits of the spatially-varying intercept (SVI), non-spatial, and SVI plus climate SDMs to  
634 the modern Forest Inventory and Analysis (FIA) occurrence data for *Fagus* and *Tsuga*.  
635 Bioclimatic variables included in the models with climatic predictors were: annual mean  
636 temperature (BIO1), mean diurnal range (BIO2), annual precipitation (BIO12), and precipitation  
637 seasonality (BIO15). Model fit was evaluated with the Deviance Information Criterion (DIC),  
638 which is the sum of  $P_D$  (the effective number of parameters) and the posterior mean of the  
639 deviance. To facilitate model comparison,  $\Delta$ DIC was also calculated, where the model with the  
640 lowest DIC has a value of zero and all other models are compared to it.

641	Model	Bioclimatic variable	Genus	$P_D$	DIC	$\Delta$ DIC
642	SVI	None	<i>Fagus</i>	247	35893	81
643	Non-spatial	1, 15	<i>Fagus</i>	3	41497	5685
644	Non-spatial	1, 2, 12, 15	<i>Fagus</i>	5	41125	5313
645	SVI-climate	1, 15	<i>Fagus</i>	248	35812	0
646	SVI-climate	1, 2, 12, 15	<i>Fagus</i>	251	35826	14
647	SVI-climate	None	<i>Tsuga</i>	170	23685	0
648	Non-spatial	1, 15	<i>Tsuga</i>	3	30025	6340
649	Non-spatial	1, 2, 12, 15	<i>Tsuga</i>	5	29715	6030
650	SVI-climate	1, 15	<i>Tsuga</i>	164	23708	23
651	SVI-climate	1, 2, 12, 15	<i>Tsuga</i>	160	23727	42



**Table 4.** Model performance as measured by Area Under the Receiver Operating Curve (AUC), false negative rates (FNR), and false positive rates (FPR) for the non-spatial model, spatially-varying intercept (SVI) model, SVI plus climate, and multilevel B-spline fit to modern *Fagus* and *Tsuga* occurrence data from the Forest Inventory and Analysis (FIA) data. Predictions of the models for modern time were validated with a 10% hold-out dataset from the FIA data. Hindcasts were validated with data from the fossil pollen record provided by the Neotoma database using the “high” pollen thresholds for both genera. The numbers behind the AUC, FNR, and FPR values in parentheses for the Bayesian models represent the standard error calculated from 1000 random draws from the post burn-in MCMC iterations. For the FIA multilevel B-spline approximation there is no standard error as there were no MCMC iterations to draw from.

<b>Genus</b>	<b>Performance Measure</b>	<b>Time (kaBP)</b>	<b>Non-spatial</b>	<b>SVI</b>	<b>SVI-climate</b>	<b>FIA</b>
<i>Fagus</i>	AUC	0	0.87 ( $4 \times 10^{-4}$ )	0.91 (0.01)	0.92 (0.01)	0.91
		1	0.89 ( $5 \times 10^{-4}$ )	0.87 (0.02)	0.87 (0.02)	0.86
		2	0.90 ( $4 \times 10^{-4}$ )	0.88 (0.02)	0.88 (0.02)	0.86
		3	0.89 ( $6 \times 10^{-4}$ )	0.88 (0.01)	0.88 (0.02)	0.86
		4	0.88 ( $6 \times 10^{-4}$ )	0.87 (0.02)	0.87 (0.02)	0.84
		5	0.85 ( $1 \times 10^{-3}$ )	0.85 (0.02)	0.84 (0.02)	0.83
		6	0.84 ( $2 \times 10^{-3}$ )	0.84 (0.02)	0.83 (0.03)	0.83
		7	0.81 ( $1 \times 10^{-3}$ )	0.80 (0.02)	0.80 (0.03)	0.78
		8	0.73 ( $2 \times 10^{-3}$ )	0.76 (0.01)	0.74 (0.02)	0.71
<i>Fagus</i>	FNR	0	0.22 (0.01)	0.14 (0.04)	0.14 (0.03)	0.11
		1	0.20 (0.01)	0.23 (0.04)	0.22 (0.09)	0.26

	2	0.19 (0.02)	0.21 (0.05)	0.20 (0.09)	0.24
	3	0.19 (0.01)	0.19 (0.04)	0.21 (0.09)	0.23
	4	0.22 (0.01)	0.20 (0.04)	0.22 (0.09)	0.23
	5	0.28 (0.02)	0.24 (0.04)	0.25 (0.10)	0.26
	6	0.26 (0.01)	0.25 (0.05)	0.27 (0.10)	0.24
	7	0.30 (0.01)	0.31 (0.05)	0.32 (0.10)	0.31
	8	0.34 (0.03)	0.33 (0.04)	0.35 (0.07)	0.38
<i>Fagus</i> FPR	0	0.23 (0.01)	0.14 (0.02)	0.14 (0.02)	0.12
	1	0.21 (0.02)	0.23 (0.04)	0.22 (0.05)	0.23
	2	0.20 (0.02)	0.21 (0.04)	0.20 (0.06)	0.22
	3	0.20 (0.01)	0.19 (0.03)	0.21 (0.06)	0.22
	4	0.24 (0.02)	0.19 (0.04)	0.22 (0.07)	0.25
	5	0.28 (0.03)	0.24 (0.03)	0.25 (0.07)	0.26
	6	0.27 (0.02)	0.25 (0.04)	0.26 (0.07)	0.28
	7	0.26 (0.02)	0.31 (0.04)	0.30 (0.07)	0.29
	8	0.35 (0.01)	0.33 (0.04)	0.34 (0.07)	0.40
<i>Tsuga</i> AUC	0	0.85 ( $3 \times 10^{-3}$ )	0.95 (0.02)	0.95 ( $8 \times 10^{-3}$ )	0.97
	1	0.85 ( $3 \times 10^{-3}$ )	0.91 (0.01)	0.91 (0.02)	0.82
	2	0.86 ( $4 \times 10^{-4}$ )	0.89 (0.01)	0.89 (0.02)	0.81
	3	0.87 ( $4 \times 10^{-4}$ )	0.88 (0.01)	0.87 (0.02)	0.80
	4	0.83 ( $3 \times 10^{-3}$ )	0.86 (0.02)	0.85 (0.02)	0.80
	5	0.84 ( $3 \times 10^{-3}$ )	0.90 (0.02)	0.89 (0.02)	0.84
	6	0.86 ( $2 \times 10^{-3}$ )	0.91 (0.02)	0.90 (0.02)	0.80

	7	0.85 ( $5 \times 10^{-3}$ )	0.88 (0.02)	0.87 (0.02)	0.80
	8	0.76 ( $5 \times 10^{-3}$ )	0.89 (0.02)	0.88 (0.02)	0.79
<i>Tsuga</i> FNR	0	0.20 (0.03)	0.11 (0.04)	0.11 (0.04)	0.05
	1	0.16 (0.07)	0.16 (0.04)	0.18 (0.03)	0.20
	2	0.19 (0.02)	0.18 (0.04)	0.20 (0.03)	0.21
	3	0.19 (0.03)	0.18 (0.04)	0.20 (0.04)	0.20
	4	0.21 ( $3 \times 10^{-3}$ )	0.20 (0.05)	0.21 (0.04)	0.21
	5	0.25 (0.02)	0.17 (0.04)	0.18 (0.04)	0.20
	6	0.20 (0.02)	0.16 (0.04)	0.18 (0.03)	0.20
	7	0.25 (0.01)	0.18 (0.04)	0.19 (0.03)	0.24
	8	0.30 (0.01)	0.19 (0.05)	0.19 (0.04)	0.33
<i>Tsuga</i> FPR	0	0.22 (0.01)	0.11 (0.03)	0.11 (0.03)	0.09
	1	0.19 (0.03)	0.16 (0.04)	0.17 (0.04)	0.23
	2	0.16 (0.01)	0.18 (0.04)	0.19 (0.03)	0.20
	3	0.19 ( $1 \times 10^{-3}$ )	0.18 (0.04)	0.19 (0.03)	0.22
	4	0.23 (0.01)	0.20 (0.03)	0.21 (0.03)	0.26
	5	0.24 (0.02)	0.17 (0.04)	0.18 (0.04)	0.23
	6	0.19 (0.01)	0.16 (0.05)	0.17 (0.04)	0.18
	7	0.23 (0.01)	0.18 (0.04)	0.18 (0.03)	0.22
	8	0.32 (0.01)	0.20 (0.04)	0.21 (0.03)	0.31

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**Figure 1.** Map of the study extent in the eastern United States showing Forest Inventory and Analysis (FIA) plots (hollow circles) and Neotoma pollen sites (solid triangles) snapped to a resolution of 0.5-degrees (Alber's Equal Area Conic projection).

**Figure 2.** Numbers of sites with presences (black fill) or absences (white fill) of *Fagus* (a and c) and *Tsuga* (b and d) based on the low and high pollen thresholds from present to 21 kiloannums before present (kaBP) based on fossil pollen data from the Neotoma database. Data extending beyond 8 kaBP were not used in the analyses due to the low number of presences of *Fagus* and *Tsuga* beyond that time.

**Figure 3.** Maps of a) a surface approximation of the probability of occurrence of *Fagus* generated by a multilevel B-spline fit to the raw FIA data and the predicted probability of presence of the b) non-spatial, c) spatially-varying intercept, and d) spatially-varying intercept plus climate SDMs to modern *Fagus* FIA data (Alber's Equal Area Conic Projection). The surface approximation in a) was calculated with the MBA package in R.

**Figure 4.** Maps of a) a surface approximation of the probability of occurrence of *Tsuga* generated by a multilevel B-spline fit to the raw FIA data and the predicted probability of presence of the b) non-spatial, c) spatially-varying intercept, and d) spatially-varying intercept plus climate SDMs to modern *Tsuga* FIA data (Alber's Equal Area Conic Projection). The surface approximation in a) was calculated with the MBA package in R.

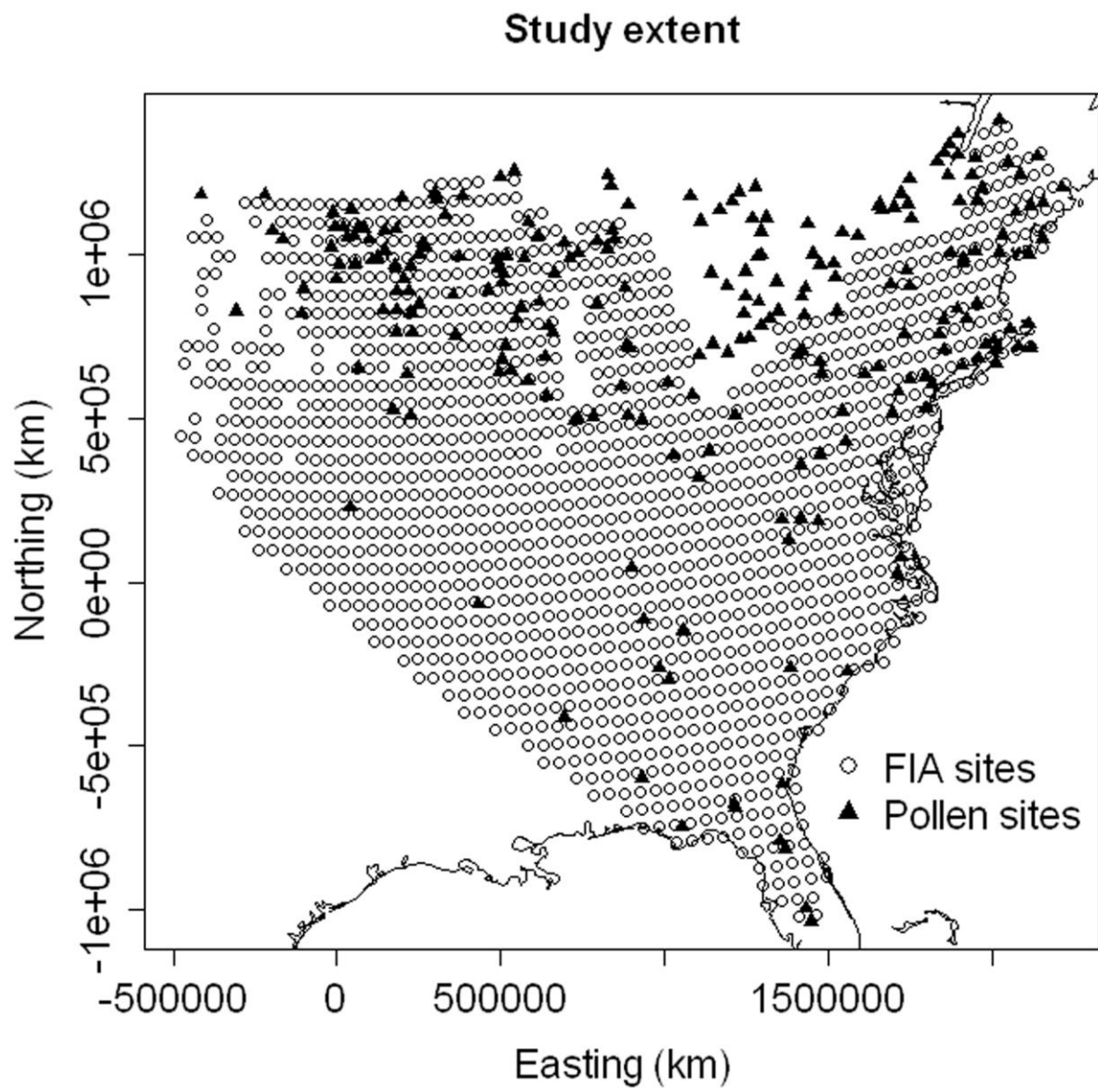
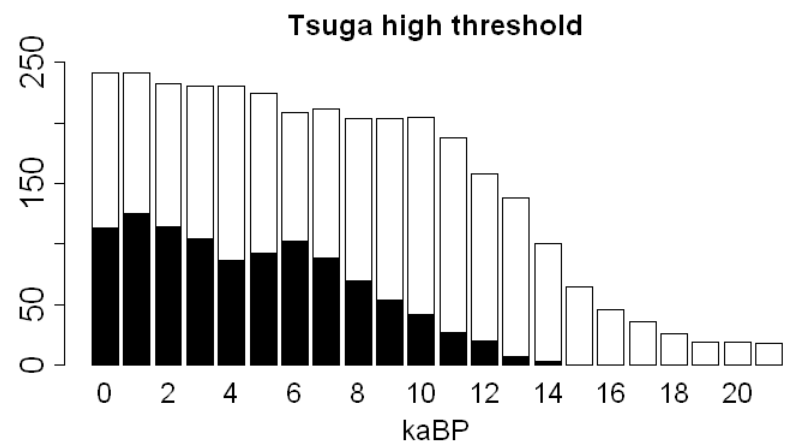
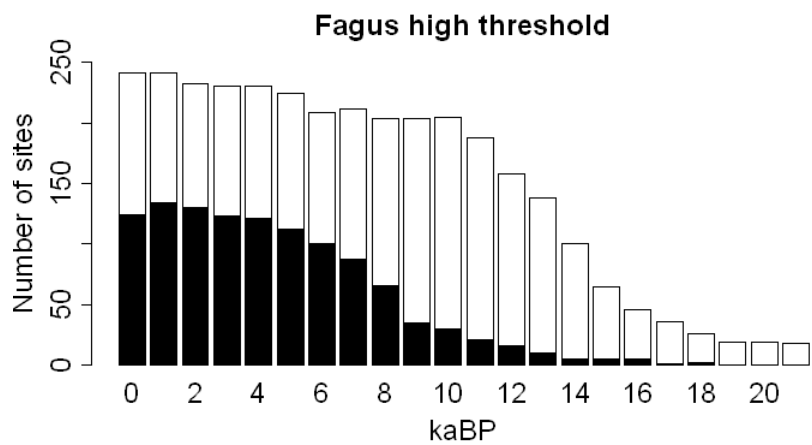
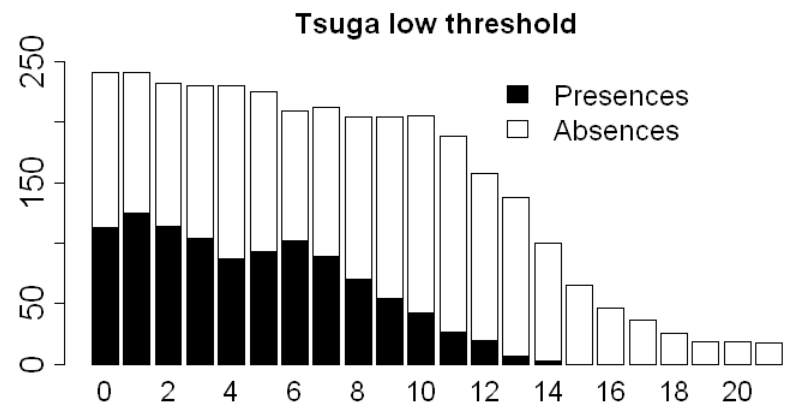
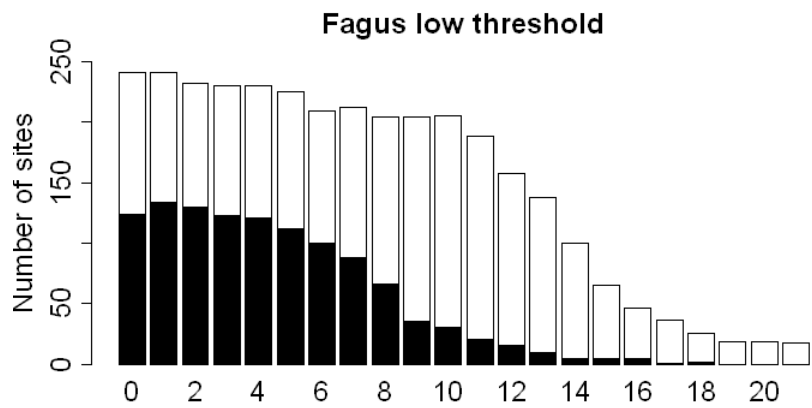


Figure 1



**Figure 2**

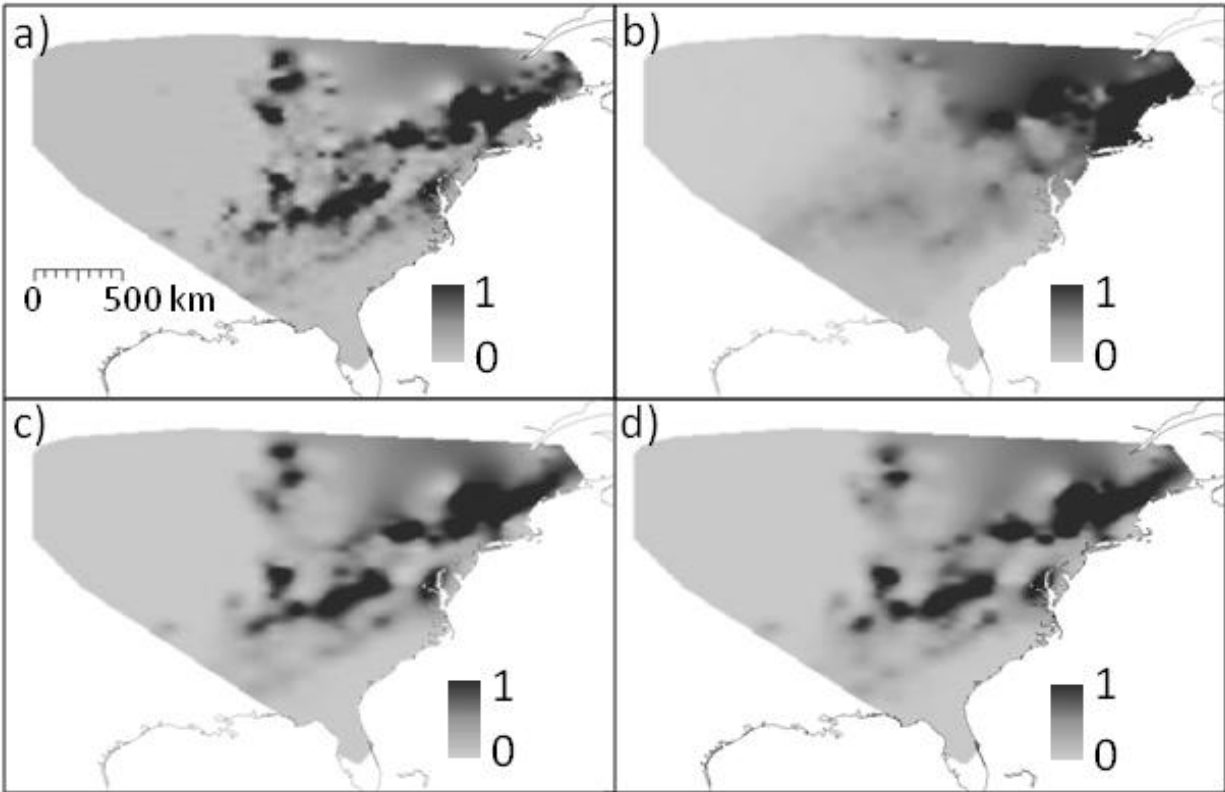
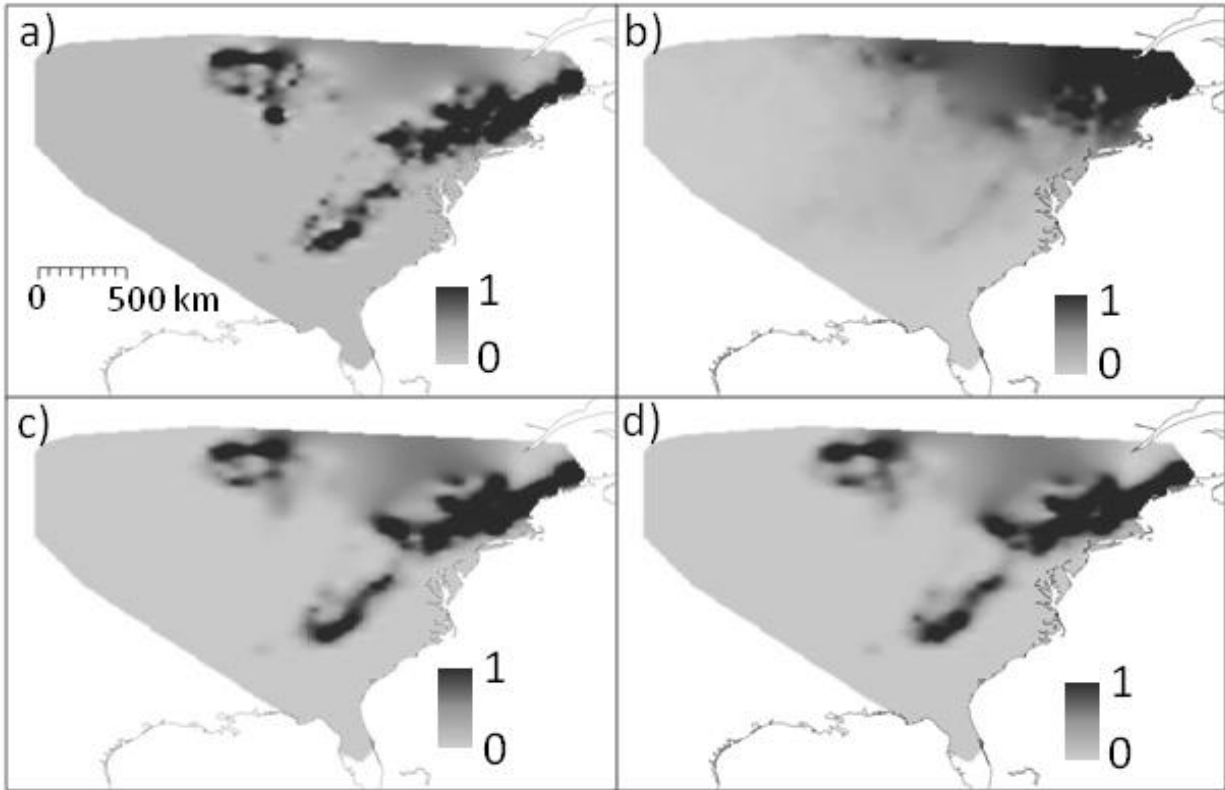


Figure 3



**Figure 4**