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

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(Article begins on next page)

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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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>). 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 0.5×0.5 -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 ≥ 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 Δ 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 ΔDIC
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 Δ 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 Δ 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

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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.

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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 σ^2 and ϕ , respectively.

572	Model	β Parameter	2.5%	50.0%	97.5%
574	SVI	Intercept	-7.23	-5.28	-2.72
575	SVI	σ^2	8.11	12.90	20.24
576	SVI	ϕ	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	σ^2	6.35	10.32	17.25
589	SVI 2	φ	$1.15 \cdot 10^{-6}$	$1.90 \cdot 10^{-6}$	$3.20 \cdot 10^{-6}$
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	σ^2	5.53	10.50	17.78
596	SVI 4	φ	$1.14 \cdot 10^{-6}$	$1.91 \cdot 10^{-6}$	$3.69 \cdot 10^{-6}$

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 σ^2 and ϕ , respectively.

607	Model	β Parameter	2.5%	50%	97.5%
608					
609	SVI	Intercept	-9.10	-7.68	-4.15
610	SVI	σ^2	12.6	22.3	36.4
611	SVI	ϕ	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	σ^2	10.86	18.57	32.11
624	SVI 2	φ	$1.09 \cdot 10^{-6}$	$1.68 \cdot 10^{-6}$	$2.96 \cdot 10^{-6}$
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	σ^2	5.94	10.58	17.86
631	SVI 4	φ	$1.14 \cdot 10^{-6}$	$1.89 \cdot 10^{-6}$	$3.43 \cdot 10^{-6}$

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, Δ 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	Δ 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.

Genus Performance	Time	Non-spatial	SVI	SVI-climate	FIA
Measure	(kaBP)				
<i>Fagus</i> AUC	0	0.87 (4×10^{-4})	0.91 (0.01)	0.92 (0.01)	0.91
	1	0.89 (5×10^{-4})	0.87 (0.02)	0.87 (0.02)	0.86
	2	0.90 (4×10^{-4})	0.88 (0.02)	0.88 (0.02)	0.86
	3	0.89 (6×10^{-4})	0.88 (0.01)	0.88 (0.02)	0.86
	4	0.88 (6×10^{-4})	0.87 (0.02)	0.87 (0.02)	0.84
	5	0.85 (1×10^{-3})	0.85 (0.02)	0.84 (0.02)	0.83
	6	0.84 (2×10^{-3})	0.84 (0.02)	0.83 (0.03)	0.83
	7	0.81 (1×10^{-3})	0.80 (0.02)	0.80 (0.03)	0.78
	8	0.73 (2×10^{-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 (3×10^{-3})	0.95 (0.02)	0.95 (8×10^{-3})	0.97
	1	0.85 (3×10^{-3})	0.91 (0.01)	0.91 (0.02)	0.82
	2	0.86 (4×10^{-4})	0.89 (0.01)	0.89 (0.02)	0.81
	3	0.87 (4×10^{-4})	0.88 (0.01)	0.87 (0.02)	0.80
	4	0.83 (3×10^{-3})	0.86 (0.02)	0.85 (0.02)	0.80
	5	0.84 (3×10^{-3})	0.90 (0.02)	0.89 (0.02)	0.84
	6	0.86 (2×10^{-3})	0.91 (0.02)	0.90 (0.02)	0.80

	7	0.85 (5×10^{-3})	0.88 (0.02)	0.87 (0.02)	0.80
	8	0.76 (5×10^{-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 (3×10^{-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 (1×10^{-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

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.

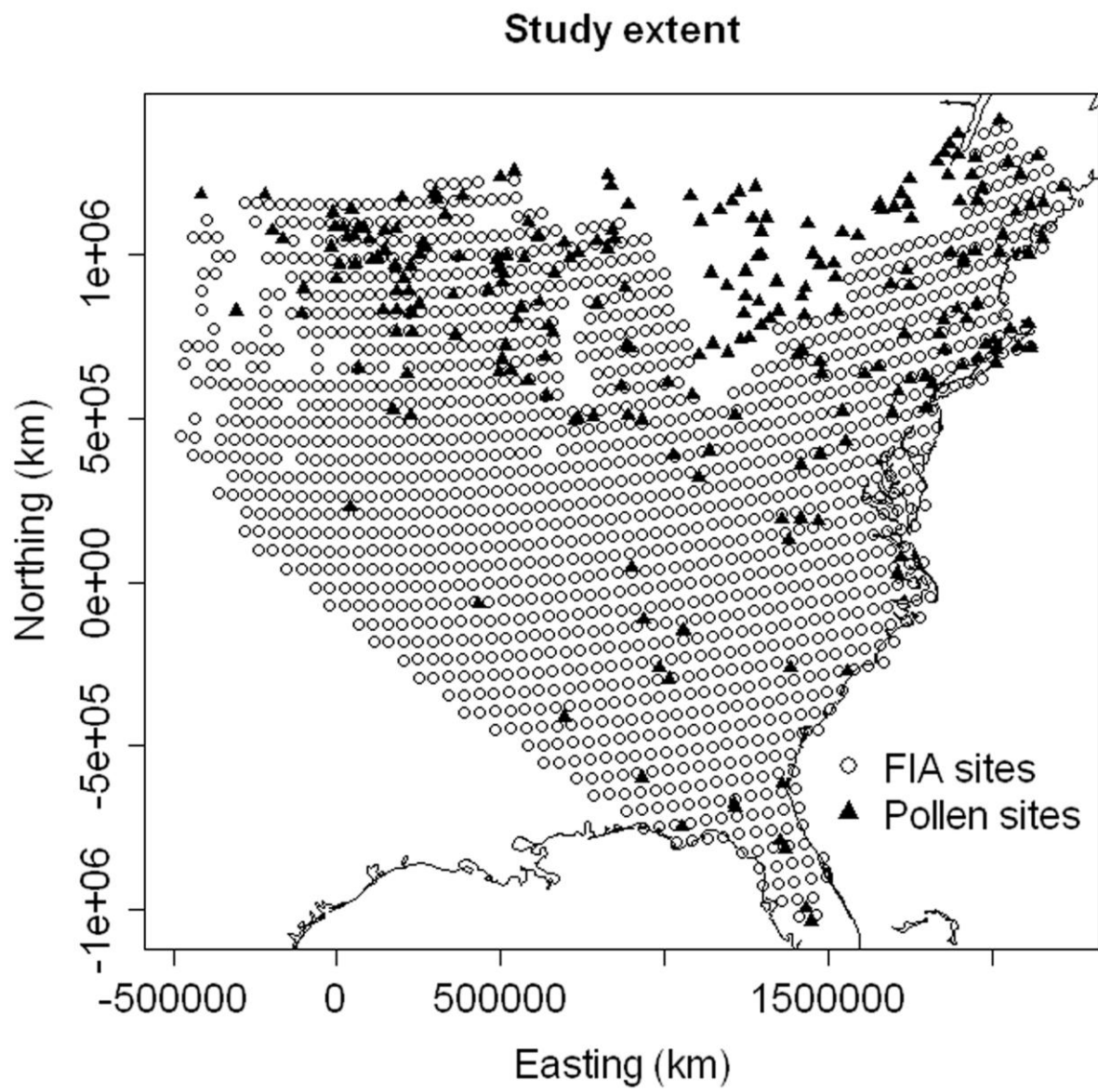


Figure 1

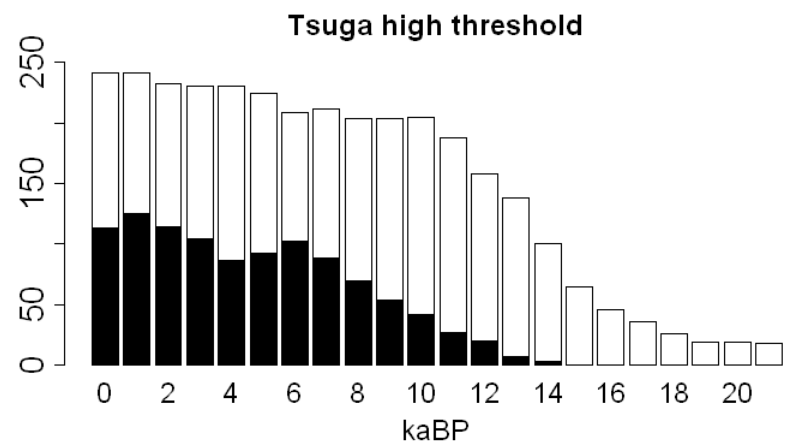
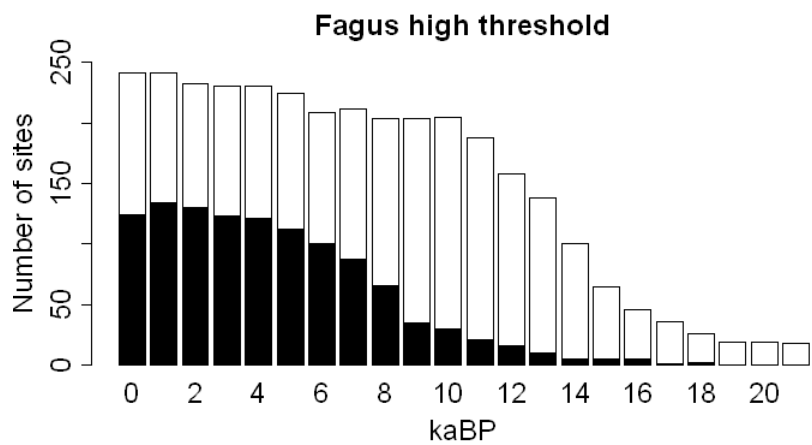
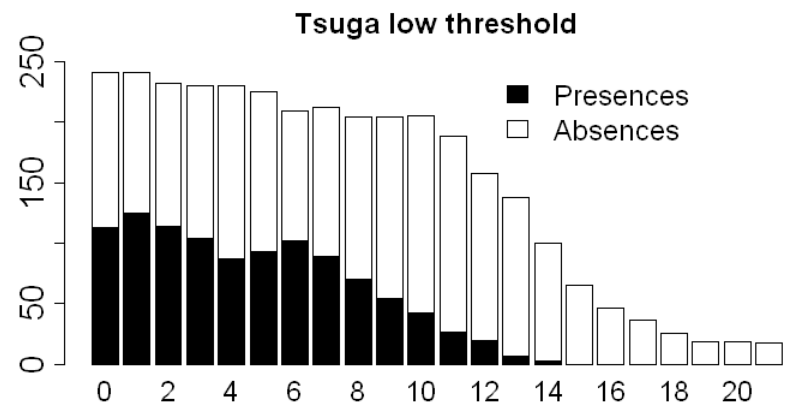
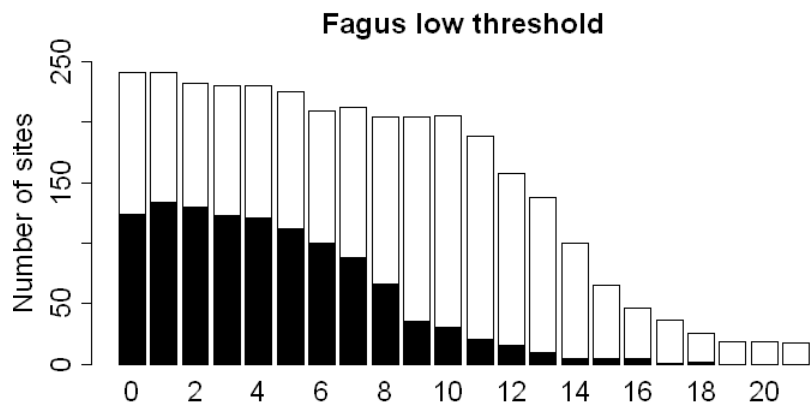


Figure 2

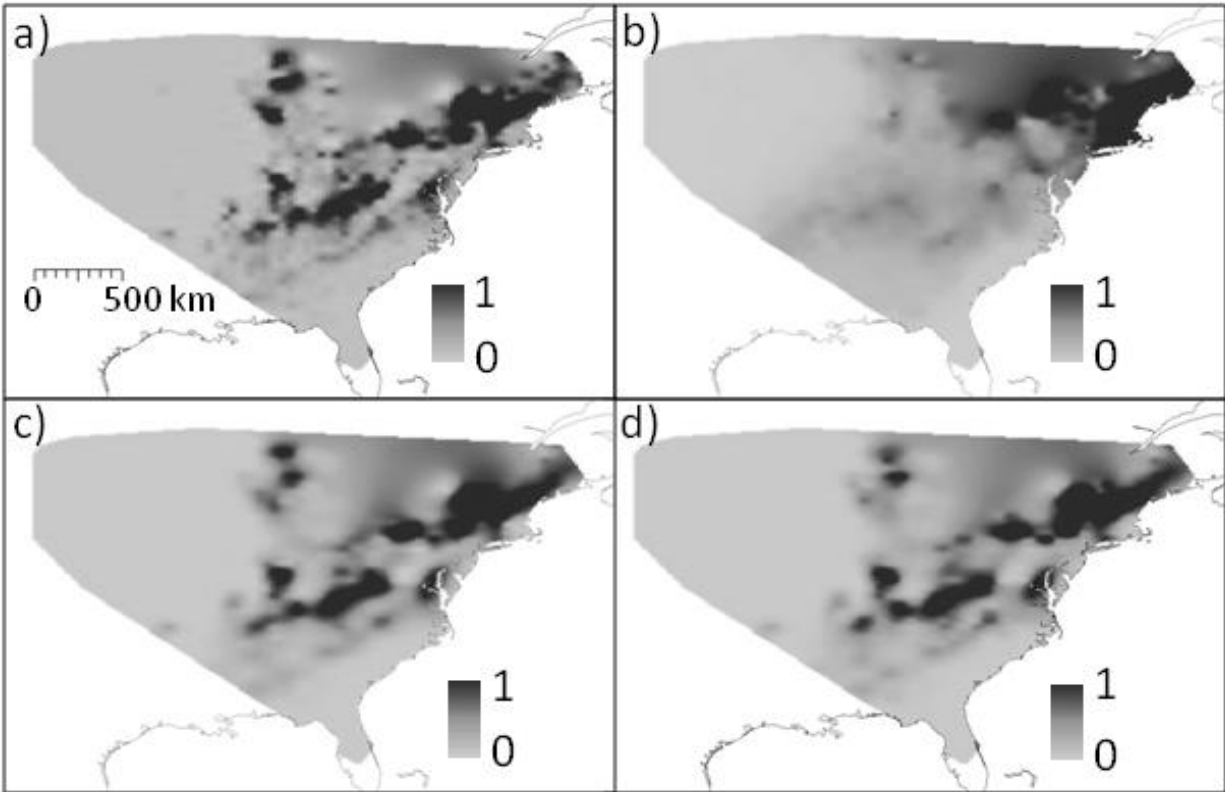


Figure 3

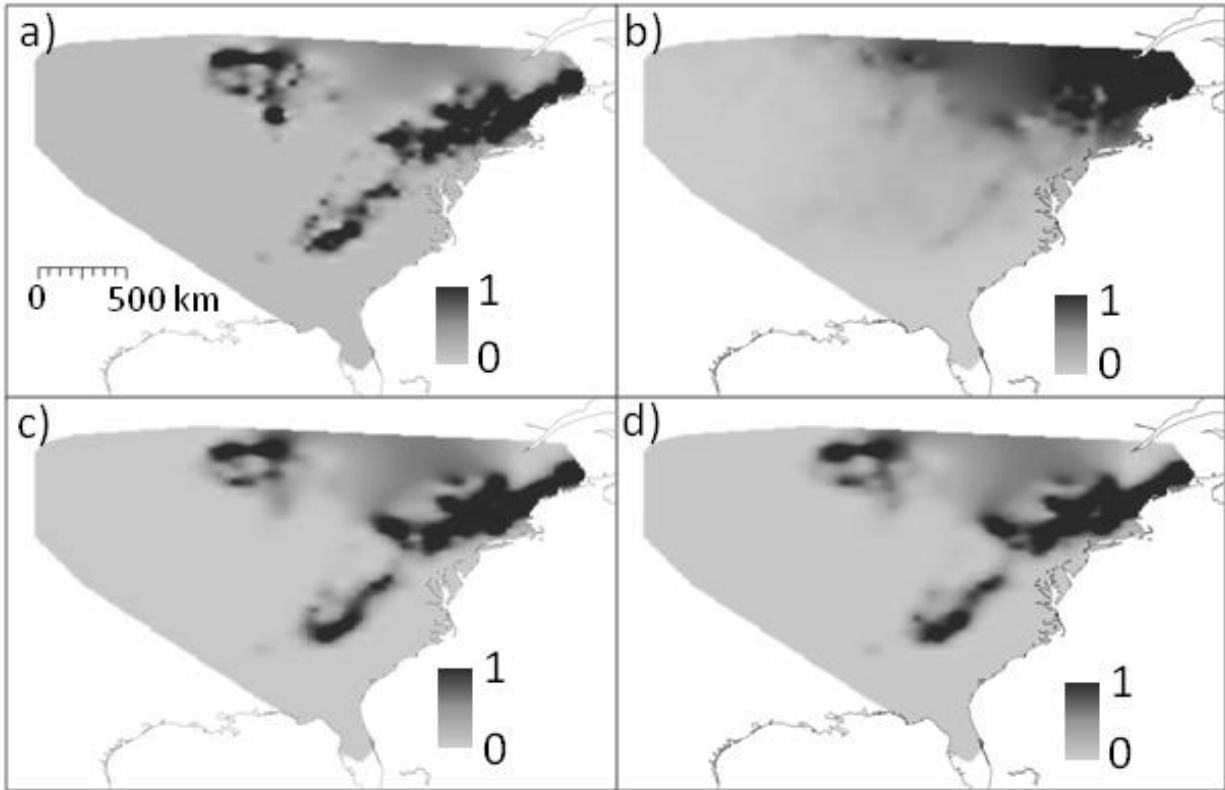


Figure 4