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## Modeling Range Dynamics In Heterogeneous Landscapes: Invasion Of The Hemlock Woolly Adelgid In Eastern North America

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3 **MODELING RANGE DYNAMICS IN HETEROGENEOUS LANDSCAPES: INVASION OF THE**  
4 **HEMLOCK WOOLLY ADELGID IN EASTERN NORTH AMERICA**

5  
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24 ABSTRACT

25 Range expansion by native and exotic species will continue to be a major component of global  
26 change. Anticipating the potential effects of changes in species distributions requires models  
27 capable of forecasting population spread across realistic, heterogeneous landscapes and subject  
28 to spatiotemporal variability in habitat suitability. Several decades of theory and model  
29 development, as well as increased computing power and availability of fine-resolution GIS data,  
30 now make such models possible. Still unanswered, however, is the question of how well this new  
31 generation of dynamic models will anticipate range expansion. Here we develop a spatially  
32 explicit stochastic model that combines dynamic dispersal and population processes with fine-  
33 resolution maps characterizing spatiotemporal heterogeneity in climate and habitat to model  
34 range expansion of the hemlock woolly adelgid (HWA, *Adelges tsugae*). We parameterize this  
35 model using multi-year datasets describing population and dispersal dynamics of HWA and apply  
36 it to eastern North America over a 57-year period (1951-2008). To evaluate the model, the  
37 observed pattern of spread of HWA during this same period was compared to model predictions.  
38 Our model predicts considerable heterogeneity in the risk of HWA invasion across space and  
39 through time, and suggests that spatiotemporal variation in winter temperature, rather than  
40 hemlock abundance, exerts a primary control on the spread of HWA. Although the simulations  
41 generally matched the observed current extent of the invasion of HWA and patterns of  
42 anisotropic spread, it did not correctly predict when HWA was observed to arrive in different  
43 geographic regions. We attribute differences between the modeled and observed dynamics to an  
44 inability to capture the timing and direction of long-distance dispersal events that substantially  
45 affected the ensuing pattern of spread.

46

47 KEY WORDS: Biological invasions, range shift, bioclimate envelopes, species distribution  
48 models, population dynamics, spread model, global warming, landscape epidemiology, species  
49 migration, climate change, metapopulation model, *Adelges tsugae*

## 50 INTRODUCTION

51           Across the globe, species are actively expanding their geographic ranges, some in  
52 response to recent climatic change (Walther et al. 2002; Parmesan and Yohe 2003) and others as  
53 the result of introductions into new regions (Mack 1996). In order to anticipate the potential  
54 effects of ongoing and future changes in the distributions of native and invasive species, there is  
55 increasing need to understand which factors influence the dynamics of range expansion and to  
56 develop models to forecast population spread. However, species most likely to exhibit dramatic  
57 range expansion and to therefore be of greatest interest in management contexts often possess  
58 characteristics that make changes in their distributions difficult to predict, notably spread driven  
59 by rare, long-distance dispersal events and rapid population growth (Hastings et al. 2005). The  
60 interaction between landscape heterogeneity and spread dynamics adds a layer of complexity that  
61 is rarely incorporated into models, but may be critical to developing adequate forecasts of range  
62 expansion at regional scales (Turner et al. 1993; With 2002; Hastings et al. 2005).

63           Multiple approaches have been used to model changes in species distributions at a variety  
64 of temporal and spatial scales. Given their relative simplicity, computational efficiency, and  
65 benign data requirements, species distribution models (SDMs) remain a common technique  
66 generally regarded as providing a useful first estimate of potential changes in species  
67 distributions at the broadest of spatial extents (Pearson and Dawson 2003). SDMs rely on static  
68 correlations between species occurrences and environmental characteristics to predict  
69 distributions of species. In essence, SDMs produce mapped predictions of the geographic ranges  
70 species would occupy if distributions were constrained by abiotic factors alone. Such correlative  
71 models will accurately predict changes in species distributions only if the observed species-  
72 environment relationships correspond to processes and factors that constrain the range and these

73 relationships remain unchanged in new ecological settings (Guisan and Thuiller 2005;  
74 Broennimann et al. 2007; Fitzpatrick et al. 2007). Even when these conditions are met, SDMs  
75 rarely incorporate the underlying processes that drive spread dynamics, most notably population  
76 and dispersal processes (Gallien et al. 2010). Therefore, although SDMs can predict potential  
77 changes in geographic distributions of species through time (e.g., Fitzpatrick et al. 2008), unless  
78 predictions from SDMs are coupled to dynamic population growth and dispersal models (e.g.,  
79 Keith et al. 2008, Anderson et al. 2009), they can reveal little about the extent to which spreading  
80 populations could actually attain these changes. As a result, SDMs are more suited to mapping a  
81 species' potential range within a study region rather than determining the probability of  
82 establishment or the likely timing of arrival in a specific location.

83         Forecasting actual changes in the geographic distribution of populations requires the  
84 development of models that integrate habitat suitability with dynamic dispersal and population  
85 processes (Thuiller et al. 2008; Elith et al. 2010; Franklin 2010; Huntley et al. 2010). General  
86 theoretical models of spread that incorporate population growth and dispersal have been used by  
87 ecologists for decades (e.g., Fisher 1937; Skellam 1951; Kot et al. 1996), but these existing  
88 models rarely consider temporal and spatial heterogeneity in habitat suitability that may  
89 profoundly influence spread dynamics (Higgins et al. 1996; With 2002; Meentemeyer et al.  
90 2008, 2011). As a result, general models of spread provide considerable theoretical insight but  
91 offer little in terms of applied practical utility and specific predictions regarding range expansion  
92 in a region of interest.

93         Developing models of range expansion that incorporate the dynamics of population  
94 growth and dispersal, as well as shifting habitat suitability and realistic landscape heterogeneity,  
95 could substantially improve our ability to understand and predict range expansion (Thuiller et al.

96 2008). Few such models have been developed and applied to large heterogeneous landscapes  
97 (but see Keith et al. (2008), Anderson et al. (2009), and Meentemeyer et al. (2011) for notable  
98 exceptions). Because long-term observational datasets documenting range expansion are rare,  
99 there have been even fewer direct comparisons of predictions from dynamic models to long-term  
100 records of spread (but see Pitt et al. 2009). Although incorporating greater realism into models  
101 may improve our understanding of range expansion, it is still unclear whether this improved  
102 understanding will translate into better forecasts, especially for those species capable of rapid  
103 spread.

104         Here we describe a model to predict the geographic spread of the hemlock woolly adelgid  
105 ('HWA', *Adelges tsugae* Annand; Hemiptera: Adelgidae), an introduced forest pest that threatens  
106 eastern hemlock (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*Tsuga caroliniana*  
107 Englemann) in eastern North America (Orwig et al. 2002). The model combines dynamic  
108 dispersal and population processes with fine-resolution maps characterizing spatiotemporal  
109 heterogeneity in climate and habitat to model range expansion across large, heterogeneous  
110 landscapes. We parameterize our model using field datasets on the population and spread  
111 dynamics of HWA, and we evaluate the predictions of the model against a 60-year record of  
112 HWA spread across eastern North America. These long-term empirical observations of spread  
113 provide a rare opportunity to evaluate how well dynamic spread models might anticipate range  
114 expansion. Although several studies have investigated the relationships between HWA spread  
115 and a variety of environmental factors (Koch et al. 2006; Evans and Gregoire 2007; Morin et al.  
116 2009; Fitzpatrick et al. 2010), these studies have either been limited in geographic extent and/or  
117 to a coarse spatial resolution. Further, correlations between environmental parameters and  
118 hemlock abundance have hindered the ability of regression models to draw inferences regarding

119 the processes influencing the spread of HWA (Morin et al. 2009). Specifically, our objectives are  
120 threefold: (1) parameterize a model using field data on population growth and historic spread  
121 patterns of HWA, (2) use this model to investigate range expansion of HWA across the range of  
122 hemlock, and (3) compare the simulated pattern of spread against the observed pattern. Of  
123 particular interest is how temporal and spatial heterogeneity in habitat suitability affect range  
124 expansion. In addition to providing taxon-specific information regarding HWA range expansion,  
125 our approach represents a general framework for developing dynamic spread models that  
126 explicitly incorporate environmental heterogeneity.

127

## 128 METHODS

### 129 *Study System*

130 HWA is a small (1 mm adult) flightless insect native to Japan and China that was first  
131 collected from hemlock in the eastern United States in spring of 1951, in Richmond, Virginia  
132 (Stoetzel 2002). By 1969 HWA had spread to Philadelphia, Pennsylvania (G. Miller personal  
133 communication) and southern New England by 1985 (McClure 1990). The invaded range now  
134 stretches from Maine, New Hampshire, and Vermont in the north to Georgia in the south.

135 HWA is a bivoltine insect that has a holocyclic lifecycle in its native range but is  
136 obligately parthenogenetic in its invaded range. The parthenogenetic nature of HWA in eastern  
137 North America means that even a single colonizing individual can start a new infestation; as a  
138 result, Allee effects at range margins are unlikely to affect spread dynamics (*cf.* Johnson et al.  
139 2006). Adelgid have two generations per year comprised of three life forms, the sistens, present  
140 from July to June, the progrediens, present from April to July, and the winged sexuparae, which  
141 emerge concurrently with the progrediens in spring. In Asia, the winged sexuparae fly to spruce



142 and reproduce sexually. Since sexuparae do not survive on spruce species found in North  
143 America (McClure 1989), this actively mobile life stage does not play a role in the invasion of  
144 HWA, and acts as a population sink. Progrediens are sessile hemlock feeders that settle  
145 exclusively on foliage from the previous year's growth. They mature by June and give rise to the  
146 next generation of sistens. The sistens generation develops during autumn and winter, following  
147 a summer aestivation period. About 85% of sistens settle on new growth produced by the tree in  
148 spring (McClure 1991) and the remainder on older growth. In spring, the sistens produce eggs  
149 that develop into either progrediens or sexuparae, thereby completing the life cycle. Sistens tend  
150 to produce more numerous offspring than progrediens (McClure 1989). Feeding progrediens and  
151 sistens do not move between branches, so the 'crawler' nymphs (life stage between eggs and  
152 sessile adults) and potentially eggs are the sole dispersal stages in eastern North America.  
153 Dispersal is passive, with wind, birds, deer, and humans thought to act as the primary dispersal  
154 agents (McClure 1990). See McClure (1989; 1991) for additional details regarding the life cycle  
155 of HWA.

156

### 157 *General framework*

158 We develop a spatially explicit, discrete space-time stochastic model that links within-  
159 patch population dynamics and between-patch propagule dispersal with fine-resolution maps  
160 characterizing spatiotemporal variability in climate and hemlock abundance to simulate range  
161 expansion of HWA across the heterogeneous landscape of eastern North America. The model  
162 incorporates the influence of four heterogeneous factors on HWA spread: (i) hemlock abundance,  
163 (ii) winter temperature, (iii) population growth, and (iv) dispersal. Hemlock abundance and  
164 winter temperature are characterized as raster maps comprised of 1 km × 1 km cells (details

165 regarding the creation of these maps, which are available online from the Harvard Forest LTER  
166 data archive, can be found in Appendix A); it is across these maps that the model simulates HWA  
167 population growth and dispersal on an annual time step. Hemlock abundance in each cell (Fig. 1)  
168 determines the probability that dispersing adelgids establish in a location and also sets the upper  
169 limit to HWA population growth once a cell becomes infested. Hemlock abundance declines  
170 annually in infested cells and, for tractability, is assumed to remain constant elsewhere. Winter  
171 temperatures (Fig. A1), which change annually following observed temperature fluctuations,  
172 influence population growth by limiting the proportion of overwintering sistens that survive to  
173 produce progrediens in the next year. Mortality rates of progrediens (which includes production  
174 of sexuparae, a demographic dead end) and sistens are drawn from appropriate probability  
175 distributions. Dispersal between cells is simulated using a function parameterized from multiple  
176 datasets documenting the spread of HWA across different regions of the eastern U.S.

177         A single simulation of the model proceeds as follows. To initiate a simulation, a random  
178 number of HWA are introduced to a cell containing hemlock near Richmond, Virginia, the  
179 location of the first documented infestation of HWA in eastern North America (Stoetzel 2002).  
180 The simulation continues thereafter for 58 annual time steps, representing the period from 1951  
181 (date of first HWA collection in the eastern United States) through 2008, with time steps  
182 beginning with production of progrediens in the spring by overwintering sistens and ending with  
183 winter mortality of sistens. First, sistens in infested cells that have survived the winter produce  
184 the next generation of progrediens crawlers, a portion of which disperse to neighboring cells  
185 either through local diffusion or via long-distance dispersal described using a distance-based  
186 probability density function. Dispersing individuals can either initiate new infestations in  
187 uninfested cells containing hemlock, re-establish in the cell from which they originated, or die if

188 they fail to establish in a cell with hemlock or if they disperse to a cell without hemlock. The  
189 probability that dispersing individuals establish is equivalent to the fraction of the cell covered  
190 by hemlock crown and is therefore related to hemlock abundance. Carrying capacity of HWA  
191 populations is also determined by hemlock abundance and after dispersal, the surplus of  
192 individuals larger than the carry capacity of the cell die. The remaining population is then  
193 subjected to stochastic mortality. Surviving progrediens reproduce to create the next generation  
194 of sistens crawlers. Sistens follow the same cycle of dispersal, establishment, and mortality as  
195 progrediens, including limiting population size to carrying capacity, but with sistens being  
196 subjected to two additional forms of mortality: summer aestivation and overwintering. Hemlock  
197 abundance, and therefore carrying capacity and probability of establishment, declines each year  
198 in infested cells as a function of HWA population density. Stochasticity enters the model via  
199 random sampling from appropriate probability distributions that influence population growth and  
200 mortality, dispersal and establishment. These components are described in more detail in the next  
201 sections. The parameters of the model are summarized in Table 1. Simulations were constrained  
202 to the region of eastern North America encompassing the natural distribution of hemlock (Fig. 1).  
203 We used the results of the 1000 stochastic simulations to obtain an average representation of  
204 HWA spread. The model was written in the statistical language R (R Development Core Team  
205 2009) and the code is available from the online supplement.

206

### 207 *Hemlock abundance*

208 We mapped geographic variation in hemlock abundance ( $B_i$ ) as  $m^2$  of basal area in each  
209  $1 \text{ km} \times 1 \text{ km}$  cell  $i$  following the procedures described in Appendix A. The amount of hemlock in  
210 a cell determines both the number of HWA the cell can support and the probability that

211 dispersing HWA encounter hemlock. HWA attach themselves at the base of needles, typically at a  
212 rate of one individual per needle. Thus, the number of needles in a stand can serve as a  
213 reasonable estimate of the carry capacity of HWA populations. To estimate the number of needles  
214 in each stand, we used allometric relationships to compute leaf area from basal area (Kenefic and  
215 Seymour 1999) and the number of needles ( $L_i$ ) from the mean leaf area per needle (Santee and  
216 Monk 1981). Because sistens feed predominantly on new growth, typically at a rate of 85% on  
217 new growth and 15% on older foliage (McClure 1991, Paradis et al. unpublished), we used field  
218 surveys of uninfested hemlocks to estimate the proportion of total leaf area in new growth ( $\omega_i$ ).  
219 This quantity varied by tree size and site conditions, but we estimated it to be between one and  
220 ten percent. Together, these quantities allowed us to estimate the carrying capacity of progrediens  
221 ( $K_{Pi}$ ), which settle exclusively on the previous years' growth and therefore can be approximated  
222 as  $K_{Pi} = L_i$ , and sistens the carrying capacity of progrediens as  $K_{Si} = 0.85L_i\omega_i + 0.15L_i$ . To  
223 estimate probability of establishment, we used allometric relationships to compute crown area  
224 ( $C_i$ ) in  $m^2$  from basal area (Santee and Monk 1981). We assumed the probability that dispersing  
225 HWA establish in a cell is equivalent to the ratio of  $C_i$  to cell area in  $m^2$ . Therefore, the number  
226 of HWA that establish in a cell is simply  $C_i$  multiplied by the number of HWA dispersing to that  
227 location. In infested cells, temporal variation in hemlock abundance in each year  $t$  was  
228 introduced by reducing hemlock abundance as a function of HWA population density, thereby  
229 also reducing carry capacity and probability of establishment in the next year. See Appendix B  
230 for a description of how hemlock decline was estimated. For tractability, hemlock abundance  
231 was assumed to remain constant in uninfested cells throughout the simulation.

232

233 *Winter temperature*

234           Of the causes of HWA mortality, winter temperatures are thought to be the most  
235 important and most variable in space. The relationship between HWA mortality and temperature  
236 has been assessed in both the laboratory and the field (Parker et al. 1999; Skinner et al. 2003;  
237 Shields and Cheah 2005; Paradis et al. 2008; Trotter and Shields 2009). Winter temperatures can  
238 cause considerable mortality and trigger dramatic population declines, with southern populations  
239 typically experiencing significantly less mortality than those in the north (Shields and Cheah  
240 2005; Trotter and Shields 2009).

241           Paradis et al. (2008) explored the relationship between winter temperature and HWA  
242 overwintering mortality and determined that of eight different measures of winter temperature  
243 they considered, average daily mean winter (December-March) temperature had the greatest  
244 explanatory power. To account for the geographic variability in HWA winter mortality, we used  
245 the best-fit regression equation from Paradis et al. (2008) to express overwintering mortality  
246 ( $M_{Swit}$ ) in cell  $i$  in year  $t$  as a function of temperature ( $W_{it}$ , °C), or:  $M_{Swit} = 0.507 - 0.078*W_{it}$ . To  
247 incorporate stochasticity in  $M_{Swit}$ , we used values for the slope and intercept drawn from the 95%  
248 confidence intervals reported by Paradis et al. (2008). See Appendix C for details regarding the  
249 creation of annual mean winter temperature maps.

250

### 251 *Within-cell population dynamics*

252           We used multi-year surveys of HWA reproduction and survival rates in Massachusetts  
253 and Connecticut to estimate mean values of parameters for the life stages of HWA. See Appendix  
254 D for details regarding how these data were collected. Using these data, we estimated probability  
255 distributions that were sampled to estimate stochastic reproduction and mortality of the sistens  
256 and progrediens generations in each cell  $i$  in year  $t$ . For the progrediens generation, these

257 parameters included average number of progrediens produced by each overwintering sistens ( $P_{it}$ )  
258 and the mortality rate of progrediens ( $M_{Pit}$ ). For the sistens generation, parameters included the  
259 average number of sistens produced by progrediens ( $S_{it}$ ) and the mortality rates of dispersing,  
260 aestivating, and overwintering sistens ( $M_{Sit}$ ,  $M_{Sait}$ ,  $M_{Swit}$ , respectively, with  $M_{Swit}$  calculated as  
261 described in the previous section). To model stochastic population growth, we sampled Poisson  
262 distributions with means  $P_{it}$  or  $S_{it}$  and multiplied these values by the existing population size of  
263 either sistens ( $N_{Sit}$ ) or progrediens ( $N_{Pit}$ ). Binomial distributions with means  $M_{Pit}$ ,  $M_{Sit}$ , or  $M_{Sait}$   
264 were used to model mortality of progrediens and sistens. We incorporated the influence of  
265 density dependence on population dynamics by allowing HWA density to increase to the carry  
266 capacity set by hemlock abundance as described above and by reducing hemlock abundance in  
267 infested cells as described in Appendix B.

268

### 269 *Between-stand dispersal*

270 Range expansion of organisms is often driven by multiple mechanisms that operate at  
271 different scales (Higgins et al. 2003; Hastings et al. 2005), a process termed stratified dispersal  
272 (Hengeveld 1988). The biology and historic pattern of spread of HWA is consistent with this  
273 form of dispersal. Dispersal within hemlock stands is facilitated by progrediens and sistens  
274 nymphs crawling along branches or between proximate trees, whereas wind, birds, humans or  
275 other agents facilitate rare long-distance dispersal between stands (McClure 1990). Our model  
276 characterized stratified dispersal by allowing local diffusion between neighboring cells and by  
277 using historic data on HWA spread to fit a function that models long-distance dispersal events.

278 To fit a function representing the frequency distribution of between-stand dispersal  
279 distances, hereafter termed the distance-based probability density function or ‘distance-pdf’, we

280 used multiple datasets describing the historic spread of HWA (Table 2). Note that a distance-pdf  
281 differs from a dispersal kernel, which describes the density of propagules as a function of the  
282 distance from a source (Cousens et al. 2008). The datasets describing spread varied in their  
283 geographic focus and their spatial and temporal coverage (Table 2), but all represent either  
284 purposeful or ad hoc surveys of regionally distributed hemlock stands rather than trees within  
285 stands and therefore represent a sample of *successful* between-stand dispersal events. Appendix  
286 E describes how these data were fit to a set of candidate distance-pdfs using maximum  
287 likelihood. Given their coarse spatial resolution, we did not use the existing USFS county-level  
288 spread dataset (<http://na.fs.fed.us/fhp/hwa/maps/distribution.shtm>) to inform the distance-pdf.  
289 These data were, however, used in model evaluation.

290 For both between-cell and long-distance movements, it was assumed a small fraction of  
291  $N_{Sit}$  (population size of sistens) and  $N_{Pit}$  (population size of progrediens) was subject to dispersal.  
292 These proportions of dispersing individuals were drawn from different uniform probability  
293 distributions for local diffusion ( $\phi_{it}$ ) and long-distance dispersal ( $\gamma_{it}$ ) and were multiplied by  $N_{Sit}$   
294 and  $N_{Pit}$  to calculate the number of dispersing HWA in each generation. Ideally these proportions  
295 could be estimated using maximum likelihood approaches, but the data necessary to fit such a  
296 likelihood function currently are not available for HWA. To estimate the proportions of  
297 dispersing individuals, we therefore performed a sensitivity analysis that confirmed spread rate  
298 was indeed sensitive to these parameters and that reasonable results (spread rate of  
299 approximately 10-20 km per year, Evans and Gregoire 2007) were obtained if we assumed one  
300 individual in a million diffused to neighboring cells and if one individual in 100 million was  
301 subjected to long-distance dispersal as described by the distance-pdf.

302

303 *Model evaluation*

304 We evaluated predictive performance of the model in two ways. First, to assess spatial  
305 accuracy, we used the Area Under the Curve of the Receiver Operating Characteristics curve  
306 (AUC; Fielding and Bell 1997) to compare the predicted probability of infestation with the  
307 observed spatial pattern of HWA infestations in three locations: the northern extent of the range  
308 in New England, near the center of the range in Pennsylvania, and the southern extent of the  
309 range in Georgia. Second, to assess temporal accuracy, we compared the predicted timing of first  
310 infestation to the observed year of infestation using the 60-year record of spread from the USFS  
311 county-level dataset. We used the following procedure to address the scale mismatch between the  
312 model (1 km<sup>2</sup> cells) and the observation data (county-level, >10<sup>3</sup> km<sup>2</sup>). Given the size of  
313 counties, each contained numerous cells. Each cell within a county had a predicted year of first  
314 infestation for each of the 1000 simulations. For each county, we obtained the predicted years of  
315 first infestation across all cells within the county and across all 1000 simulations. Cells that did  
316 not become infested were ignored. Thus, if a county had 100 cells, all of which were infested in  
317 all 1000 simulations, we obtained a distribution of predicted years of infestation for the county  
318 comprised of  $1 \times 10^5$  data points. To evaluate the extent to which the predicted dates of  
319 infestation compared to the observed date, we determined whether the 95% confidence interval  
320 of the distribution of predicted years contained the observed year.

321

322 **RESULTS**

323 The maximum-likelihood estimation of the distance-pdf determined a log-normal  
324 function with a mean dispersal distance of 4.73 [4.5, 5.0] km provided the most plausible fit to  
325 the observed HWA spread data (Fig. E1). Application of the model to spatially and temporally



326 heterogeneous hemlock abundance (Fig. 1) and mean winter temperature (Fig. C1) over the 57-  
327 year simulation period suggested the probability of infestation was greatest from central  
328 Pennsylvania to the southernmost extent of the geographic range of hemlock in northern Georgia  
329 (red-yellow shading, Fig. 2, see Fig. F1 in the Appendices for an animated version of this figure).  
330 Regions of southern New York and New England, portions of which currently are infested by  
331 HWA, were generally predicted to have very low probabilities ( $< 1\%$ ) of invasion (blue shading,  
332 Fig. 2), whereas most of northern New England, Wisconsin and the upper peninsula of Michigan,  
333 and southern Canada had zero probability of infestation. In the southern portion of the study  
334 region, probabilities of infestation generally increased with time, before gradually declining as  
335 hemlock was lost from the region (animated Fig. F1, Appendices). In contrast, probabilities of  
336 infestation did not increase above zero in southern New England until late in the simulation,  
337 where invasion risk tended remain low and fluctuate yearly in response to year-to-year changes  
338 in winter temperature. Geographic and temporal variation in HWA population size tended to  
339 follow the pattern of probability of infestation, with population sizes being greatest south of  
340 central Pennsylvania and remaining relatively small in the north (animated Fig. G1, Appendices).

341       Earliest infestations were concentrated in the central Appalachians, with subsequent  
342 spread to the south and followed by later spread to the north (Fig. 3). In general, HWA was not  
343 predicted to arrive in northern Pennsylvania and southern New England until after year 2000. On  
344 average, the model predicted an overall increase in infested area beginning around 1970 and  
345 continuing to increase throughout the simulation period (Fig. 4). Simulated spread was most  
346 rapid in the southwest and was slowest in the north and northeast (slopes of curves, Fig. 5).

347       The spatial accuracy of the model measured using AUC varied by geographic region (Fig.  
348 6). AUC was highest in New England (NE, solid line Fig. 6) and Georgia (GA, dashed line Fig.

349 6), where the model had excellent to good discrimination (Pearce and Ferrier 2000). In contrast,  
350 model performance was poor (less than 0.5) in Pennsylvania (PA, dotted line Fig. 6), where the  
351 model over-predicted the observed extent of the invasion in the northwestern portion of the state.

352         Of the 325 counties that were known to be infested by HWA in 2008, the observed year  
353 of first infestation fell within the 95% confidence interval of the simulated year for only 37  
354 (11.4%) (Fig. 7, hatched counties). There was no discernable geographic patterning to these 37  
355 counties, which tended to be scattered throughout the study area. In contrast, there were strong  
356 geographic patterns in model error. In general, the model predicted arrival later than observed  
357 (Fig. 7, purple shading) in the north and earlier than observed (Fig. 7, green shading) in the  
358 south. In some instances the difference between the observed and modeled year of first  
359 infestation differed by more than 15 years. Most notably, HWA was predicted to arrive much  
360 later than observed in counties surrounding New York, NY and the city of Philadelphia,  
361 Pennsylvania. In addition, there were 13 known-infested counties that the model did not predict  
362 would become infested (Fig. 7, black-shaded counties). These areas included Philadelphia  
363 County, PA as well as counties containing New York, NY.

364

## 365 DISCUSSION

366         The objectives of this study were to develop a process-based, stochastic model to  
367 simulate range expansion of HWA across the large heterogeneous landscape of eastern North  
368 America, examine how environmental heterogeneity affected spread dynamics, and to compare  
369 the predictions of the model to the observed pattern of range expansion. Taken together, our  
370 model predicts considerable heterogeneity in the risk of HWA invasion across space and through  
371 time, with spatiotemporal variation in winter temperature, rather than hemlock abundance,

372 exerting a primary control on simulated spread dynamics. The simulated dynamics match some  
373 aspects of the observed pattern of range expansion, most notably the extent of invasion and  
374 anisotropic spread, but our model did not correctly predict the timing of HWA's arrival in  
375 different geographic regions.

376 Ours joins a growing list of range expansion models that integrate temporal and spatial  
377 heterogeneity in habitat suitability with dynamic population and dispersal processes (Dullinger et  
378 al. 2004; Keith et al. 2008; Anderson et al. 2009; Meentemeyer et al. 2011). However,  
379 evaluations of dynamic models against long-term records of observed spread histories remain  
380 rare (but see Pitt et al. 2009) and such comparisons are sorely needed to quantify the extent to  
381 which dynamic models might anticipate rapid range expansion. HWA provides a particularly  
382 good study system because its population dynamics are strongly influenced by temperature and it  
383 is limited to discrete habitat patches of its host plant (hemlock). Most importantly in the context  
384 of model evaluation, the introduction and spread history of HWA are relatively well known, and  
385 therefore provides a unique opportunity to ask: Given what we know today, how well could we  
386 have anticipated the spread of HWA across eastern North America? This question can be  
387 considered in the context of (i) extent of infestation, (ii) rate of spread, and (iii) timing of arrival.

388 In terms of extent of invasion, our simulations generally agree with the observed current  
389 extent of HWA's spread (Figs. 2, 6) and suggest that there are few remaining opportunities for  
390 widespread invasion of HWA. The model suggests that lethal winter temperatures are likely to  
391 limit additional northward spread of HWA beyond its current northern limit. Northwestern  
392 Pennsylvania and southern New York represent notable exceptions, though invasion risks are  
393 rather low or zero across most of New York. Elsewhere, the invasion largely has already reached  
394 the extent of its potential range as determined by availability of hemlock.

395           The model predicted anisotropic spread (Fig. 5), generally matching the observed pattern  
396 of most rapid spread in the south and lower rates of spread elsewhere (Fitzpatrick et al 2010).  
397 Our model predicted HWA to spread most rapidly across the southern Appalachians – where  
398 winters are relatively warm and hemlock is relatively abundant. Despite an abundance of  
399 hemlock in New England, HWA was predicted to spread slowly in this region, highlighting the  
400 importance of winter temperatures in limiting range expansion. It is worth noting that our  
401 findings contrast with regression-based analyses of the observed pattern of anisotropy, which  
402 suggest that, although spread rates of HWA were relatively rapid in the south, they were greatest  
403 in the northeast (Morin et al. 2009). However, this finding may in part be an artifact of the  
404 regression approach implemented by Morin et al. (2009), which assumes spread rates are  
405 constant and therefore can overestimate spread rates if long-distance dispersal events to a  
406 particular region are followed by slower diffusion (i.e., if invasion speed varies in time). This is  
407 the case with the dispersal of HWA to the northeast, which was facilitated by early, long-distance  
408 dispersal, followed by much slower rates of diffusion (Fitzpatrick et al. 2010).

409           Despite generally matching the observed extent of the invasion of HWA and the pattern  
410 of anisotropic spread, our model did a poor job of predicting the timing of arrival – a failure we  
411 attribute to an inability of the model to adequately capture both the timing and direction of early,  
412 rare long-distance dispersal events. Much has been written regarding the inherent difficulties of  
413 accurately measuring and modeling infrequent long-distance dispersal events and of the  
414 importance of such rare events in determining spread rate and ultimately timing of arrival of an  
415 organism undergoing range expansion (e.g., Clark et al. 1998; Higgins and Richardson 1999;  
416 Clark et al. 2001; Clark et al. 2003; Skarpaas and Shea 2007). For the most part, discussions  
417 regarding modeling long-distance dispersal have been one-dimensional in that they mainly have

418 considered the shape of the probability function describing the distribution of dispersal distances.  
419 A less appreciated aspect of modeling range expansion is that for models to be successful, they  
420 must also accurately model dispersal *direction* (i.e., anisotropy). In the case of HWA, data  
421 suggest populations spread from Richmond, VA to Philadelphia, PA then eventually to New  
422 York, NY. These early, long-distance movements to densely populated regions of the northeast  
423 were not captured in our simulations (black shading; Fig. 7), which may explain why the  
424 simulations predicted later arrival in the northeast than was observed. In fact, none of our  
425 simulations predicted that Philadelphia County, PA and the counties surrounding New York, NY  
426 would become infested. These findings can be attributed in part to the failure of our hemlock  
427 map to capture urban hemlock density. Of equal or greater importance could be the role of long-  
428 distance dispersal vectors that increase the likelihood of spread to the east and northeast, most  
429 notable of which are wind and birds (McClure 1990). Dispersing progrediens hatch during the  
430 time of spring bird migration from south to north, and McClure (1990) found HWA attached to  
431 forest birds. Bird migration may be a particularly important dispersal vector in unforested areas  
432 such as cities as isolated hemlocks likely have much higher bird visitation rates per tree than  
433 trees embedded in a forest. During the time of both progrediens and sistens dispersal, dominant  
434 winds are mainly out of the west and southwest (Klink 1999). Consistent with the observed  
435 pattern of range expansion of HWA, the dominant winds and bird migrations would tend to  
436 reduce the probability of spread to the south and west, thereby delaying arrival in the southern  
437 Appalachians, while increasing spread potential to north and east. The failure to incorporate wind  
438 patterns may also explain why the model predicted a high probability of spread to upwind  
439 portions of northwestern Pennsylvania that are not currently known to be invaded (B. Register,  
440 pers. comm.). The movement of hemlock for landscaping purposes may also play a role in

441 facilitating long distance dispersal of HWA, though the directionality of such movements are less  
442 clear. Taken together, the inability of the model to reproduce the observed timing of arrival in  
443 different regions seems to largely result from an inability to capture early dispersal events to  
444 northeastern cities and an overestimation of the frequency of long distance dispersal events to the  
445 south and west.

446         Although the model failed to capture aspects of the spread of HWA, it is reasonable to  
447 ask: Within the context of the model, how likely was the observed pattern of spread? Invasion  
448 dynamics are dependent on a number of highly stochastic processes that pose major challenges to  
449 developing realistic models of range expansion. Vagaries of population dynamics and dispersal,  
450 particularly at early stages of range expansion (Higgins and Richardson 1999), can play a  
451 disproportionate role in determining the ensuing pattern of spread. It is reasonable to assume that  
452 small changes to any of these early dynamics could result in strikingly different patterns of range  
453 expansion. More broadly, the ecological patterns we observe, and on which models are  
454 parameterized, represent a single realization of a multitude of possible realizations, some more  
455 likely than others. It is critical to note that although running many simulations can reduce the  
456 influence of model stochasticity on the predicted outcome, as well as provide an indication of  
457 uncertainty, model averaging may not necessarily bring us any closer to predicting the observed  
458 pattern. In fact, it could do just the opposite as averaging multiple simulations reduces the  
459 influence of uncommon, but highly consequential, events.

460         Knowledge of when and where an invasive species is likely to spread is critical to  
461 management efforts. In the case of HWA, there appears to be little potential for additional spread,  
462 at least under current climatic conditions, and therefore correspondingly small remaining  
463 opportunities for management intervention at the landscape scale. However, given the limiting

464 effects of temperature on HWA range dynamics in New England, increases in winter temperature  
465 in this region could lead to the rapid spread of HWA (Paradis et al. 2008) and subsequent loss of  
466 hemlock. Planned applications of our model to scenarios of future climate in the northeastern US  
467 and southern Canada will explore these dynamics in greater detail.

468         As global change continues to alter the distributions of native and exotic species, there is  
469 an increasing need for spatially explicit forecasts of range expansion. Here, we combined  
470 existing techniques for modeling population growth and dispersal with fine-resolution maps  
471 characterizing spatial and temporal variability in climatic and habitat suitability to model species  
472 spread over a large heterogeneous region. Ours is the sort of integrated model recently  
473 envisioned by Huntley et al. (2010), who, like many others, have argued that dynamic models are  
474 needed to provide more realistic forecasts of changes in species distributions, such as species  
475 responses to climatic change. Validation remains a central challenge however, as it is not possible  
476 to validate predictions of events that may not occur for decades. In contrast, invasive species  
477 offer a unique opportunity to observe range expansion over relatively short time scales and can  
478 therefore serve as a means to assess dynamic models of range expansion. Our results suggest  
479 that, by some measures, dynamic models can provide useful predictions of changes in species  
480 distributions in space broadly consistent with observed patterns. However, in instances where  
481 range expansion is driven by rare events with large consequences, for models to be successful in  
482 predicting timing of arrival, they must incorporate an improved understanding of the drivers of  
483 anisotropy. In the context of the range dynamics of HWA, this would include the role of passive  
484 dispersal vectors in driving long-distance dispersal events to cities in the northeastern US and  
485 preventing spread to highly suitable locations elsewhere.

486

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496

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641

642 ECOLOGICAL ARCHIVES MATERIAL

643 Appendix A. Description of how maps of hemlock distribution and abundance were developed.

644 Appendix B. Description of how hemlock mortality in infested cells was modeled.

645 Appendix C. Description of how annual maps of mean winter temperature were developed

646 (contains Figure B1).

647 Appendix D. Description of field data collection and analyses used to estimate HWA

648 reproduction and survival rates.

649 Appendix E. Description of the estimation of the dispersal-distance probability density function

650 using maximum likelihood (contains Figure E1).

651 Appendix F. Animated version of Fig. 2 (probability of HWA infestation).

652 Appendix G. Animation of spatiotemporal changes in HWA population size.

653 Supplement 1: R code used for spread simulations.

654 Table 1. Overview of default and fitted parameter values of the HWA range expansion model.

Symbol	Parameter	Type	Value, range, or distribution
General			
$i$	index of a particular cell	index	—
$j$	index of a particular year	index	1951 – 2008
Population dynamics			
$N_0$	Initial population size in Richmond, VA in 1951	random	$\sim$ Pois(1000)
$K_{Pit}$	Carrying capacity of progrediens in cell $i$ in year $t$ , equal to $L_{it}$	modeled	—
$K_{Sit}$	Carrying capacity of sistens in cell $i$ in year $t$ , function of $L_{it}$ and $\omega_{it}$	modeled	—
$N_{Pit}$	Progrediens population size in cell $i$ in year $t$	modeled	$[0, K_{Pit}]$
$N_{Sit}$	Sistens population size in cell $i$ in year $t$	modeled	$[0, K_{Sit}]$
$W_{it}$	Winter temperature in cell $i$ in year $t$	observed	—
$P_{it}$	Number of progrediens produced by each sisten in cell $i$ in year $t$	random	$\sim$ Pois(142.7)
$S_{it}$	Number of sistens produced by each progredien in cell $i$ in year $t$	random	$\sim$ Pois(22.2)
$M_{Pit}$	Mortality rate of established progrediens in cell $i$ in year $t$	random	$\sim$ Binom(0.98)
$M_{Sit}$	Mortality rate of established sistens in cell $i$ in year $t$	random	$\sim$ Binom(0.64)



$M_{Sai}$	Mortality rates of sistens during aestivation in cell $i$ in year $t$	random	$\sim\text{Binom}(0.71)$
$M_{Swit}$	Overwintering mortality rate of sistens in cell $i$ in year $t$ , function of $W_{it}$	modeled	[0, 1]

#### Host dynamics

$B_{it}$	Basal area of hemlock in cell $i$ year $t$	modeled	—
$L_{it}$	Leaf area in cell $i$ in year $t$ , function of $B_{it}$	modeled	—
$C_{it}$	Crown area in cell $i$ in year $t$ , function of $B_{it}$	modeled	—
$\omega_{it}$	Proportion of $L_{it}$ that is new growth	random	$\sim\text{Uniform}(0.01, 0.05)$

#### Dispersal dynamics

$\mu$	Mean of the log-normal dispersal pdf	modeled	4.73 km
$\sigma$	Standard deviation of the log-normal dispersal pdf	modeled	3.27 km
$\phi_{it}$	Proportion of individuals diffusing to adjacent cells in cell $i$ in year $t$	random	$\sim\text{Uniform}(0, 1 \times 10^{-6})$
$\gamma_{it}$	Proportion of long-distance dispersers in cell $i$ in year $t$	random	$\sim\text{Uniform}(0, 1 \times 10^{-8})$

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655

656

657 Table 2. Datasets describing the spread of hemlock woolly adelgid at the landscape scale that  
658 were used to parameterize the dispersal probability density function. See acknowledgements for  
659 data sources. Published sources are footnoted.

Region	Number of locations	Year of first/last observation
Georgia	1057	2003/2006
Southwestern Virginia	98	1997/2007
Pennsylvania	1598	1982/2006
Connecticut & Massachusetts*	142	1998/2007
New Hampshire	73	2000/2008

660 \* Preisser et al. (2008)

661

662 Figure 1. Eastern North America showing modeled hemlock abundance at 1km  $\square$  1km  
663 resolution versus the geographic range of hemlock (USGS 1999). The red star indicates the  
664 location of Richmond, Virginia where introduced populations of hemlock woolly adelgid were  
665 first collected in 1951.

666

667 Figure 2. Predicted probability of infestation of hemlock stands by hemlock woolly adelgid  
668 averaged over 1000 simulations of range expansion initiated in Richmond, Virginia, using annual  
669 winter temperatures experienced during the period 1951-2008. The observed extent of the  
670 invasion in 2008 is delineated by the bold gray line. Hemlock stands not predicted to become  
671 infested in any of the 1000 simulations are shown in black. Unshaded regions do not contain  
672 hemlock.

673

674 Figure 3. Total area infested versus time for each of the 1000 individual simulations (dashed gray  
675 lines) and the mean (solid black line) total area infested.

676

677 Figure 4. Predicted year of infestation of hemlock stands by hemlock woolly adelgid averaged  
678 over 1000 simulations of range expansion initiated in Richmond, Virginia using annual winter  
679 temperatures experienced during the period 1951-2008. The observed extent of the invasion in  
680 2008 is delineated by the bold gray line. Hemlock stands not predicted to become infested in any  
681 of the 1000 simulations are shown in black. Unshaded regions do not contain hemlock.

682

683 Figure 5. Area of hemlock infested versus year averaged over 1000 simulations within different  
684 geographic regions defined by dividing the study area into 22.5° intervals (16 cardinal directions)

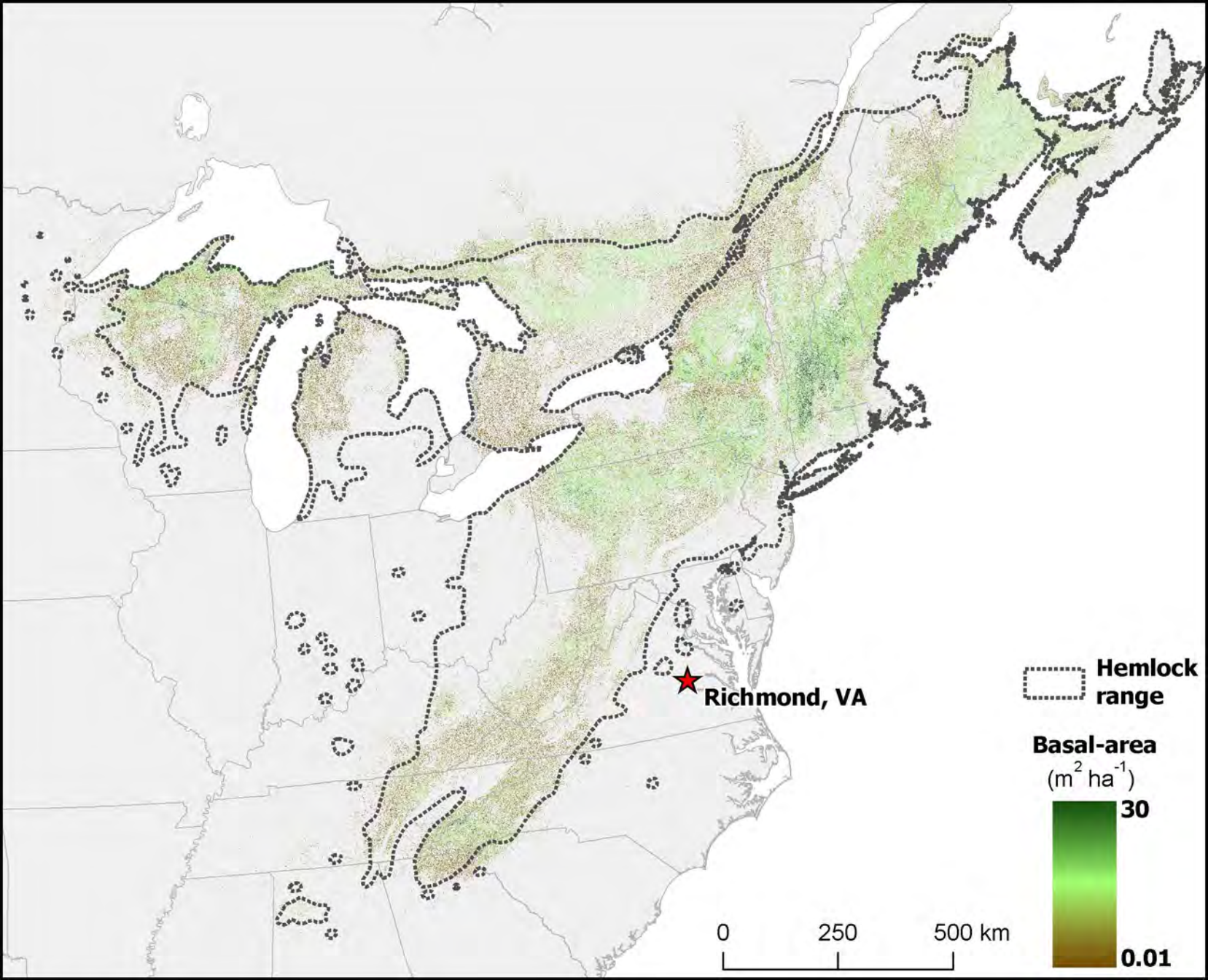
685 using Richmond, Virginia as the origin. The rate of spread, indicated by the slope of the line in  
686 each panel, is most rapid in the southwest and slowest in the northeast.

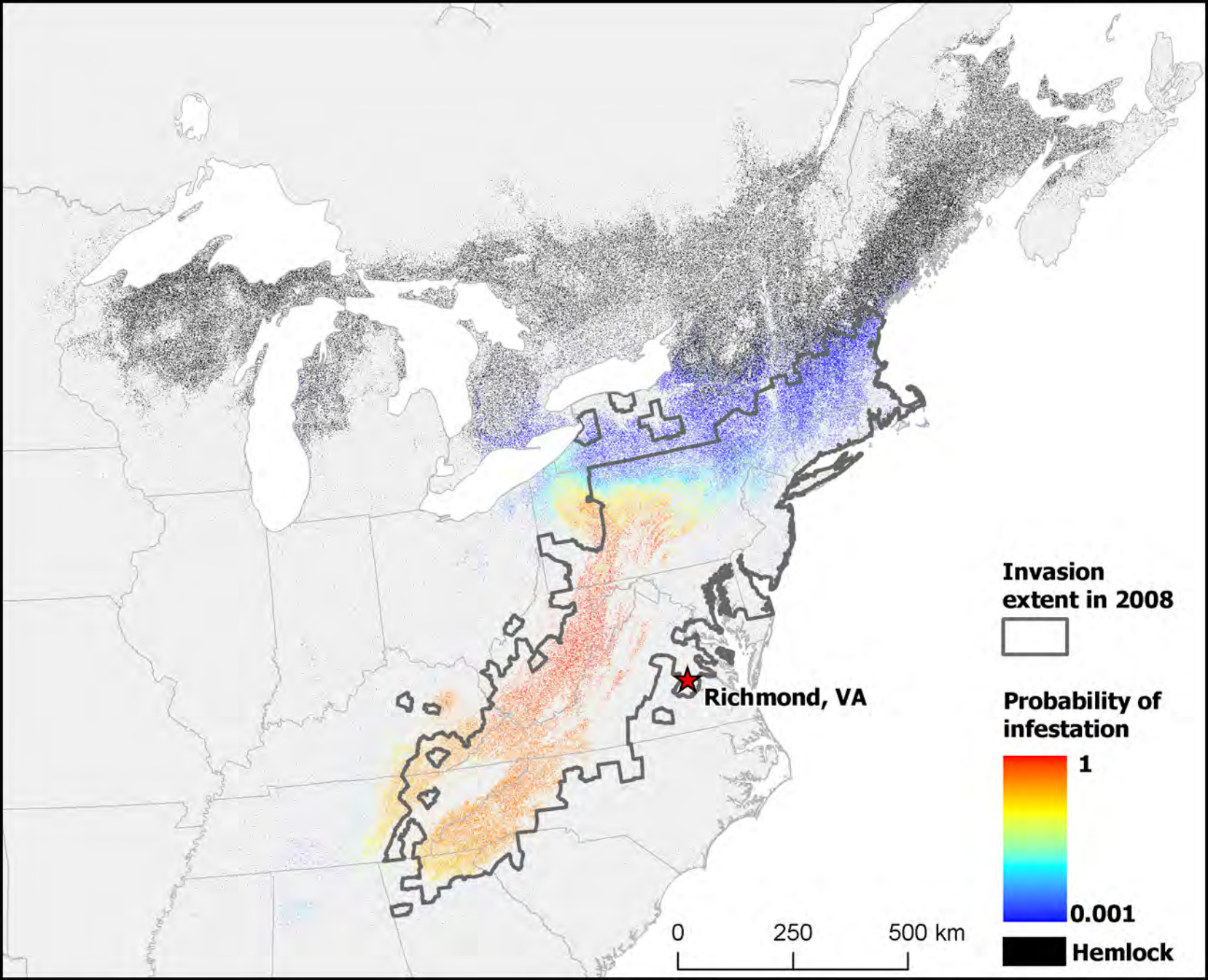
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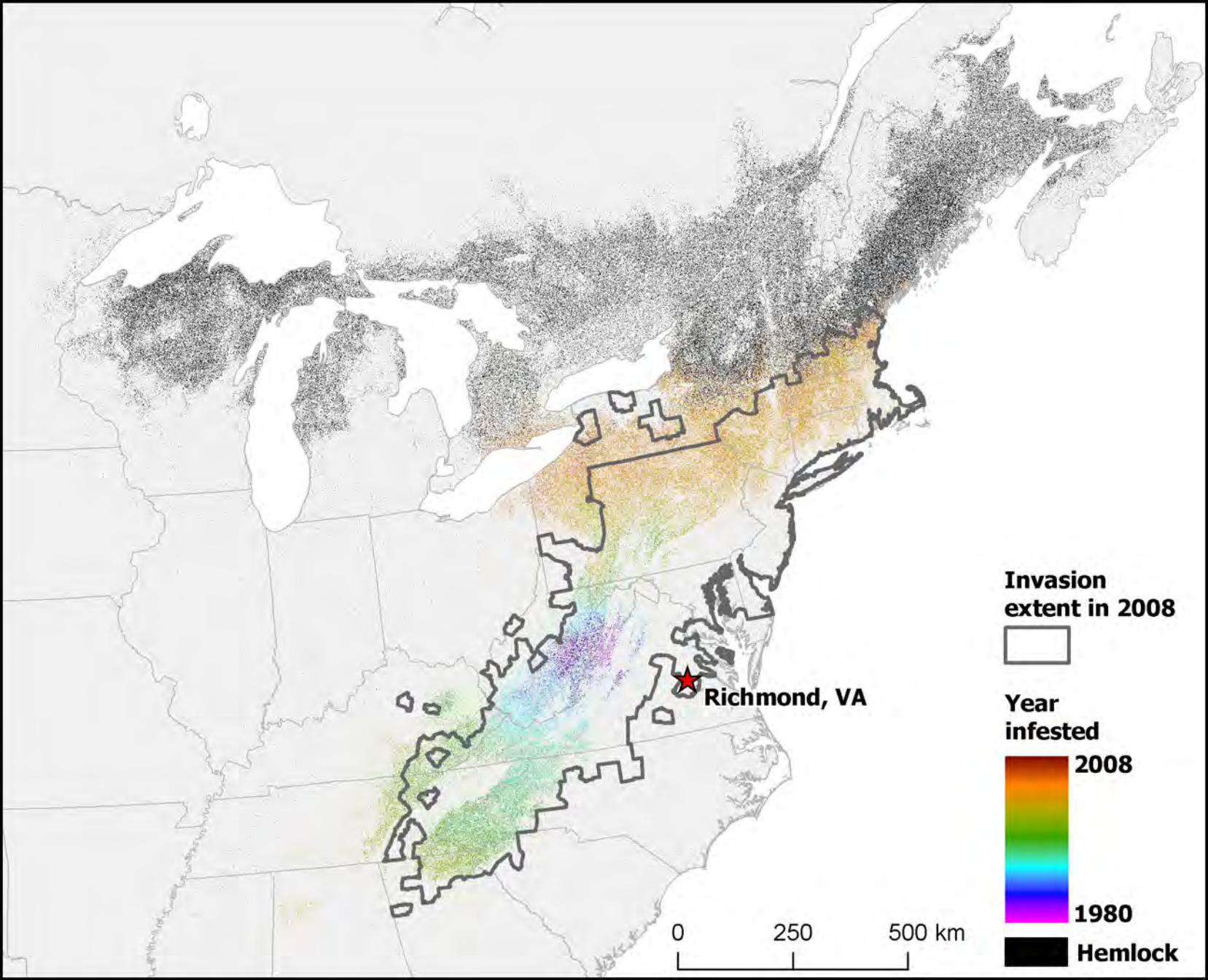
688 Figure 6. Receiver Operating Characteristics (ROC) curves showing model performance in three  
689 geographic regions, including New England (NE), Georgia (GA) and Pennsylvania (PA).

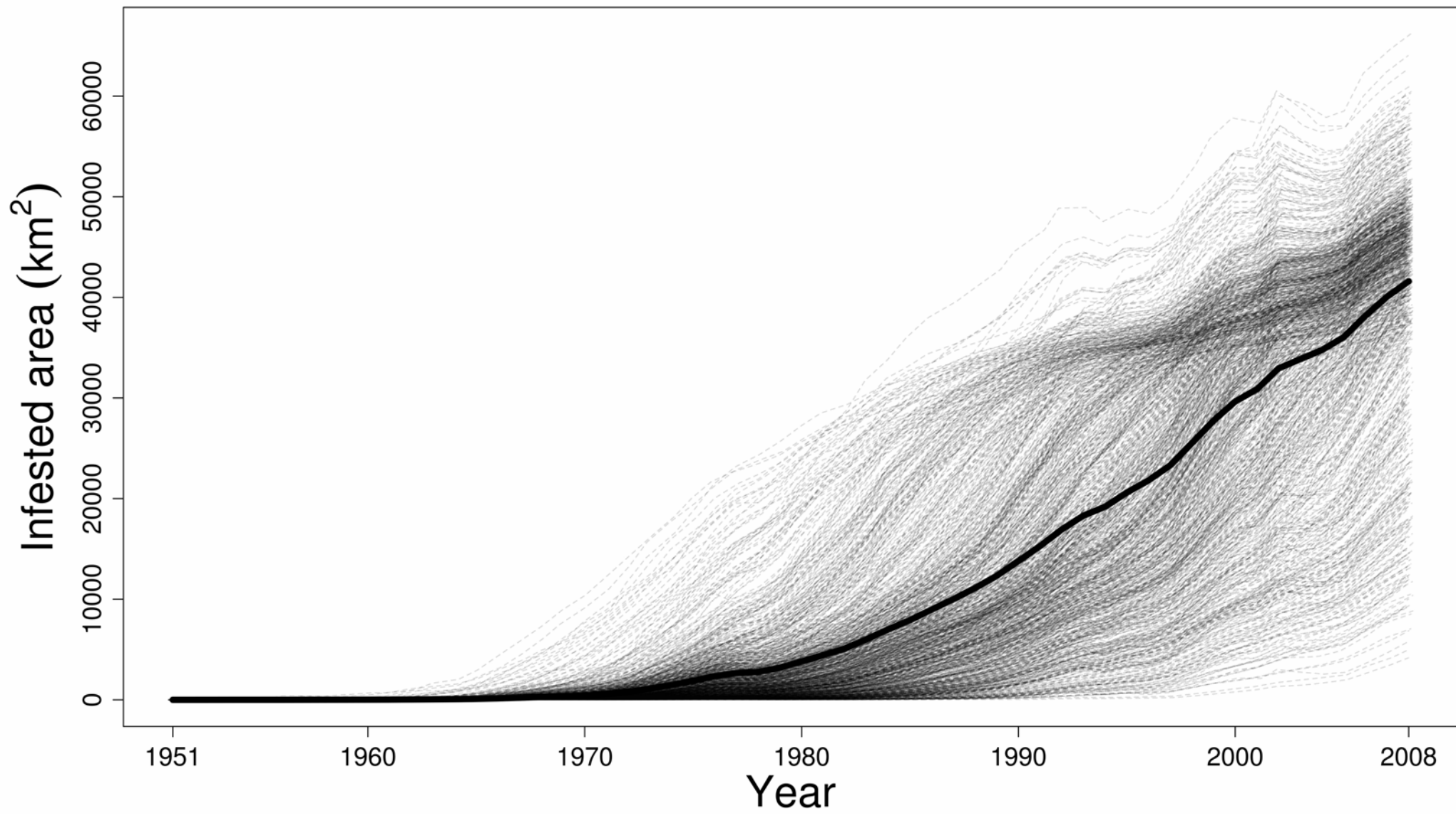
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691 Figure 7. Map of the difference between the observed (inset) and mean simulated year of  
692 infestation for counties infested by the hemlock woolly adelgid up to year 2008. Green/purple  
693 shading indicates counties for which the model predicted a county to become infested  
694 earlier/later than was observed. Grey shading indicates counties for which the simulated data fell  
695 within one year of the observed date. Hatching highlights those counties for which the observed  
696 year of infestation fell within the 95% confidence interval of the simulated year. Black shading  
697 represent counties where HWA has been observed, but which none of the 1000 simulations  
698 predicted to become infested.

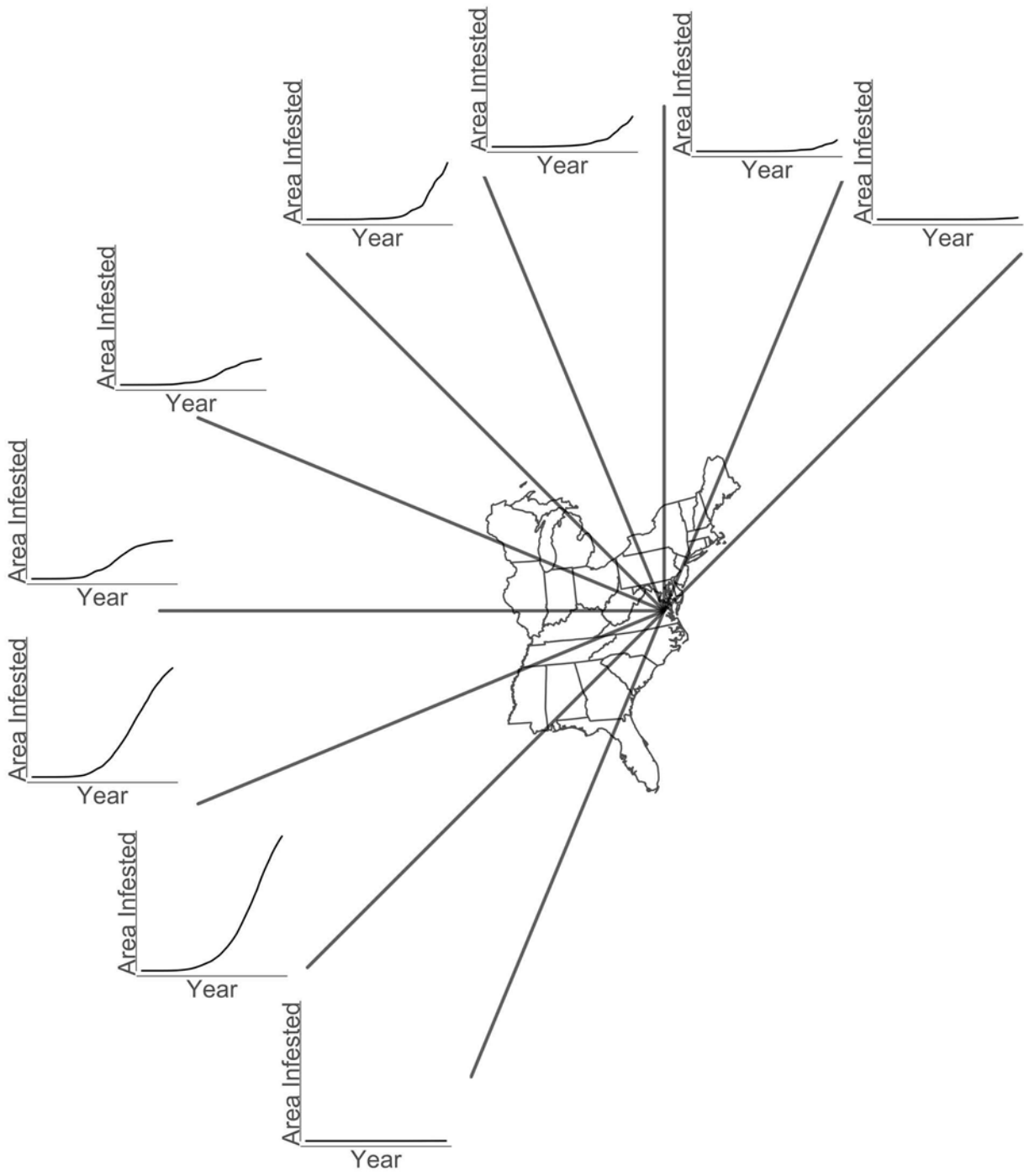


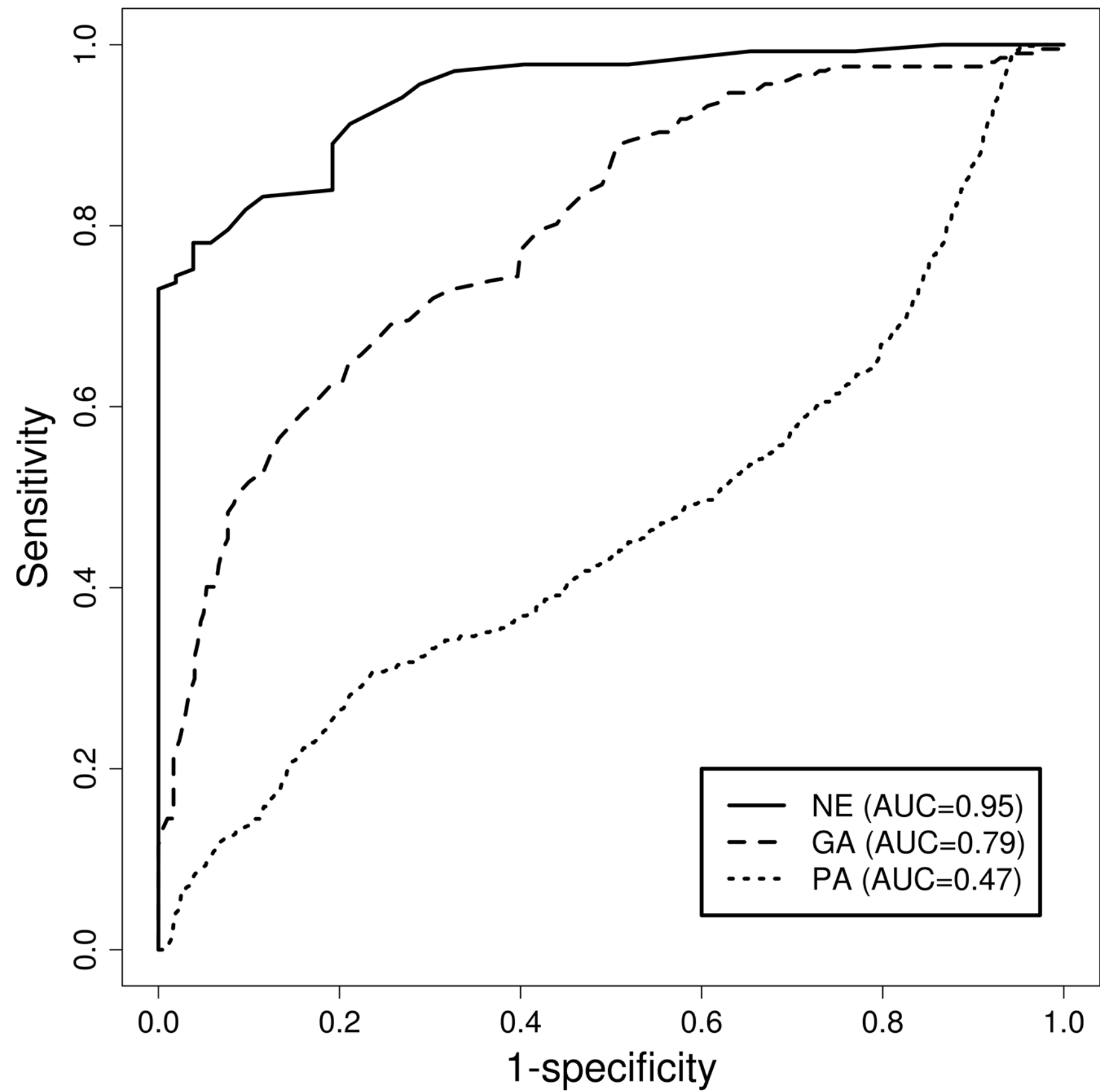


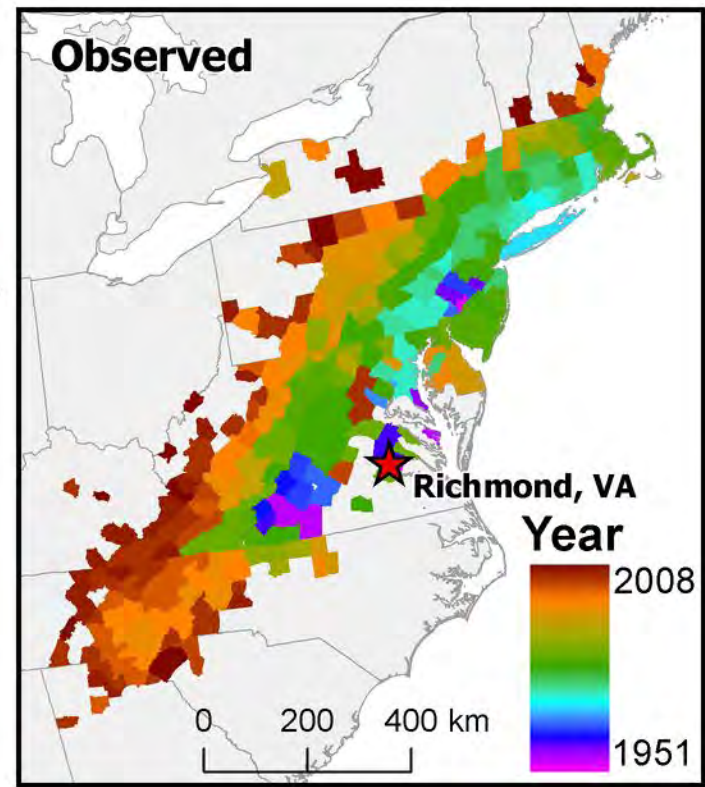
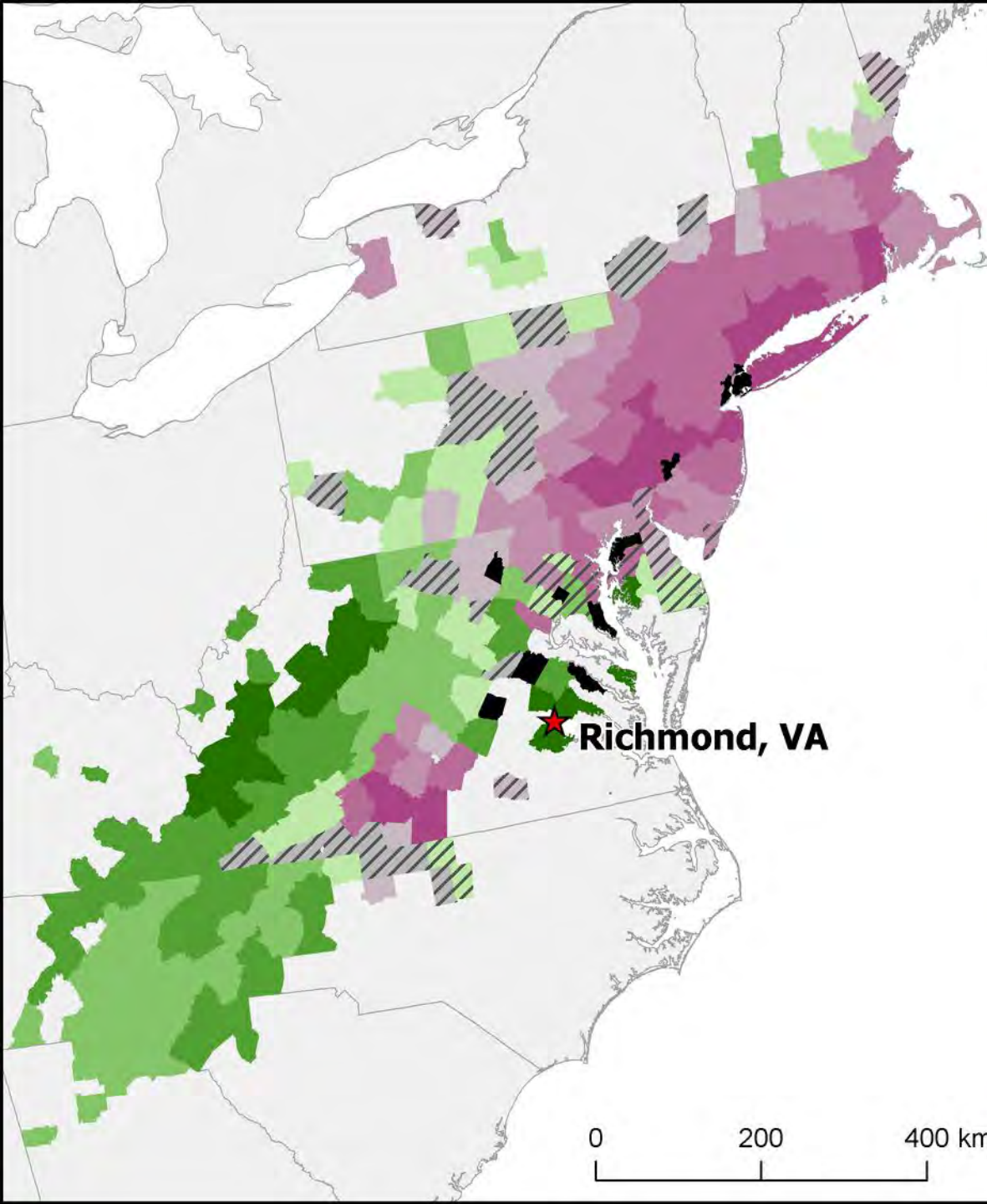












### Difference

(Observed - Simulated)

