*Ecology*, 91(12), 2010, pp. 3448–3455

# Ecological boundary detection using Bayesian areal wombling

MATTHEW C. FITZPATRICK,[1,2,3,7] EVAN L. PREISSER,[2] ADAM PORTER,[4] JOSEPH ELKINTON,[4] LANCE A. WALLER,[5]
BRADLEY P. CARLIN,[6] AND AARON M. ELLISON[3]

[1]*University of Maryland Center for Environmental Science, Appalachian Lab, Frostburg, Maryland 21532 USA*
[2]*Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881 USA*
[3]*Harvard University, Harvard Forest, Petersham, Massachusetts 01366 USA*
[4]*Department of Plant, Soil, and Insect Sciences, University of Massachusetts, Amherst, Massachusetts 01003 USA*
[5]*Department of Biostatistics, Rollins School of Public Health, Emory University, Atlanta, Georgia 30322 USA*
[6]*Division of Biostatistics, School of Public Health, University of Minnesota, Minneapolis, Minnesota 55455 USA*

*Abstract*. The study of ecological boundaries and their dynamics is of fundamental importance to much of ecology, biogeography, and evolution. Over the past two decades, boundary analysis (of which wombling is a subfield) has received considerable research attention, resulting in multiple approaches for the quantification of ecological boundaries. Nonetheless, few methods have been developed that can simultaneously (1) analyze spatially homogenized data sets (i.e., areal data in the form of polygons rather than point-reference data); (2) account for spatial structure in these data and uncertainty associated with them; and (3) objectively assign probabilities to boundaries once detected. Here we describe the application of a Bayesian hierarchical framework for boundary detection developed in public health, which addresses these issues but which has seen limited application in ecology. As examples, we analyze simulated spread data and the historic pattern of spread of an invasive species, the hemlock woolly adelgid (*Adelges tsugae*), using county-level summaries of the year of first reported infestation and several covariates potentially important to influencing the observed spread dynamics. Bayesian areal wombling is a promising approach for analyzing ecological boundaries and dynamics related to changes in the distributions of native and invasive species.

*Key words:* Adelges tsugae; *boundary analysis; ecotones; edge detection; hemlock woolly adelgid; invasive species; spatial statistics.*

## INTRODUCTION

A central challenge in ecology is determining the factors influencing species distributions and how these factors change across space and time (Holt and Keitt 2005). The increasingly serious threats to natural systems posed by global change emphasize the practical importance of identifying the environmental factors associated with range edges (e.g., Gavin and Hu 2006) and of determining how environmental factors may influence the distributions of both native and invasive species. At its core, understanding the dynamics of species distributions is both a statistical problem of identifying boundaries between where a species is present (or abundant) and absent (or rare), and an ecological problem of determining environmental factors associated with these boundaries (Gaston 2003, Fortin et al. 2005).

Two major challenges limit detailed analysis of ecological and evolutionary processes underlying the formation, persistence, and change of range edges. First, the spatiotemporal data required for inference are lacking (Parmesan et al. 2005). When such data are available, it is most common for them to be spatially homogenized as summaries over geopolitical or ecological regions such as counties, states, or biomes. Such aggregation obscures fine-scale spatiotemporal characteristics in the data. Second, data arising from neighboring regions are often more similar than those from distant neighbors. The spatial structure inherent in the data is often of ecological interest, but must be accounted for to make valid inferences (Legendre 1993). Acknowledging spatial structure is particularly important when considering the spread of invasive species because ecological dynamics are inherently correlated in space and time.

Over the last decade a large body of ecological research has addressed boundary analysis with a corresponding increase in the number of analytical approaches available for detecting and analyzing boundaries (see Jacquez et al. [2000] and Fagan et al. [2003] for recent reviews and Jacquez et al. [2008] for a recent special issue on the topic). Wombling, a type of boundary analysis named in recognition of a pioneer in the field (Womble 1951), is a technique for determining zones of rapid change of a quantity of interest as it varies across some geographical or Euclidean space (Fortin and Dale 2005). A common secondary concern

Manuscript received 22 April 2010; revised 21 July 2010; accepted 27 July 2010. Corresponding Editor: J. Elith.

[7] E-mail: mfitzpatrick@umces.edu

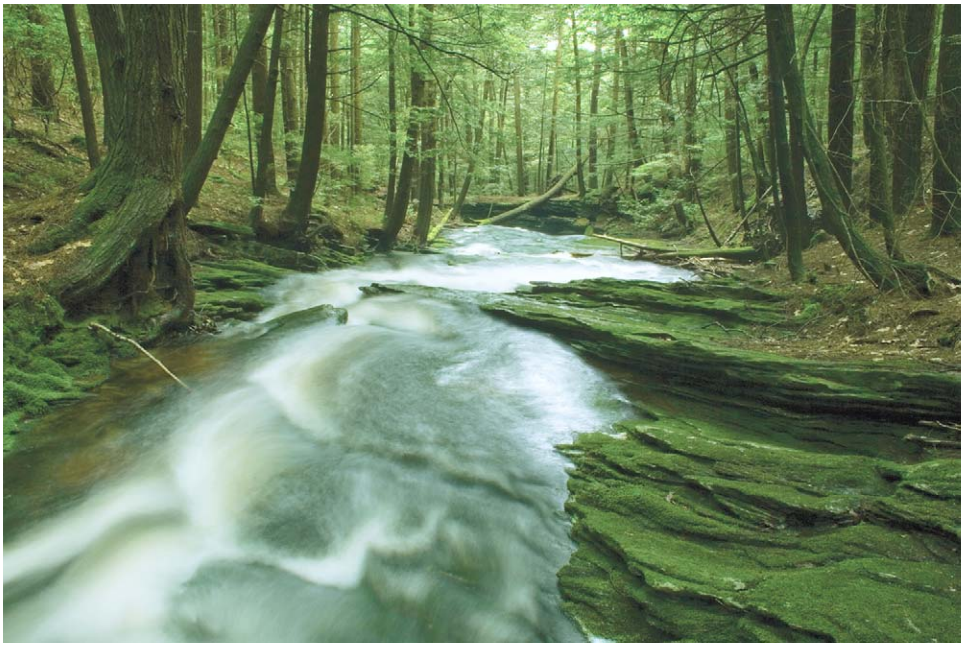

PLATE 1. A monospecific stand of eastern hemlock (*Tsuga canadensis*) at Dean Brook, Shutesbury, Massachusetts (USA). Hemlock is a late-successional conifer that by virtue of its structural and functional attributes supports unique terrestrial and aquatic ecological communities. As no other co-occurring tree species fill the same ecological role as hemlock, its removal from the landscape by the hemlock woolly adelgid (*Adelges tsugae*) is likely to acutely and chronically impact ecosystem processes, hydrology, and biodiversity. Photo credit: M. C. Fitzpatrick.

is to assign statistical significance or probabilities to the identified boundaries.

At present, much of the published literature on boundary analysis in ecology considers point-referenced data (i.e., geostatistical data comprised of spatial locations of points with known coordinates, such as latitude–longitude) that are either regularly (lattice or grid) or irregularly spaced. Although point-referenced data are becoming increasingly accessible (Graham et al. 2004), ecological data covering broad spatial and temporal scales are more commonly available as summaries over geographic regions. For example, locality information for plants from herbaria or from the USDA PLANTS database (*available online*)[8] is often provided as county- or state-level summaries rather than specific locations from where the plants were observed. Boundary analysis of such *areal* data is well-developed in public health fields, but it has received minimal attention in ecology. Further, most of the boundary analysis approaches in current use in ecology assign significance or probabilities to detected boundaries using null distributions; such inferences are relative to predetermined and often subjective choices.

Here we describe a promising technique for ecological analysis of areal data developed by public heath researchers (e.g., Lu and Carlin 2005, Ma et al. 2006, Wheeler and Waller 2008) that has as yet seen little use by ecologists. The method employs a Bayesian hierarchical framework that (1) uses areal data; (2) accounts for spatial structure in these data and the spatial and nonspatial uncertainty associated with them; and (3) provides a natural means of assigning probabilities to boundaries using posterior estimates of the modeled parameters. As examples, we analyze simulated spread data and the historic pattern of spread of the invasive hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). Although this pest threatens hemlock forests (both eastern hemlock, *Tsuga canadensis* and Carolina hemlock, *Tsuga caroliniana*, are susceptible; see Plate 1) throughout eastern North America (Orwig et al. 2002) and is of great concern to both researchers and land managers, data on HWA spread exists primarily as county-level summaries documenting the year HWA infestations were reported in that area. Such reporting is ad hoc and thus not equally spaced in time. In contrast to classical approaches, the Bayesian framework incorporates prior information (in this case, the likely correlation between year of first HWA infestation in spatially adjacent regions) in order to produce improved estimates of all underlying model parameters. These parameters are themselves regarded as having probability distributions in light of the data (posterior distributions), which among other things permits direct estimation of the probability that two geographic regions are separated by a boundary while simultaneously accounting for spatial dependencies (Lu and Carlin 2005). Our goal is to improve inference between

---

[8] ⟨http://plants.usda.gov⟩

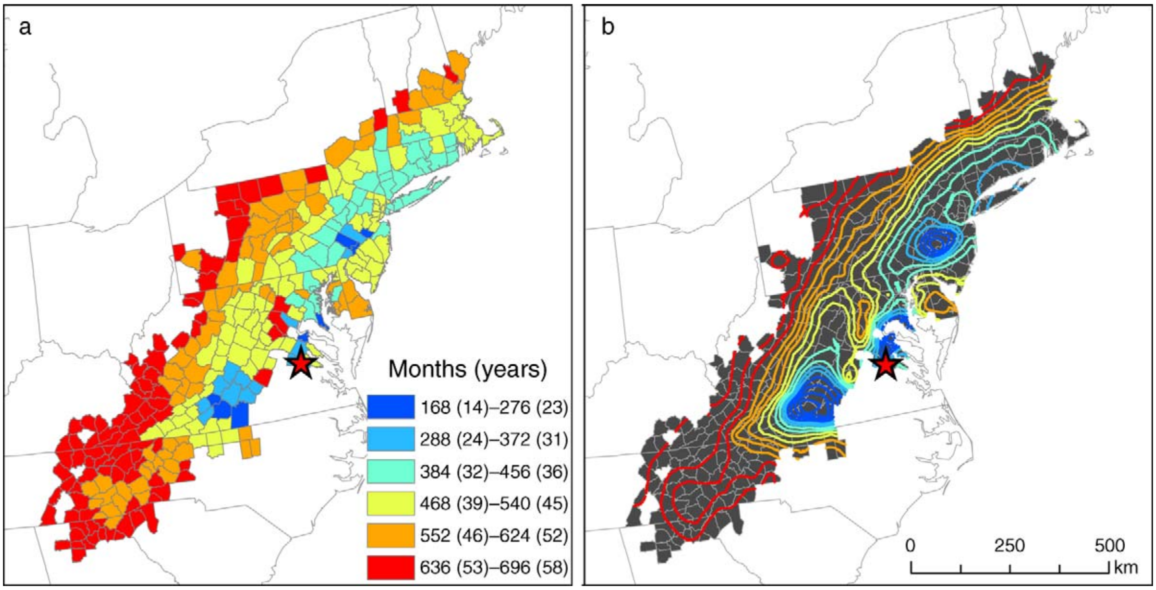

FIG. 1. Observed pattern of spread of the hemlock woolly adelgid (a) at the county level and (b) smoothed using ordinary kriging of these dates. Colors indicate time elapsed between the initial infestation in Richmond, Virginia, USA (indicated by red star) in 1951 and each county's first reported infestation.

observed spread patterns and underlying ecological processes by identifying boundaries across which spread is slower than expected and to determine whether such boundaries are associated with aspects of the environment.

## METHODS

*Study system*.—HWA is a small, flightless insect native to Asia that was first collected from hemlock in the eastern United States in 1951 in Richmond, Virginia. HWA infestations were collected next in 1969 in Philadelphia, Pennsylvania, followed shortly thereafter by counties southwest of Richmond, Virginia (Fig. 1a, see the Appendix for a detailed description of these data). The observed pattern of county-level spread following these early events largely mimics a diffusive process although outlying infestations also have appeared in northwestern New York State. As an exploratory tool, ordinary kriging on the county-level spread pattern shows slow initial spread from the three distinct early infestations, followed by spread to the northeast and southwest (Fig. 1b). Compressed contours along the Appalachian Mountains suggest that environmental or topographic aspects of this feature may be associated with reduction of spread rate to the west. In contrast, spread has been relatively rapid in the southeastern Appalachians, where contours are spaced broadly, suggesting topography alone may not influence spread rate. Despite their proximity to the initial infestation, counties south of Richmond, Virginia remain uninfested presumably because of a lack of hemlock.

Although population and dispersal dynamics of HWA remain poorly understood, we expect the pattern of spread to be a function of both environmental and social factors. Environmental factors such as hemlock abundance and winter temperature (Paradis et al. 2008, Trotter and Shields 2009) may alter spread rate by influencing population and dispersal dynamics. Social factors such as human population density may influence the pattern of spread both by altering the environment (e.g., by reducing forest cover or planting hemlocks as landscape trees) and by influencing the detection and reporting of HWA infestations. To account for these processes, we generated a set of covariates for each county that could influence the spread and detection of the advancing HWA front, including mean winter (December–March) temperature, human population density, and hemlock abundance (see the Appendix for details regarding the calculation of these variables). We did not consider physical barriers to spread such as rivers or mountains (e.g., Wheeler and Waller 2008) in this analysis because passive dispersal of HWA by wind and birds is unlikely to be influenced by such features at the county level.

*Bayesian areal wombling*.—We follow recent work by Lu and Carlin (2005) and use a Bayesian hierarchical model to perform areal wombling. Wheeler and Waller (2008) extended Lu and Carlin's (2005) research on human disease incidence to the spread of rabies using county-level reporting of rabid raccoons. Following Wheeler and Waller (2008), we modeled $Y_i$, the number of months elapsed between the first reported HWA infestation in the study region in 1951 and the first reported HWA infestation in each county $i$ as follows:

$$Y_i \sim \mathcal{N}\left(\mu_i, \frac{1}{\tau}\right) \tag{1}$$

where

$$\mu_i = \alpha + \mathbf{x}_i\boldsymbol{\beta} + \phi_i \tag{2}$$

is the expected number of months elapsed to first reported HWA infestation in county $i$, $\alpha$ is an intercept, $\tau$ is the precision, $\mathbf{x}_i$ is a vector of the covariates, and $\phi_i$ is a spatial random effect. The spatial random effect $\phi_i$ is given an intrinsic conditionally autoregressive (CAR) prior expressed as

$$\phi \sim \mathrm{CAR}(\tau_C) \tag{3}$$

$$\phi \mid \boldsymbol{\phi}_{j \neq i} \sim \mathcal{N}\left(\bar{\phi}_i, \frac{1}{(\tau_C m_i)}\right) \tag{4}$$

where $m_i$ is the number of counties neighboring county $i$ and $\tau_C$ is the precision. The use of a CAR prior for the random effects serves two functions. Foremost, invasive spread is a spatial process, with neighboring counties more similar in date of first infestation than distant counties. Second, the CAR prior provides a degree of spatial smoothing and thereby may prevent the erroneous detection of barriers that arise from spurious departures from the overall spatial trend. For example, detection and reporting of HWA infestations could be delayed in counties where populations remain at low densities (Fitzpatrick et al. 2009) because of scarcity of hemlock or where winter temperatures cause high mortality (Paradis et al. 2008, Trotter and Shields 2009). In our analysis, we consider counties to be neighbors if they share a common boundary; more sophisticated choices such as inverse distance weighting warrant investigation.

The above framework provides a smoothed expected value for the number of months to HWA infestation in each county. Although spread rate is itself of ecological interest, our goal is to identify barriers that separate counties with substantially different times to first infestation and to assign probabilities to these boundaries. A boundary likelihood value (BLV) for boundary $(i, j)$ can be defined as the absolute difference in months (Lu and Carlin 2005) of first HWA infestation reported in neighboring counties $i$ and $j$ as

$$\Delta_{ij} = |Y_i - Y_j|. \tag{5}$$

Estimates of $\Delta_{ij}$ can be obtained using a Markov chain Monte Carlo (MCMC) algorithm to draw $G$ samples of the modeled response $\mu_i^{(g)}$, $g = 1, \ldots, G$ from the posterior distribution $\mathrm{p}(\mu_i \mid y)$ (where $y$ represents observations of the response variable, in this case, the number of months to first infestation) for each county $i$ and each MCMC iteration $g$ to obtain

$$\Delta_{ij}^{(g)} = |\mu_i^{(g)} - \mu_j^{(g)}|. \tag{6}$$

Boundary probabilities are then estimated by counting the number of samples of $\Delta_{ij}^{(g)}$ that exceed a threshold $c$, where $c$ is some number of months of interest. For example, if we wanted to know which county boundaries were associated with preventing spread for five years (i.e., the difference in the date of first reported HWA infestation between adjacent counties is five years), $c$ would equal 60 months. To estimate the boundary probability for this value of $c$, we would draw $G$ samples ($G$ equaled 2000 in our analysis) from the posterior distribution of the differences in date of first infestation ($\Delta_{ij}^{(g)}$), count the number of these samples that exceed 60 months (i.e., $\Delta_{ij}^{(g)} > 60$), and divide this number by total number of samples $G$, or

$$\hat{p}_{ij} \equiv \hat{P}(\Delta_{ij} > c \mid y) = \frac{\Delta_{ij}^{(g)} > c}{G}. \tag{7}$$

This approach to determining boundary probabilities is known as fuzzy wombling. Alternatively, crisp wombling can be performed if boundaries are assigned a value of 1 when the BLV exceeds some predetermined threshold (e.g., 0.5) or 0 otherwise.

Although BLVs based on the expected values $\mu_i$ offer one means of investigating boundary probabilities, a potentially more informative approach is to calculate BLVs using the spatial random effects $\phi_i$. In essence, the $\phi_i$ can be interpreted as spatial residuals. High-probability boundaries based on residuals delineate regions that differ in their unmodeled heterogeneity and thus highlight boundaries that are not explained by the covariates. In contrast, if few boundaries exist in a map of residual-based boundaries, then the covariates explain (or are at least correlated with factors that explain) detected boundaries. Close examination of boundary probabilities based on spatial residuals could prove extremely useful in ecological studies where the goal is to elucidate the factors determining range edges and how these vary across space.

The model described above can be fit in WinBUGS (Spiegelhalter et al. 2003) and output analyzed and plotted in R (R Development Core Team 2009). For all models described below we used a burn-in period of 100 000 iterations and an additional 100 000 iterations were used to estimate model parameters (see Bolker 2008:233–238). For calculation of BLVs, we sampled 2000 iterations (the value of $G$ in Eq. 7) from the posterior distributions of $\mu$ and $\phi$. We assessed model convergence using the Gelman-Rubin potential scale reduction statistic (Brooks and Gelman 1998). Details of model construction and selection of priors are available from the code provided in the Supplement.

## EXAMPLE ANALYSES

*Simulation study.*—Our first example considers an analysis of simulated county-level spread data. We simulated, with added noise, the number of months to infestation as a linear function of distance from

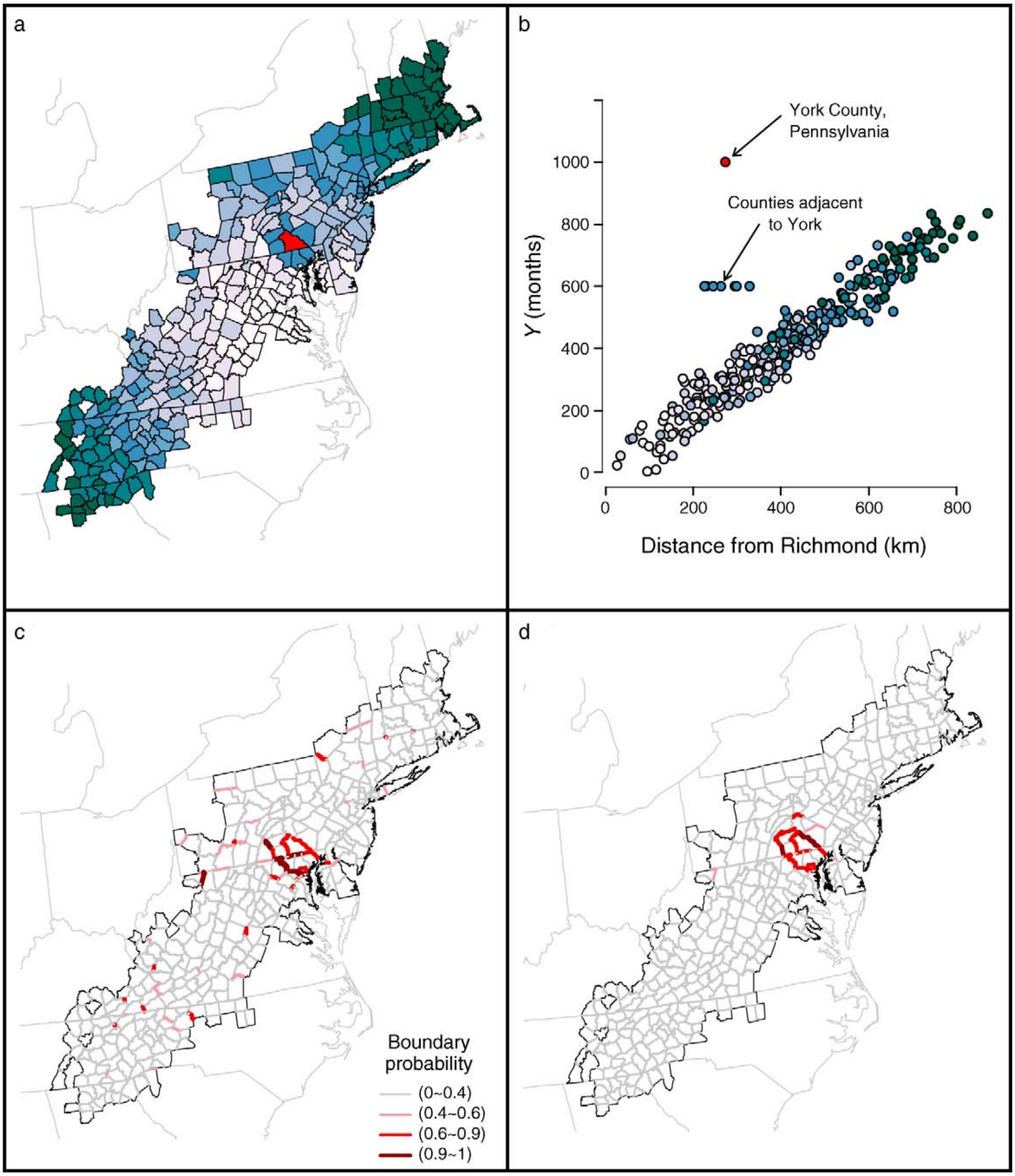

FIG. 2. Bayesian areal wombling on (a) simulated dates of infestation; and (b) a single simulated covariate related to distance from Richmond, Virginia. By design, York County, Pennsylvania (red shading) and counties immediately adjacent, do not follow the simulated pattern and are expected to be separated by high probability boundaries. Panels c and d show posterior probabilities for boundaries for the expected values μ and the spatial residuals ϕ, respectively, and a threshold of 60 months. Darker shades of red indicate high boundary probabilities.

Richmond, VA (Fig. 2a). By design, York County, Pennsylvania and counties adjacent, do not follow this pattern (Fig. 2b). Because distance from Richmond should not explain the detected boundaries around these outlier counties, even after smoothing, we expect high probability boundaries in the vicinity of York County, Pennsylvania for both μ- and ϕ-based BLVs. We found the expected pattern: nearly all of the detected boundaries (Fig. 2c) are explained by the distance covariate other than those surrounding York County, Pennsylvania (Fig. 2d).

*Historic spread of HWA*.—A model fit to the observed HWA spread data incorporated three covariates: human population density, mean winter temperature, and

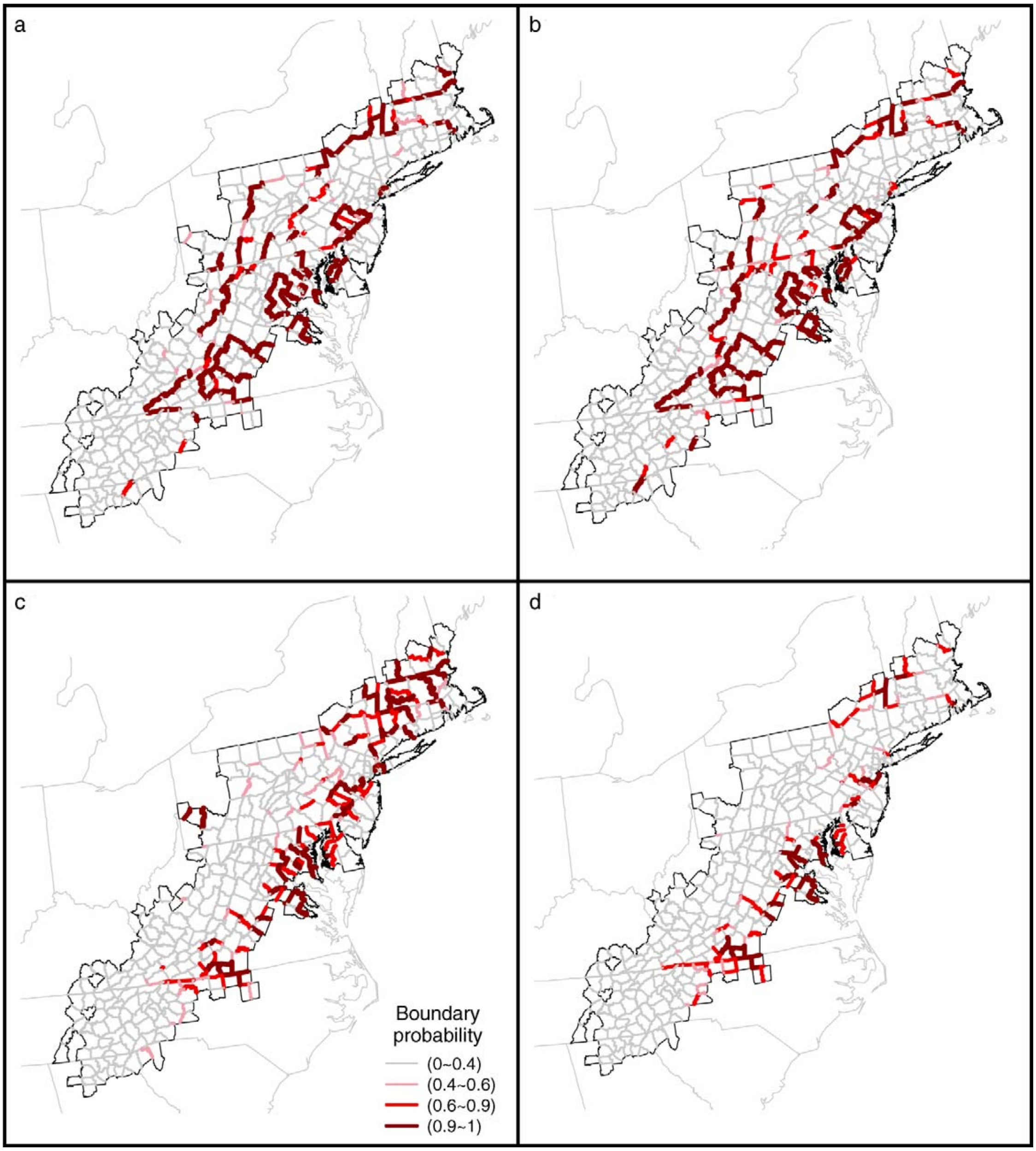

FIG. 3. Posterior probabilities for Bayesian areal wombling boundaries calculated using either (a) the expected values μ or (b) the spatial residuals ϕ and a threshold of 60 months, and posterior probabilities for Bayesian local edge wombling boundaries calculated using either (c) the expected values δ or (d) the spatial residuals ψ and a threshold of 36 months. Darker shades of red indicate high boundary probabilities.

hemlock abundance. This model suggests several features of the spread of HWA (Fig. 3a). Most notably, boundary probabilities are highest (1) in the vicinity of counties where HWA first established and where spread may have been slow due to lag effects (Kowarik 1995) related to HWA population dynamics, (2) along ridges of the Appalachian Mountains north of Tennessee, and (3) in the northernmost portions of HWA's range in New England. In contrast there are few barriers south of Virginia's southern border, where spread has been rapid. However, mean winter temperature and hemlock abundance are not significantly associated with barriers to spread; only the coefficient for human population density emerged as significantly different from zero. Except in some northern counties and those in central Pennsylvania, boundary probabilities based on the spatial residuals (Fig. 3b) largely reflect those calculated using the expected value μ (Fig. 3a), demonstrating that the covariates do not explain most of the detected boundaries.

In retrospect, the failure of temperature and hemlock abundance to explain barriers to spread of HWA may not be surprising. Global covariates, though useful in detecting and visualizing boundaries, do not couple regional heterogeneity in environmental conditions to local barriers to spread. For example, HWA can spread rapidly under warm temperatures only where hemlock is available. In addition, spread patterns are strongly a function of where propagules are first introduced. In the case of HWA, the earliest dates of infestation are found in counties with little or no naturally occurring hemlock.

To better model the landscape influences that hinder spread, Bayesian spatially varying coefficient models (Banerjee et al. 2004) can be used for wombling (e.g., Wheeler and Waller 2008), although these models offer greater technical challenges. Alternatively, rather than modeling the data arising from areal units, wombling can be performed on the county borders themselves (Ma et al. 2006, 2010). In this approach, every boundary segment is a data point and the response for each segment is the difference in the modeled value of interest between adjacent units. In the context of invasive spread, "local edge wombling" is likely to be ecologically more sensible because differences (or similarities) between adjacent areal units may be more important for, and therefore may better explain, spread dynamics than mean values of covariates within counties. This approach also provides a more straightforward means to represent physical barriers such as rivers, mountains or urban areas as binary indicator variables.

We modified our model (Eqs. 1–3) for local edge wombling by examining the difference in months to first infestation between adjacent counties:

$$D_{ij} = Y_i - Y_j \tag{8}$$

$$D_{ij} \sim \mathcal{N}\left(\delta_{ij}, \frac{1}{\tau}\right) \qquad i \text{ adjacent to } j \tag{9}$$

where

$$\delta_{ij} = \alpha + \mathbf{x}_{ij}\boldsymbol{\beta} + \psi_{ij}. \tag{10}$$

As before, a spatial random effect ($\psi$) is included and is given a CAR prior. The vector of covariates $\mathbf{x}_{ij}$ in this model represents *differences* in covariates across borders. Because the response is the difference in months to first infestation across borders, the calculation of BLVs is simplified slightly. Here, BLVs are determined using the absolute values of the posterior estimates of $\delta_{ij}$ (or $\psi_{ij}$ for residual-based boundaries) themselves as opposed to *post hoc* calculation of these differences as in Eq. 6. Code for fitting this model is provided in the Supplement.

A local edge wombling model incorporating as covariates differences in population density, mean winter temperature, and hemlock abundance across county borders reveals similar results to those derived from the areal wombling model: high probability boundaries are concentrated in the east and northeast (Fig. 3c). However, in this model the coefficients for hemlock abundance and population density are significantly different from zero and as a result, there are few boundaries that remain unexplained (Fig. 3d). As before, boundaries associated with early spread in the eastern portion of the study region remain after accounting for the effects of the covariates, potentially reflecting demographic lag effects unrelated to environmental factors (Kowarik 1995).

## CONCLUSIONS

Bayesian areal wombling is promising approach for analyzing ecological boundaries and the dynamics of range expansion. Many other applications for areal wombling can be envisioned. For example, wombling is commonly used in public health research to identify boundaries where disease incidence is higher/lower than expected. The same principle can be applied in ecology to understand patterns of both invasive species richness and distribution as well as patterns of diversity of native species (e.g., Is species richness higher/lower than expected at the biome level and what explains differences in richness across biomes?). Important targets for future improvement of these models in ecology include exploration of alternate parameterizations for spatial smoothing, such as distance weighting or to estimate smoothing parameters from the data (Ma et al. 2010).

By providing probability distributions for the modeled parameters and accounting for spatial dependencies, wombling in a Bayesian framework permits direct estimation of boundary probabilities and the uncertainty associated with them—something that is not possible with classical approaches. Although classical models can declare the "statistical significance" of a potential boundary, they cannot estimate the probability that any particular segment is part of the boundary. Bayesian models can also estimate missing data over space and time. However, it is difficult to make generalizations regarding the quality of data (in terms of number of observations in space and time) needed for Bayesian wombling as it will depend on particulars of the study system. Although there is not yet a single software package or R library that can be used to perform Bayesian areal wombling analyses of the sort described here, the code and data provided in the Supplement illustrate how to integrate several software packages to implement areal wombling models. Additional statistical challenges remain. The use of a CAR prior encourages local smoothing of dates of infestation toward those of neighboring counties. Ideally, this accounts for uncertainty in detection, if, for example, a single county reports a much later date of first infestation than its neighbors. Local smoothing can, however, have unanticipated effects. For example, a county that is colonized early but that is surrounded by counties with much later dates of colonization could have a modeled (smoothed) later date of first infestation. Although it is possible for the actual date of first infestation to be earlier than the reported date, it is unlikely that the actual date of first infestation would be later than the reported date (barring misidentification or data entry errors). Finally, the incorporation of spatially correlated errors may alter estimates of fixed-effects coefficients in ways that are only beginning to be explored and which could lead to misinterpretation of residual-based wombling maps. Despite these issues, Bayesian areal wombling should be considered a complement to existing methods for ecological boundary analysis as an approach that can explore dynamics related to changes in the distributions of native and invasive species using coarse resolution datasets common in ecology and biogeography.

## ACKNOWLEDGMENTS

We thank D. Wheeler and M. Levine for statistical advice and assistance with coding. J. Elith and two anonymous reviewers provided comments that improved the manuscript. C. Burnham, B. Burns, J. Denham, J. Johnson, T. McAvoy, G. Miller, D. Orwig, and B. Regester kindly provided local HWA spread records that were used to update the USFS county-level spread map provided by A. Steketee. This research was funded by NSF DEB-0715504 to E. L. Preisser and by funding from UMCES-AL to M. C. Fitzpatrick. This is UMCES Appalachian Laboratory Scientific Contribution No. 4440.

## LITERATURE CITED

Banerjee, S., B. P. Carlin, and A. E. Gelfand. 2004. Hierarchical modeling and analysis for spatial data. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Bolker, B. 2008. . Ecological models and data in R. Princeton University Press, Princeton, New Jersey, USA.

Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Fagan, W. F., M. J. Fortin, and C. Soykan. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. BioScience 53:730–738.

Fitzpatrick, M. C., E. L. Preisser, A. M. Ellison, and J. S. Elkinton. 2009. Observer bias and the detection of low-density populations. Ecological Applications 19:1673–1679.

Fortin, M., and M. R. T. Dale. 2005. Spatial analysis. Cambridge University Press, Cambridge, UK.

Fortin, M. J., T. H. Keitt, B. A. Maurer, M. L. Taper, D. M. Kaufman, and T. M. Blackburn. 2005. Species' geographic ranges and distributional limits: pattern analysis and statistical issues. Oikos 108:7–17.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.

Gavin, D. G., and F. S. Hu. 2006. Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. Journal of Biogeography 33: 1384–1396.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution 19:497–503.

Holt, R. D., and T. H. Keitt. 2005. Species' borders: a unifying theme in ecology. Oikos 108:3–6.

Jacquez, G., M. Fortin, and P. Goovaerts. 2008. Preface to the special issue on spatial statistics for boundary and patch analysis. Environmental and Ecological Statistics 15:365–367.

Jacquez, G. M., S. Maruca, and M. Fortin. 2000. From fields to objects: a review of geographic boundary analysis. Journal of Geographical Systems 2:221–241.

Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. Pages 15–38 *in* P. Pysek, K. Prach, M. Rejmanek, and M. Wade, editors. Plant invasions. General aspects and special problems. SPB Academic Publishing, Amsterdam, The Netherlands.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Lu, H., and B. P. Carlin. 2005. Bayesian areal wombling for geographical boundary analysis. Geographical Analysis 37: 265–285.

Ma, H., B. P. Carlin, and S. Banerjee. 2010. Hierarchical and joint site-edge methods for Medicare hospice service region boundary analysis. Biometrics 66:355–364.

Ma, H., B. A. Virnig, and B. P. Carlin. 2006. Spatial methods in areal administrative data analysis. Italian Journal of Public Health 3:94–103.

Orwig, D. A., D. Foster, and D. L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography 29:1475–1487.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58–75.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨www.r-project.org⟩

Spiegelhalter, D., A. Thomas, N. Best, and D. Lunn. 2003. WinBUGS users manual, v 1.4.3. ⟨www.mrc-bsu.cam.ac.uk/bugs⟩

Trotter, R. T., and K. S. Shields. 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environmental Entomology 38:577–587.

Wheeler, D., and L. Waller. 2008. Mountains, valleys, and rivers: the transmission of raccoon rabies over a heterogeneous landscape. Journal of Agricultural, Biological, and Environmental Statistics 13:388–406.

Womble, W. H. 1951. Differential systematics. Science 114:315–322.

## APPENDIX

Detailed description of data and covariates used for wombling (*Ecological Archives* E091-246-A1).

## SUPPLEMENT

Data and the R and WinBUGS code used in the paper (*Ecological Archives* E091-246-S1).