Intervention Analysis of Hurricane Effects on Snail Abundance in a Tropical Forest Using Long-Term Spatiotemporal Data

Marcos O. PRATES, Dipak K. DEY, Michael R. WILLIG, and Jun YAN

Large-scale natural disturbances, such as hurricanes, have profound effects on populations, either directly by causing mortality, or indirectly by altering ecological conditions or the quantity, quality, and spatial distribution of resources. In the last 20 years, two major disturbances, Hurricane Hugo in 1989 and Hurricane Georges in 1998, struck the Luquillo Mountains of Puerto Rico, providing an unique opportunity to understand the long-term effects of recurrent disturbances on the abundance of species. *Nenia tridens* is one of the most abundant and pervasive terrestrial gastropods in the Luquillo Mountains. Estimates of yearly abundance of *N. tridens* from 40 sites on the Luquillo Forest Dynamics Plot from 1991 to 2007 facilitate the development of a spatiotemporal model with intervention effects on the mean abundance over time in response to each hurricane. Intervention effects characteristically decay over time, similar to those in a time series analysis. Model parameters were estimated in a Bayesian framework. Model comparison and diagnostics suggest that our intervention model provides a plausible description of hurricanes effects on the abundances of *N. tridens* and may be useful for studying long-term spatiotemporal dynamics from the perspective of disturbance and succession.

Key Words: Bayesian method; Disturbance ecology; Long-term ecological data; MCMC; Spatiotemporal model.

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1. INTRODUCTION

The role of disturbance in affecting the spatial and temporal dynamics of ecosystems has gained sharpened focus in ecology. Disturbances can be natural or human-induced, differing in frequency, scale, and intensity, leading to different short-term and long-term responses. Large-scale natural disturbances, such as hurricanes, have profound effects on populations, either directly by causing mortality through action of wind or rain, or indirectly, by altering the abiotic environment, habitat structure, resource availability, or density of predators or competitors (Bloch and Willig 2006). In the last 20 years, two major hurricanes, Hugo in 1989 and Georges in 1998, both in September, struck the island of Puerto Rico. Hurricane Hugo, a category 4 storm, was much more intense than Hurricane Georges, a category 3 storm. Because of the infrequent nature of such large-scale disturbances and lack of associated long-term data, few ecological studies have examined the long-term responses of the biota to multiple hurricanes.

Long-term censuses of terrestrial snails, *Nenia tridens*, occurred in the Luquillo Forest Dynamics Plot (LFDP; 18°20′N, 65°49′W), a 16-ha grid in the northwest of the Luquillo Experimental Forest (LEF), in the Luquillo Mountains of northeastern Puerto Rico (see Willig et al. 1998). The LFDP lies in tabonuco forest, a subtropical wet forest type (Ewel and Whitmore 1973) found below 600 m of elevation. Precipitation is substantial throughout the year. Although a modestly drier period typically extends from January to April, rainfall generally remains higher than 20 cm in all months (Brown et al. 1983).

Within the LFDP (Figure 1), 40 circular plots of 3 m radius were spaced evenly in a rectilinear grid system such that 60 m separated adjacent points along a row or column. The elevation of the 40 plots ranged less than 75 m from 345.6 m to 418.2 m (mean = 378.06; SD = 17.17). From 1991 to 2008, snail surveys were conducted during the summer (wet season); hurricanes occurred after the data collection in the years when hurricanes struck (1989 and 1998). This is a long-term study by ecological standards, as most ecological research projects represent only a brief snapshot in time, spanning 1 to 3 years of study (Gosz 1999). Each time a plot was sampled, two people surveyed it for a minimum of 15 minutes, during which time they searched all available surfaces (e.g., soil, litter, rock cover, vegetation) up to a height of approximately 3 m. To minimize alteration of long-term study plots, substrate was disturbed as little as possible while searching for snails. This method limits the inference space, potentially ignoring small, litter-dwelling individuals, but this is not an issue for *N. tridens*, as it is not generally a litter- or soil-dwelling species.

Resistance and resilience are two important aspects of the long-term responses of ecosystems to disturbances (Zimmerman et al. 1996). Resistance reflects the ability of a system to withstand perturbation. Resilience reflects the ability of a system recover from disturbance. These two components, in essence, address how a system responds to disturbances, and knowledge about them is key to designing reclamation and restoration efforts. In the case of *N. tridens*, we are interested in the extent to which abundance is reduced by and subsequently recovers from the hurricanes.

Since the introduction by Box and Tiao (1975), intervention analysis has been a standard methodology for assessing the effect of an intervention on the mean of a time series in

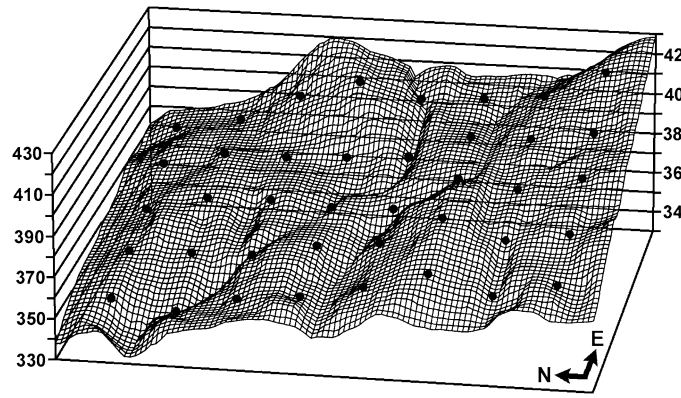

Figure 1. Topography (vertical axis is elevation in meters above the sea level) of the Luquillo Forest Dynamics Plot (LFDP; 18°20′N, 65°49′W) in tabonuco forest, Puerto Rico, showing the location of forty 3-m radius plots (filled circles) in which *N. tridens* were surveyed each wet season from 1991 to 2008. The 40 plots were arranged into an 8-by-5 lattice, with 60 m separating centers of adjacent plots in a row or column of the lattice. The long horizontal axis parallels north and the vertical axis represents elevation above the sea level in meters. For perspective, the small squares of the lattice represent 5-by-5 m areas.

many fields including ecology (Rasmussen et al. 1993). Nevertheless, intervention analysis has not been used widely with spatiotemporal data, especially in ecological studies, even though such data characterize a discipline that seeks to understand the distribution of abundance of species (Scheiner and Willig 2008). Part of the reason might be that spatiotemporal data often span a much shorter length in time than does a typical time series, and large-scale interventions are rare. A special application concerns the effect of river monitoring networks on water quality in a spatiotemporal model (Clement and Thas 2007), where traditional spatiotemporal models are not appropriate because of downstream directional spatial dependence. We incorporate intervention effects of hurricanes into a traditional spatiotemporal model for abundance of *N. tridens*. In particular, the count $Y_{s,t}$ at site s and year t is assumed to be Poisson with mean $\lambda_{s,t}$, which, after logarithmic transformation, comprises three parts: overall level, hurricane effects over time, and spatiotemporal noise. Our statistical inferences are performed in a Bayesian framework.

The contributions of this article are threefold. First, to the best of our knowledge, this is the first attempt to incorporate multiple intervention effects, similar to those in time series, into a traditional spatiotemporal model. Second, we propose a simple, easy-to-compute diagnostic tool for identifying the influence of particular observations on the overall analysis based on Markov chain Monte Carlo (MCMC) samples. Third, analytical results and model diagnostics suggest that the model provides a plausible description of hurricane effects on the abundance of this keystone snail species.

The rest of the paper is organized as follows. In Section 2, we perform exploratory analyses to understand the overall behavior of the snail population, which subsequently motivates a spatiotemporal model. The proposed model and prior selection are discussed in Section 3. Submodels arising from various constraints on the general model and model comparison techniques are described in Section 4. Results and model diagnoses are presented in Section 5. A discussion concludes in Section 6.

2. EXPLORATORY ANALYSIS

Moran's I statistic (Moran 1950) is one of the most widely used statistics to quantify spatial dependence. For abundance of *N. tridens*, p-values of the Moran's I computed at each year t, under the null hypothesis of no spatial dependence, are plotted in Figure 2(a), along with a threshold line of 0.10. For 6 of 17 years, some before and some after Hurricane Georges, the hypothesis of no spatial dependence was rejected at level 0.10. Consequently, spatial dependence should be accommodated in a realistic model.

To learn about temporal changes in overall abundance, a separate model with spatial dependence was fitted for each year. Let $Y_{s,t}$ be the observed count at site s in year t, $s = 1, \ldots, S$, $t = 1, \ldots, T$, where $S = 40$, $T = 17$, and $t = 1$ represents the year of 1991. The count data are modeled by a Poisson distribution with a log link function as

$$Y_{s,t} \sim \text{Poisson}(\lambda_{s,t}),$$

$$\log(\lambda_{s,t}) = \beta_t + \phi_{s,t},$$

$$\boldsymbol{\phi}_t \sim \text{ICAR}(\tau_\phi),$$

where $\lambda_{s,t}$ is the Poisson mean, β_t is the mean at year t on the log scale, $\boldsymbol{\phi}_t = (\phi_{1,t}, \ldots, \phi_{S,t})^\top$ is an intrinsic conditional autoregressive process (ICAR) with overall mean 0 and precision τ_ϕ (Besag and Kooperberg 1995). In particular, the ICAR process is a conditionally specified model,

$$\phi_{s,t} \sim N\left(\frac{\sum_{j\sim s} \phi_{j,t}}{\sum_{j=1}^{S} I(j \sim s)}, \frac{\tau_\phi}{\sum_{j=1}^{S} I(j \sim s)}\right),$$

where $j \sim s$ means that site j is a neighbor of site s. Note that the overall mean level of an ICAR process is unidentified, which is seen from an equivalent specification on contrasts

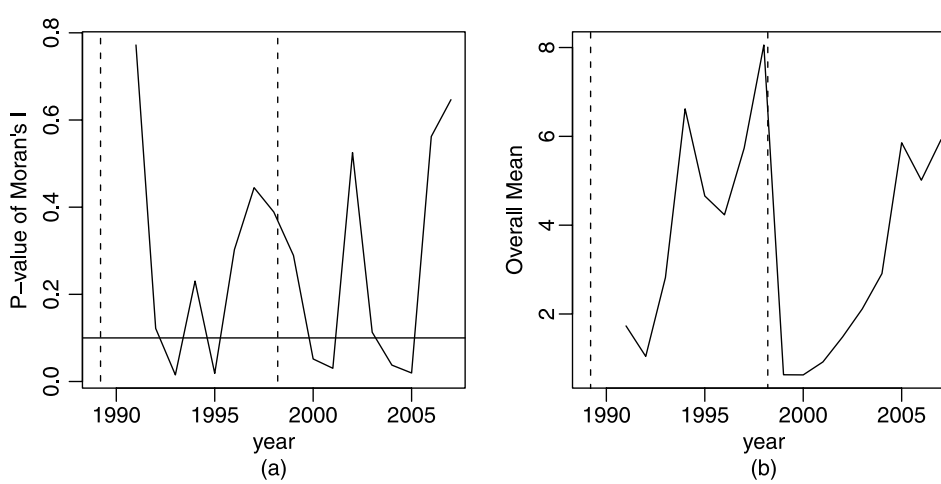

Figure 2. Exploratory results for abundance of *N. tridens* from 1991 to 2007. The vertical dashed lines show the years of Hurricane Hugo and Hurricane Georges. (a) P-values of Moran's I test for no spatial dependence; the horizontal threshold line is level 0.10. (b) Posterior median of mean abundance of *N. tridens* from separate analysis by each year.

between neighboring sites (e.g., Hodges, Carlin, and Fan 2003):

$$p(\boldsymbol{\phi}_t|\tau_\phi) \propto \tau_\phi^{(S-1)/2} \exp\left(-\frac{1}{2}\tau_\phi \sum_{i\sim j}(\phi_{i,t} - \phi_{j,t})^2\right).$$

To make β_t identifiable, we add a constraint $\sum_{s=1}^{S} \phi(s) = 0$. The neighboring structure for the ICAR model is of order 1. That is, two sites are considered as neighbors if they are adjacent either in row or column of the lattice. Neighboring sites (60 meters apart) are expected to be spatially dependent due to, for example, a large tree fall that provides resources to snails. On the other hand, sites beyond the neighboring sites may provide little information in addition to the neighboring sites. Such spatial dependence is accommodated naturally by the conditional specification of the ICAR model.

A noninformative flat prior was put on each β_t, $t = 1, \dots, 17$. A proper but vague prior $\Gamma(0.05, 0.0005)$ was put on the precision parameter τ_ϕ, where $\Gamma(a, b)$ is a Gamma distribution with shape a and rate b. We considered such a choice for hyperparameters so that τ_ϕ can vary with a wide range (with probability 95% from 0 to 532).

Figure 2(b) shows the posterior median of the overall mean abundance level, $\exp(\beta_t)$, from separate analyses for each year t. Overall abundance increased steadily after Hurricane Hugo, dropped drastically in immediate response to Hurricane Georges, and gradually recovered. By the end of the data collection period, abundance returned to pre-Georges levels.

The exploratory analysis suggests that for *N. tridens*, a plausible model for hurricane effects on abundance may be captured by a post-hurricane influence whose severity diminishes over time. The intervention should be modeled taking into account both spatial and temporal dependences.

The percentage of zero counts is 20% in the entire data set. Many zeroes (52.5%) occur in the year immediately following Hurricane Georges. For parsimony, we do not consider zero-inflated models, which may be worthy of investigation in the future.

3. SPATIOTEMPORAL MODEL WITH INTERVENTION

Intervention analysis is a standard statistical method for assessing the impact of an intervention, planned or unplanned, on a time series of outcome measures. Details about intervention analysis can be found in most textbooks on time series analysis; see, for instance, Cryer and Chan (2008) for an illustration of the impact of the terrorist attacks of September 11, 2001, on the number of air passengers. It is assumed that an intervention affects a time series by changing its mean function or trend. Many intervention models are available to capture the intervention effect whose onset may be abrupt or gradual, and whose duration may be permanent or temporary (e.g., McDowall et al. 1980). In our application, as the snail abundance is immediately reduced by the hurricanes and recovers in several years, we expect the intervention to be abrupt and temporary.

Let H_t and G_t be the impact of Hurricane Hugo and Hurricane Georges, respectively, at year t. Further, let $P_{h,t}$ and $P_{g,t}$ be the pulse function defined by Hurricane Hugo and Hurricane Georges, respectively. That is, $P_{h,t}$ ($P_{g,t}$) is 1 when t is the year following

Hurricane Hugo (Georges) and 0 otherwise. In particular for Hurricane Hugo, $P_{h,t}$ is 1 for $t = 0$ (1990) and 0 for all other years t, since the data collection started two years later. We propose to model H_t and G_t as

$$H_t = \frac{-\omega_{h,1}}{1 - \omega_{h,2}\mathrm{B}} P_{h,t},$$

$$G_t = \frac{-\omega_{g,1}}{1 - \omega_{g,2}\mathrm{B}} P_{g,t},$$

where B is the backshift operator ($BX_t = X_{t-1}$), and $\omega_{i,1} > 0$ and $\omega_{i,2} \in (0, 1)$, $i = h, g$, are model parameters. This characterization uses the notation from time series analysis. It essentially specifies a geometrically decaying hurricane impact. Consider Hurricane Hugo as an illustration. In the year immediately following it, Hurricane Hugo causes a rapid decline of size $\omega_{h,1}$, which is interpreted as a measure of resistance to the hurricane; the smaller $\omega_{h,1}$, the stronger the resistance to Hurricane Hugo. The remaining hurricane effect, after k years, is $\omega_{h,1}\omega_{h,2}^{k-1}$. The decay rate $\omega_{h,2}$ is interpreted as a measure of resilience to the hurricane. The smaller $\omega_{h,2}$, the faster the recovery of *N. tridens* after Hurricane Hugo.

The full model for snail abundance with hurricane interventions, denoted by M_1, is now defined as

$$Y_{s,t} \sim \text{Poisson}(\lambda_{s,t}), \tag{3.1}$$

$$\log \lambda_{s,t} = \beta + H_t + G_t + \alpha_t + \phi_{1,s} I(t \le 8) + \phi_{2,s} I(t > 8), \tag{3.2}$$

$$\boldsymbol{\alpha} \sim \text{CAR}(\gamma, \tau_\alpha), \tag{3.3}$$

$$\boldsymbol{\phi}_1 \sim \text{ICAR}(\tau_\phi), \tag{3.4}$$

$$\boldsymbol{\phi}_2 \sim \text{ICAR}(\tau_\phi), \tag{3.5}$$

where β is the overall mean abundance on the log scale when there were no disturbances; $\boldsymbol{\alpha} = (\alpha_1, \ldots, \alpha_T)$ introduces temporal dependence through a proper Gaussian conditional autoregressive (CAR) process with mean zero, autoregression coefficient γ, and precision τ_α; and $\boldsymbol{\phi}_1 = (\phi_{1,1}, \ldots, \phi_{1,S})$ and $\boldsymbol{\phi}_2 = (\phi_{2,1}, \ldots, \phi_{2,S})$ introduce spatial dependence before and after Hurricane Georges, respectively, specified by two ICAR processes with common precision τ_ϕ. For identification purpose, we have imposed constraints $\sum_{s=1}^{S} \phi_{1,s} = 0$ and $\sum_{s=1}^{S} \phi_{2,s} = 0$.

Priors for model parameters were selected in a manner that has a simple but clear interpretation from an ecological point of view. For the instantaneous decline in abundance after Hurricane Georges, $\omega_{g,1}$, we chose $\Gamma(1.802, 1.744)$, which assigns probability 95% to the event that the disturbance causes a reduction in abundance level between 10% and 95%. Hurricane Hugo was an extreme intervention in Puerto Rico with a much more massive killing effect than that of Hurricane Georges (Lugo and Frangi 2003; Ostertag, Scatena, and Silver 2003). Based on historic facts and expert opinion, we chose $\Gamma(7.719, 2.033)$ for $\omega_{h,1}$. This choice ensures that with 95% probability the instantaneous effect causes an overall decline in snail abundance to be between 80% and 99.9%. The

lower end (80%) is set to be the average decline from Hurricane Georges based on the exploratory analysis, while the upper end (99.9%) comes from an earlier study showing that Hurricane Hugo killed almost 100% of *N. tridens* in tabonuco forest near the site where our data were collected (Bloch and Willig 2006; Willig et al. 2007). Priors for the decay parameters $\omega_{g,2}$ and $\omega_{h,2}$ were naturally chosen to be noninformatively uniform over (0, 1), which guarantees stationarity of the recovery process. Priors for the precision parameters τ_ϕ and τ_α were selected based on their implication on the standard deviation. We chose $\Gamma(2, 2)$, which places a 99% probability that the standard deviations of ϕ_i's and α_i's are between 0.52 and 4.40; a two-standard-deviation increase (decrease) on $\log \lambda_{s,t}$ implies an increase to 2.82–6581 times (a decrease of 74–99.9% from) the overall level. For β, we placed a diffuse prior of $N(0, 100)$. Finally, for the autoregressive coefficient γ, we placed a noninformative uniform prior distribution over $(-1, 1)$.

4. MODEL COMPARISON

Model M_1, defined by Equations (3.1)–(3.5), can be simplified by imposing various constraints to obtain more parsimonious submodels, all nested in M_1. By comparing M_1 with simplified models, we evaluate the necessity of the spatiotemporal dependence and the flexibility of the spatial dependence. The following models are considered in our analysis in Section 5. In Model M_2, we change the structure of temporal dependence introduced through $\boldsymbol{\alpha}$ in M_1 by setting $\gamma = 0$ in the Gaussian CAR process, which eliminates temporal dependence. In Model M_3, we completely remove the temporal error α_t. Model M_4 carries the temporal dependence as in M_1, but instead of having two different spatial structures before and after Hurricane Georges, $\boldsymbol{\phi_1}$ and $\boldsymbol{\phi_2}$, a single spatial structure is used ($\boldsymbol{\phi_1} = \boldsymbol{\phi_2}$). Finally, in Model M_5, we simultaneously combine the constraints in Model M_2 and M_4, resulting in a model with no temporal dependence and a single spatial structure. These submodels are summarized by the constraints they impose on Model M_1 (Table 1). Model M_3 is nested in Model M_2, whereas Model M_5 is nested in both Model M_2 and Model M_4.

We propose to use the conditional predictive ordinate (CPO) criterion (e.g., Geisser 1993; Gelfand, Dey, and Chang 1992; Dey, Chen, and Chang 1997) to compare submodels with the full model M_1. Let $\boldsymbol{y}$ be the observed data $\{Y_{s,t} : s = 1, \ldots, S; t = 1, \ldots, T\}$. Let $\boldsymbol{y}_{-i}$ denote the observed data excluding the ith observation. The CPO statistic associated with the ith observation is defined as the marginal posterior predictive density of y_i,

Table 1. The four submodels nested in Model M_1 are distinguished by the constraints that they impose on Model M_1.

Submodels	Constraints
M_2	$\gamma = 0$
M_3	$\alpha_t = 0, t = 1, \ldots, T$
M_4	$\boldsymbol{\phi}_1 = \boldsymbol{\phi}_2$
M_5	$\gamma = 0$ and $\boldsymbol{\phi_1} = \boldsymbol{\phi}_2$

conditioning on $\boldsymbol{y}_{-i}$:

$$\mathrm{CPO}_i = f(y_i|\boldsymbol{y}_{-i}) = \int f(y_i|\boldsymbol{\lambda})\pi(\boldsymbol{\lambda}|\boldsymbol{y}_{-i})\,\mathrm{d}\boldsymbol{\lambda}, \tag{4.1}$$

where $\boldsymbol{\lambda} = (\lambda_{1,1}, \ldots, \lambda_{S,1}, \ldots, \lambda_{1,T}, \ldots, \lambda_{S,T})$, $f(y_i|\boldsymbol{\lambda})$ is the conditional mass function of y_i given $\boldsymbol{\lambda}$, and $\pi(\boldsymbol{\lambda}|\boldsymbol{y}_{-i})$ is the posterior density of $\boldsymbol{\lambda}$ based on data $\boldsymbol{y}_{-i}$. The intuition behind the CPO criterion is to choose a model with higher predictive power measured in terms of predictive density. The idea is similar to that of a leave-one-out cross-validation in that the predictive density of each data point is evaluated at a density fitted from all other data points.

Although a closed form of (4.1) is not available, Dey, Chen, and Chang (1997) showed that CPO_i can be estimated from a Monte Carlo integration approach and is approximated by a harmonic mean:

$$\widehat{\mathrm{CPO}_i} = B\left(\sum_{j=1}^{B}\left[\frac{1}{f(y_i|\boldsymbol{\lambda}^{(j)})}\right]\right)^{-1},$$

where B denotes the size of a MCMC sample of the posterior distribution $\pi(\boldsymbol{\lambda}|\mathbf{y})$, $\boldsymbol{\lambda}^{(j)}$ is the parameter vector $\boldsymbol{\lambda}$ in the jth MCMC sample. This approximation is valid when $Y_{s,t}$ are assumed to be conditionally independent given $\boldsymbol{\lambda}$. Since the approximation is based on the posterior given all the observations, its calculation is straightforward.

To assess the goodness-of-fit of each model, we use a summary statistic, the logarithm of the pseudo-marginal likelihood (LPML) defined as

$$\mathrm{LPML} = \sum_{i=1}^{n} \log \widehat{\mathrm{CPO}}_i.$$

The model with the largest LPML indicates the best fit of competing models.

The relative goodness-of-fit of two competing models at individual observations can be graphically compared in a CPO plot (Dey, Chen, and Chang 1997). For two competing models M_j and M_k, let $\Delta(i; j, k) = \log(\mathrm{CPO}_i|M_j) - \log(\mathrm{CPO}_i|M_k)$, the difference in $\log \mathrm{CPO}_i$ from the two models. Observation i equally supports M_j and M_k if $\Delta(i; j, k) = 0$. It supports M_j more than it supports M_k when $\Delta(i; j, k) > 0$ ($\Delta(i; j, k) < 0$), and vice versa. When we plot $\Delta(i; j, k)$ against observation number i, those points above the zero line support model M_j, and those points below the zero line support model M_k. If there are more points below the zero line and their summed magnitude is less than that for the points above the zero line, then model M_k will have a higher LPML value and is a better model than M_j.

5. ANALYSIS

For each of the 5 models in Sections 3–4, we use a Gibbs sampler to obtain MCMC samples of the model parameters. We ran the chain for 600,000 MCMC iterations. After a burn-in period of 100,000 iterations, every 100th iteration was retained, yielding a sample

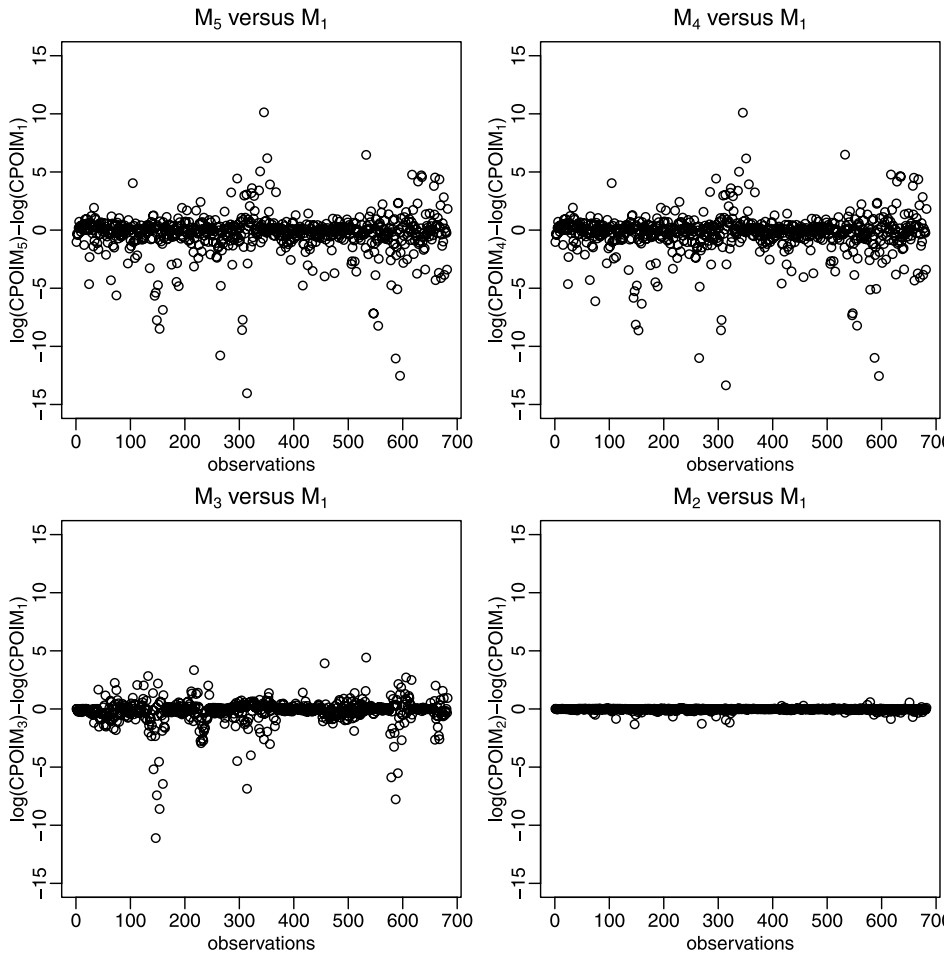

Figure 3. CPO model comparisons of each of four submodels with the full model M_1. The observations are ordered in time.

of 5,000 draws from the posterior distribution of the model parameters. The convergence was verified using Geweke's criterion (Geweke 1992).

The LPML results (-1890.0 for M_1, -1913.7 for M_2, -2034.6 for M_3, -2107.1 for M_4, and -2110.1 for M_5) suggest that M_1 is the most preferable model with the highest LPML value. Comparison of each of the four submodels with M_1 can be visualized as CPO plots (Figure 3). Clearly, M_1 is superior to M_3, M_4, and M_5, which supports that there is overdispersion from the temporal random effect and that Hurricane Georges may have changed the spatial random effect.

It is not clear if M_1 is much better than M_2 in Figure 3. By the parsimony principle, M_2 might be preferable. To further assess the difference between M_1 and M_2, we use the pseudo Bayes factor (PsBF), first used by Geisser and Eddy (1979) and developed further

Table 2. Modified Kass & Raftery's scale of evidence for pseudo Bayes factor comparing M_1 against M_2.

$2\log(\text{PsBF}_{1,2})$	Evidence against M_2
$(-1, 1]$	not worth more than to mention
$(1, 5]$	positive
$(5, 9]$	strong
$(9, \infty)$	very strong

Table 3. Posterior mean and 95% HPD credible intervals of the parameters in Model M_1.

Parameter	Mean	95% HPD credible interval
β	2.03	(1.06,3.71)
$\omega_{g,1}$	1.56	(0.36,2.64)
$\omega_{g,2}$	0.72	(0.30,1.00)
$\omega_{h,1}$	2.87	(1.23,5.23)
$\omega_{h,2}$	0.54	(0.07,1.00)
γ	0.60	(−0.08,1.00)
τ_α	3.90	(0.75, 7.56)
τ_ϕ	0.42	(0.42,0.82)

in Dey, Chen, and Chang (1997) as

$$\text{PsBF}_{1,2} = \frac{\prod_{i=1}^{n} \text{CPO}_i | M_1}{\prod_{i=1}^{n} \text{CPO}_i | M_2}.$$

For Bayes factor, Kass and Raftery (1995) presented a table on how to assess model M_1 against model M_2. For PsBF, we used the asymptotic distribution described by Gelfand and Dey (1994) to correct it and obtained a modified version (Table 2). For this application, we have $2\log(\text{PsBF}_{1,2}) = 45.2$ which, from Table 2, provides very strong evidence that M_1 is preferable over M_2. That is, allowing temporal dependence gives better fit even though the autocorrelation is weak.

Having concluded that M_1 is the best model, we summarize in Table 3 the posterior means and 95% Highest Posterior Density (HPD) credible intervals of the parameters in M_1. By exponentiating β, we have, on the original scale, a posterior median of overall mean abundance per site 7.6. Parameter $\omega_{g,1}$ represents the magnitude of the instantaneous shock initiated by Hurricane Georges, estimated to be an 80.1% reduction. The decay rate $\omega_{g,2}$ is estimated to be 0.715, which implies that, on the log scale, it takes 10 years for the decline in abundance to become 5% of the initial decline. For Hurricane Hugo, the estimated instantaneous reduction $\omega_{h,1}$ is approximately 94.3%. The decay rate $\omega_{h,2}$ is estimated to be 0.544. It takes only 6 years for the decline in abundance, on the log scale, to become 5% of the initial decline.

The estimated temporal dependence γ is 0.599 and its 95% HPD credible interval covers zero. Nevertheless, the posterior probability of $\gamma < 0$ is 6.8%. This indicates that temporal dependence is marginally important. The inverse of precision parameters τ_α and τ_ϕ describes the variance of the temporal and spatial noise, respectively. Spatial noise

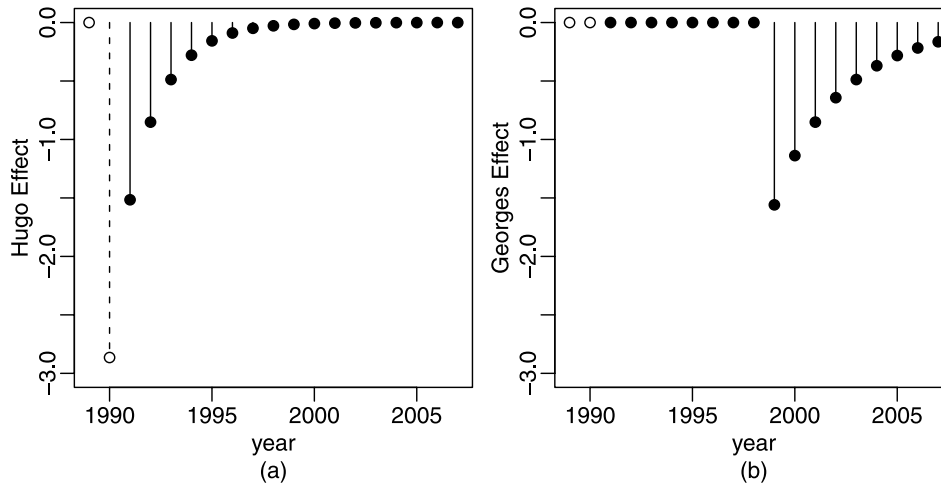

Figure 4. (a) Estimated Hurricane Hugo's effect on snail abundance over 17 years. (b) Estimated Hurricane Georges's effect on snail abundance since its occurrence in 1998.

is clearly greater than temporal noise, as evident from the precision parameter estimates (0.424 versus 3.901)

Posterior means of the intervention effects of Hurricane Hugo and Hurricane Georges over years are plotted in Figure 4. The effect of Hurricane Hugo is in its second year when data collection started, which is only slightly less than the initial effect of Hurricane Georges. It had vanished before Hurricane Georges struck the forest. Hurricane Georges's effect decays moderately, and by the end of the observation period (2007), is quite small. These results make sense ecologically. The abundance of *N. tridens* is more resistant to Hurricane Georges than to Hurricane Hugo; the initial impact of Hurricane Hugo was about twice that of Hurricane Georges. Nevertheless, *N. tridens* is more resilient to Hurricane Hugo than to Hurricane Georges.

From an ecological perspective, the model seems to capture the essence of the demographic responses of *N. tridens* to the two hurricanes. The large-scale decline in abundance shown in Figure 2(b) matches the shapes of the intervention effects shown in Figure 4. The larger initial impact of Hurricane Hugo than of Hurricane Georges is expected from our prior elicitation, but is not completely driven by the prior distributions. Greater resilience from Hurricane Hugo than from Hurricane Georges might be associated with the different historical contexts of the hurricanes. Hurricane Hugo was the first major hurricane to make landfall in north-eastern Puerto Rico in over 30 years, whereas Hurricane Georges arrived only 9 years after Hurricane Hugo. Resilience after Hurricane Hugo may have been greater than that after Hurricane Georges for two intercorrelated reasons. First, winds from Hurricane Hugo deposited massive quantities of debris on the forest floor, including leaves of sierra palms (*Prestoea montana*). Such debris represents both substrate and food for *N. tridens*, thereby enhancing individual growth rates, reproductive output, and subsequent survivorship of individuals that were alive after the hurricane's initial impact. Moreover, greater reductions in intra-specific and inter-specific competition after Hurricane Hugo—most snail species suffered massive declines in abundances (Bloch and Willig

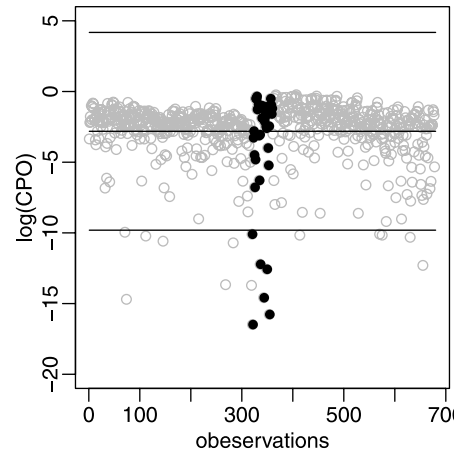

Figure 5. Control charts of $\log \mathrm{CPO}$ for detecting influential observations. Observations are ordered in time. Solid circles are observations from the year following Hurricane Georges (1999). The horizontal lines are the sample mean and 3 sample standard deviations above and below the sample mean.

2006)—compared to after Hurricane Georges would minimize density-dependent controls on population growth. In short, the demographic context after Hurricane Hugo would directly support greater rates of increase (i.e., birth rates minus death rates) and relaxed competition-related dampening of those rates by increasing the disparity between carrying capacity and abundance. Responses to disturbances on an even longer term, such as several decades, remains to be understood.

The CPO criterion can also be used to detect influential points in the data set. We propose a graphical approach similar to a control chart. Based on $\log \mathrm{CPO}_i$, $i = 1, \ldots, n$, we compute their sample mean $\hat{\mu}$ and sample standard deviation $\hat{\sigma}$. As in a control chart, any observation i such that $|\log \mathrm{CPO}_i - \hat{\mu}| > 3\hat{\sigma}$ will be considered as a possible outlier. Figure 5 shows $\log \mathrm{CPO}_i$ against observation number i, along with a mean line $\hat{\mu}$ and upper and lower 3 standard deviations bounds above and below $\hat{\mu}$. There are 16 possible outliers, representing 2.5% of the data set. Observations following Hurricane Georges contributed 6 possible outliers, which represents 37.5% of the influential points.

Our analyses used quite informative priors elicited from expert opinion and historical observation. The most informative priors are on the initial shocks of the two hurricanes, $\omega_{h,1}$ and $\omega_{g,1}$. Figure 6 shows the prior density and posterior kernel density of the two parameters. Distributions of both parameters evolved noticeably from prior to posterior, learning considerably from the data. The informative prior on $\omega_{h,1}$ is necessary to ensure that Hurricane Hugo has a more profound effect than Hurricane Georges. The posterior distribution of both parameters are not completely driven by the prior distribution. To study the sensitivity of priors, we modeled with two other priors on $\omega_{g,1}$, placing a 95% probability that Hurricane Georges causes an initial reduction between 5% and 99% or between 20% and 90%. Our results are reasonably robust.

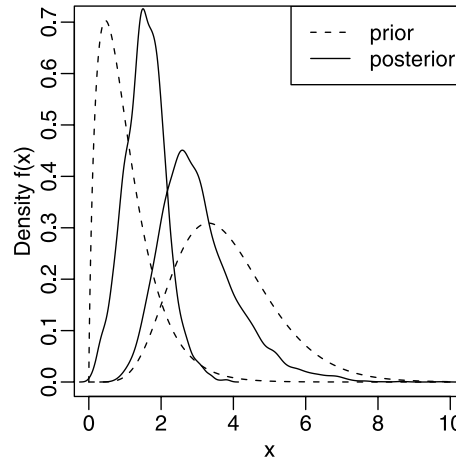

Figure 6. Prior and posterior distributions of initial shock parameters of Hurricane Hugo (2 curves on the right) and Hurricane Georges (2 curves on the left).

6. DISCUSSION

The long-term effects of natural disasters on population, community, and ecosystem properties are not well understood because of a paucity of long-term data collected in similar fashions and at comparable spatial scales. When available, such data are spatiotemporal, demanding quantitative models in which both spatial dependence and temporal dependence are accounted for appropriately. We incorporated intervention analysis from time series settings into a spatiotemporal model to assess the long-term impacts of multiple hurricanes on abundance of a terrestrial snail species. A geometrically declining intervention effect on the mean abundance level on the log scale was assumed for each hurricane. Bayesian inference and model comparison suggest that the model provides a plausible description of annual variation in snail abundance in the aftermath of recurrent disturbance from hurricanes.

The intervention effects of hurricanes on *N. tridens* are modeled by geometrically decaying shocks. It is well documented that terrestrial gastropods respond to disturbance in a species-specific manner (Willing et al. 1998, 2007; Bloch and Willig 2006); consequently, hurricane effects on other species may need to be modeled by other intervention patterns (Box and Tiao 1975). One simple modification of the geometric decaying impact is to add an extra initial decline that only affects the year following a hurricane. For the current data, however, such initial decline for Hurricane Hugo would still be unidentifiable because the data collection started two years after Hurricane Hugo struck.

Prior elicitation from expert opinion and historical observation plays an important role in the analysis. The span of 17 years is still short given that we are dealing with two hurricanes. Further, the data collection started two years after Hurricane Hugo stuck. Although both produced considerable damage to the tabonuco forest, the two hurricanes differed in intensity, extent, and severity. Hurricane Hugo, a category 4 storm with maximum sustained winds of 166 km/h (Scatena and Larsen 1991), produced larger canopy openings and deposited more debris than did Hurricane Georges, a category 3 storm (Lugo and Frangi

2003; Ostertag, Scatena, and Silver 2003). If such information were ignored and the same prior were placed on the initial declines caused by the two hurricanes, the analysis would lead to a conclusion that Hurricane Georges had a more profound impact than did Hurricane Hugo.

For the purpose of modeling, we assumed that abundance of *N. tridens* had returned to its normal stationary level before the arrival of Hurricane Georges. Without this assumption, the overall natural, stationary abundance level would be unidentifiable. This assumption seems to be reasonably supported by the data as the empirical abundance level did decrease in some of the years, as opposed to always increasing, before Hurricane Georges struck. It can be validated further when more data become available in the future.

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