

Spatial-Temporal Modeling of Forest Gaps
Generated by Colonization from Below- and
Above-ground Bark Beetle Species

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Abstract

Studies of forest declines are important, because they both reduce timber production and affect successional trajectories of landscapes and ecosystems. Of particular interest is the decline of red pines which is characterized by expanding areas of dead and chlorotic trees in plantations throughout the Great Lakes Region. Here we examine the impact of two bark beetle groups, namely red turpentine beetles and pine engraver bark beetles, on tree mortality and the subsequent gap formation over time in a plantation in Wisconsin. We construct spatial-temporal statistical models that quantify the relations among red turpentine beetle colonization, pine engraver bark beetle colonization, and mortality of red pine trees, while accounting for correlation across space and over time. For statistical inference, we adopt a Bayesian hierarchical model and devise Markov chain Monte Carlo algorithms for obtaining the posterior distributions of model parameters as well as posterior predictive distributions. Our data analysis results suggest that red turpentine beetle colonization is associated with higher likelihood of pine engraver bark beetle colonization and pine engraver bark beetle colonization is associated with higher likelihood of red pine tree mortality, whereas there is no direct association between red turpentine beetle colonization and red pine tree mortality. There is strong evidence that red turpentine beetle colonization does not kill a red pine tree directly, but rather predisposes the tree to subsequent colonization by pine engraver bark beetles. The evidence is also strong that pine engraver bark beetles are the ultimate mortality agents of red pine trees.

Keywords: Autologistic model, Bayesian inference, forest entomology, Markov chain Monte Carlo, perfect simulation, spatial-temporal processes.

1 Introduction

Studies of forest declines are of great interest to the timber industry, natural resource managers, and ecologists alike, because these declines both reduce timber production and affect successional trajectories of landscapes and ecosystems. Decline syndromes occur in forests throughout the world, and occur at a variety of scales (Auclair, 2005). Declines due to soil acidification and atmospheric pollution may affect large areas (Battles and Fahey, 2000; Drohan et al., 2002; Purdon et al., 2004) while declines due to insect and/or disease complexes may exhibit smaller mosaics of mortality such as gap formation, which is our focus here (Klepzig et al., 1991; Erbilgin and Raffa, 2003). In some systems, areas of large-scale mortality to insects and pathogens may originate from such small-scale mosaics. Characterizing spatial patterns and gaining inference about the processes that may create such patterns may assist in policy and management decisions when dealing with declines. Indeed, linking pattern and process is a key goal in ecology.

In particular we examine tree mortality and the subsequent gap formation over time in red pine forests. Decline of red pines is characterized by expanding areas, termed “pockets” of dead, slow growing, and chlorotic trees in plantations throughout the Great Lakes Region (Klepzig et al., 1991). Abiotic factors such as soil characteristics and drought stress can predispose trees to biotic mortality agents such as insects and root pathogens (Klepzig et al., 1991; Erbilgin and Raffa, 2002). Here we focus on the impact of two bark beetle groups, called “turpentine beetles” and “*Ips* spp.” (for details of the species, see Section 2), on the decline of red pines in a plantation in Wisconsin.

Past studies on red pine decline have yielded valuable insights on individual components of this system by examining multiple levels of scale, from detailed studies on individual trees (Klepzig et al., 1995; Raffa and Smalley, 1995; Klepzig et al., 1996) to regional studies comparing multiple sites (Klepzig et al., 1991; Erbilgin and Raffa, 2002, 2003). Despite these advances, elucidation of exact mechanisms of pocket development and expansion remain elusive since a single site has never been observed over more than three years. In the present study, we examine a seven-year data set of annual surveys of all trees in a plantation. Each year, each of the 2,715 trees was examined for presence/absence of *Ips* spp., tree condition (alive/dead), and the number of pitch tubes, each of which signifies colonization by a turpentine beetle. We attempt to answer several important ecological questions. Of most interest is how the mortality rate of a tree is associated with the turpentine beetle and *Ips* spp. colonization. For example, how different are the mortality rates between a tree that has been colonized by both groups and a tree that has been colonized by just one group of bark beetles? Related to these questions are the degree of association between turpentine beetle and *Ips* spp. For example, what is the likelihood of a tree that has been colonized by turpentine

beetles will be colonized by *Ips* spp. subsequently? Moreover it is also of interest to quantify the spatial and temporal relations among turpentine beetle colonization, *Ips* spp. colonization, and tree mortality.

The study of red pine declines poses statistical challenges, in that processes giving rise to patterns of mortality may act at different levels of temporal and spatial scales. Here we construct spatial-temporal models that quantify the relations among the activities of turpentine beetle, the activities of *Ips* spp., and the conditions of red pine trees. Furthermore, we introduce spatial and temporal terms into the model that account for correlations across space and over time. For statistical inference, we adopt a Bayesian hierarchical model and Markov chain Monte Carlo (MCMC) algorithms that enable us to obtain the posterior distributions of the model parameters and posterior predictive distributions. The model for *Ips* spp. also involves an unknown normalizing constant. Thus when we use a Metropolis-Hastings algorithm, we approximate a ratio of normalizing constants by path sampling (Gelman and Meng, 1998) combined with the Propp-Wilson algorithm for perfect simulation (Propp and Wilson, 1996; Møller, 1999).

The remainder of the paper is organized as follows. In Section 2, we describe some more biological background and the data. In Section 3, we specify a set of spatial-temporal models for the data. The Bayesian model and simulation algorithms are specified in Section 4. We describe the results of the data analysis and address the ecological questions in Section 5. Section 6 contains concluding remarks.

2 Bark beetle and red pine data

2.1 Background

Bark beetle species are characterized by their ability to mine and reproduce below the surface of the bark of trees. The red turpentine beetle (*Dendroctonus valens* (LeConte)), which we in short call “turpentine beetle”, is one of the most widely distributed bark beetles in North America. Colonization by turpentine beetle adults concentrate in the lower stems of pine trees. The larvae breed largely below the soil line in the root collar and primary lateral root regions. An external indicator of colonization by the turpentine beetle is a pitch tube on the outer surface of the bark just above the soil line or pitch pellets on the ground. Peak flight and colonization in Wisconsin occur in late April and May. Turpentine beetles colonize primarily trees that are weakened by drought and fire, for example, but may also colonize apparently healthy trees. These beetles vector the staining fungi *Leptographium terebrantis* and *L. procerum* (Klepzig et al., 1991). It is hypothesized that a colonization of a healthy tree by turpentine beetles does not kill the

tree but may predispose it to subsequent colonization by other bark beetles such as engraver beetles.

Engraver beetles (predominantly *Ips pini* (Say), although additionally some *Ips grandicollis* (Eichhoff) in our study site (Klepzig et al., 1991)), which we in short call “*Ips* spp.”, may have up to three generations from spring to early fall (Erbilgin et al., 2002; Erbilgin and Raffa, 2002; Aukema et al., 2005). Successful colonization by the *Ips* spp. is indicated by fine sawdust shavings pushed to the outer surface of the bark and galleries inside the tree. *Ips* spp. beetles produce aggregation pheromones as they enter host trees, thus attacking trees *en masse* over very short periods. These mass attacks typically result in complete utilization of the resource within a single generation, making it unlikely that subsequent *Ips* spp. or turpentine beetles will enter. *Ips* spp. also vector the fungal associate *Ophiostoma ips*, whose colonization may impede the upward flow of water to the tree crowns. Lack of water leads the needles to wither and die while the color characteristically fades from green to red to brown. *Ips* spp. brood adults leave the tree through emergence holes on the surface of the outer bark, the most apparent external indicator that a tree has been colonized by *Ips* spp. The tree is most likely to die within a few weeks after an attack.

2.2 Description of data

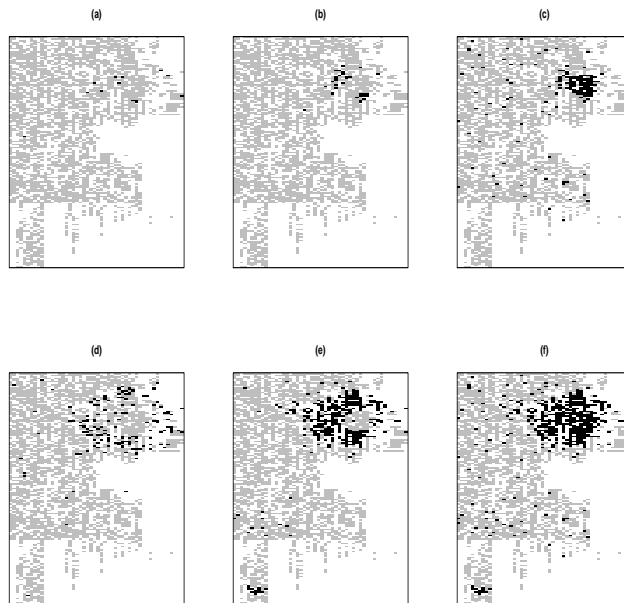
The study area is a red pine plantation near Spring Green, Wisconsin. In 1986, each of the 2,715 trees in the plantation was surveyed and its condition (alive/dead) was recorded. From 1987 to 1992, subsequent surveys were conducted not only of the tree condition, but also about the colonization of turpentine beetles and *Ips* spp. For turpentine beetles, the number of pitch tubes on the outer surface of a bark was recorded, while for *Ips* spp., an indicator variable of *Ips* spp. colonization (yes/no) was recorded. The survey took place in autumn of each year, after beetles had become dormant.

Selected image plots in Figure 1 illustrate the nature of the data. For 1987, colonization of turpentine beetles (zero or positive number of pitch tubes), colonization of *Ips* spp. (yes/no), and condition of trees (alive/dead) are shown (Figure 1(a)–(c)). For 1992, similar plots are shown, except that colonization of *Ips* spp. here includes colonization from 1987 to 1992 (Figure 1(d)–(f)). There is clear indication of spatial dependence among tree conditions, *Ips* spp. colonization, and turpentine beetle colonization. A gap of dead trees was evident in the southeastern part of the plantation in the beginning and expanded over the years. Furthermore there was a strong association between the spatial pattern of *Ips* spp. colonization and that of tree mortality, but the link was not as obvious between turpentine beetle colonization and tree mortality.

There were 126 dead trees in 1986. From 1987 to 1992, a total of 344 trees died,

339 trees were colonized by *Ips* spp., and 152 trees were colonized by turpentine beetles. Among the 344 dead trees, a majority of 330 were colonized by *Ips* spp. and 73 were colonized by turpentine beetles. Only 9 out of 339 trees that were colonized by *Ips* spp. survived by 1992, whereas 79 out of 152 of the trees that were colonized by turpentine beetles survived. *Ips* spp. colonization seemed to associate more with those trees with a larger number of pitch tubes of turpentine beetles, although the evidence was subtle due to the small number of trees that had a large number of pitch tubes.

Figure 1: (a) and (d) turpentine beetle colonization, (b) and (e) *Ips* spp. colonization, and (c) and (f) tree condition by 1987 (top row) and 1992 (bottom row). The site of a tree is colored black if the tree was colonized by turpentine beetles ((a) and (d)), colonized by *Ips* spp. ((b) and (e)), or dead ((c) and (f)); all other sites are colored grey.



3 Observation model

3.1 Notation

Let $t = -1, 0, \dots, 5$ index the time of survey from 1986 to 1992 and let $i = 1, \dots, 2715$ index the sites of 2,715 red pine trees in the plantation that were surveyed. For the purpose of modeling, we consider time points $t = \dots, -1, 0, 1, \dots$ and define $x_{t,i}$, $y_{t,i}$, $z_{t,i}$, and $u_{t,i}$ as follows. Since the survey was conducted in autumn, after insect and tree dormancy for any given year, the data reflect insect activities and tree conditions throughout that year. At time t and site i , let $x_{t,i}$ denote the turpentine beetle colonization variable such that $x_{t,i}$ is the cumulative number of turpentine beetle pitch tubes on the bark. Further, let $y_{t,i}$ denote the *Ips* spp. colonization variable such that $y_{t,i} = 0, 1, 2$ correspond respectively to no *Ips* spp. colonization, colonization by *Ips* spp. in year t , and colonization by *Ips* spp. in a previous year. Let $u_{t,i}$ denote an indicator variable of whether *Ips* spp. colonization took place during year t at site i , i.e. $u_{t,i} = 1$ if $y_{t,i} = 1$ and $u_{t,i} = 0$ otherwise. In consistency with the data, we assume that *Ips* spp. colonization could only occur once at a given site and after colonization of a tree, *Ips* spp. leaves the tree before the end of the flight season of the same year (before the annual survey). Thus $u_{t,i} = 1$ for at most one year t . Finally, let $z_{t,i}$ denote the tree condition variable such that $z_{t,i} = 0$ if the tree was alive and $z_{t,i} = 1$ if the tree was dead at time t and site i .

We let $x_t = (x_{t,1}, \dots, x_{t,2715})$, $y_t = (y_{t,1}, \dots, y_{t,2715})$, and $z_t = (z_{t,1}, \dots, z_{t,2715})$ denote the vectors of respectively the turpentine beetle colonization variables, the *Ips* spp. colonization variables, and the tree condition variables at time t and all the sites. Further, let $u_t = (u_{t,1}, \dots, u_{t,2715})$ and $w_t = (x_t, y_t, z_t)$. Since turpentine beetle colonization typically precedes *Ips* spp. colonization, which in turn precedes the death of a tree, we order the variables x_t, y_t, z_t such that x_t precedes y_t and y_t precedes z_t . Thus, the data under study are ordered as $(z_{-1}, x_0, y_0, z_0, \dots, x_5, y_5, z_5)$, while the unobserved data in the past are ordered as $(\dots, x_{-2}, y_{-2}, z_{-2}, x_{-1}, y_{-1})$.

3.2 Temporal model

In Sections 3.3–3.5, we shall construct a set of spatial-temporal models to capture the relations among the variables $x_{t,i}$, $y_{t,i}$, and $z_{t,i}$, while accounting for spatial and temporal dependence. Before specifying these details, it is useful to give a brief description of the temporal process w_t and how the likelihood factorizes.

In equations (1)–(3) below we naturally consider a sequential model construction such that for each time t , we specify the conditional distribution of x_t first, y_t second, z_t third given the relevant past. The detailed model descriptions (5), (8), and (12) in Sections 3.3–3.5 imply the following conditional independence

structure for the temporal process. Let $[a|b]$ denote the conditional distribution of a random component a given another random component b . For the turpentine beetle colonization variables at time t ,

$$[x_t|(w_s)_{s=t-1,t-2,\dots}] \sim [x_t|x_{t-1}, z_{t-1}] \quad (1)$$

depends on a parameter θ as specified in Section 3.3; for the *Ips* spp. beetle colonization variables at time t ,

$$[y_t|x_t, (w_s)_{s=t-1,t-2,\dots}] \sim [y_t|x_t, y_{t-1}, z_{t-1}] \quad (2)$$

depends on a parameter ψ (Section 3.4); for the tree condition variables at time t ,

$$[z_t|x_t, y_t, (w_s)_{s=t-1,t-2,\dots}] \sim [z_t|x_t, y_t, z_{t-1}] \quad (3)$$

depends on a parameter φ (Section 3.5). For the corresponding likelihood terms, we write $L^{(1)}(\theta) = L^{(1)}(\theta; x_t|x_{t-1}, z_{t-1})$, $L^{(2)}(\psi) = L^{(2)}(\psi; y_t|x_t, y_{t-1}, z_{t-1})$, and $L^{(3)}(\varphi) = L^{(3)}(\varphi; z_t|x_t, y_t, z_{t-1})$.

For statistical inference we condition on

$$e = (z_{-1}, x_0, y_0)$$

since by (1)–(3), the remaining data

$$d = (z_0, x_1, y_1, z_1, \dots, x_5, y_5, z_5)$$

are conditionally independent of the unobserved $(\dots, x_{-2}, y_{-2}, z_{-2}, x_{-1}, y_{-1})$. We let $L(\theta, \psi, \varphi) = L(\theta, \psi, \varphi; d|e)$ denote the likelihood based on the conditional distribution of d given e . By (1)–(3), this factorizes into

$$L(\theta, \psi, \varphi; d|e) = L^{(1)}(\theta)L^{(2)}(\psi)L^{(3)}(\varphi)$$

given by the likelihood terms for each type of data

$$L^{(1)}(\theta) = \prod_{t=1}^5 L_t^{(1)}(\theta), \quad L^{(2)}(\psi) = \prod_{t=1}^5 L_t^{(2)}(\psi), \quad L^{(3)}(\varphi) = \prod_{t=0}^5 L_t^{(3)}(\varphi), \quad (4)$$

where $L_t^{(1)}(\theta) = L_t^{(1)}(\theta; x_t|x_{t-1}, z_{t-1})$, $L_t^{(2)}(\psi) = L_t^{(2)}(\psi; y_t|x_t, y_{t-1}, z_{t-1})$, and $L_t^{(3)}(\varphi) = L_t^{(3)}(\varphi; z_t|x_t, y_t, z_{t-1})$ are specified at the end of Sections 3.3–3.5.

In Sections 3.3–3.5, our strategy is for each time, site, and type of data $x_{t,i}$, $y_{t,i}$, or $z_{t,i}$ to specify a “local characteristic” which only depends on “local information”. For example, by the local characteristic of $y_{t,i}$, we mean the conditional distribution of $y_{t,i}$ given the other $y_{t,j}$, $j \neq i$ and the previous history $x_t, (w_s)_{s=t-1,t-2,\dots}$. We express the local information with respect to the grid of tree locations and consider for site i its first-, second-, \dots order neighbors which are the (up to) four nearest, four second nearest, \dots sites to i .

3.3 Likelihood based on turpentine beetle colonization

The cumulative number of turpentine beetles at time t and site i is assumed to depend on local information such that

$$[x_{t,i} | (x_{t,j})_{j \neq i}, (w_s)_{s=t-1,t-2,\dots}] \sim [x_{t,i} | x_{t-1,N_i^x}, z_{t-1,i}] \quad (5)$$

where x_{t-1,N_i^x} is the vector of variables x_j with $j \in N_i^x$. Here N_i^x consists of i and its neighbors up to the fifth order, and we assume that the conditional distribution of turpentine beetle colonization at time t depends only on turpentine beetle colonization at time $t-1$ and at sites in N_i^x , since this neighborhood is fairly large but is still interpretable biologically (see Section 5 for further details). Since turpentine beetles colonize red pines during only one brief period per year, and a tree can be colonized by multiple turpentine beetles, we assume conditional independence among nearby sites within the same year. On the other hand, turpentine beetles that colonize a tree in one spring tend to colonize nearby trees in the next spring. Thus we build into the model a possible relation between turpentine beetle colonization at time t and at time $t-1$.

The local characteristic $[x_{t,i} | x_{t-1,N_i^x}, z_{t-1,i}]$ is specified as follows. If the tree at site i was dead at time $t-1$ (i.e. $z_{t-1,i} = 1$), the local characteristic is deterministic with $x_{t,i} = x_{t-1,i}$, since turpentine beetles will not colonize a dead tree. Turpentine beetles could theoretically colonize a tree that dies from competitive thinning, i.e., a process in which the growth of neighboring trees blocks out necessary sunlight. However, such events were rare in the stand, as the insects would likely colonize the weakened tree in advance of tree death. Moreover, the diameter and subcortical tissues of trees that have been crowded to death are frequently too thin to serve as a suitable breeding substrate for this insect. Turpentine beetles could also colonize a healthy tree that was killed suddenly, such as by a lightning strike or during a wind storm. However, we did not find any visual evidence of lightning (e.g., shredded bark, burn marks, or shattered limbs) or windthrow (other than trees that had already been killed) in any of our annual surveys. Hence, focusing on the colonization of live trees, if the tree at site i was alive at time $t-1$ (i.e. $z_{t-1,i} = 0$), we assume that

$$[x_{t,i} - x_{t-1,i} | x_{t-1,N_i^x}, z_{t-1,i} = 0] \sim \text{Poisson}(\lambda_{t,i})$$

where

$$\log(\lambda_{t,i}) = \theta_0 + \theta_1 \sum_{j \in N_i^x} x_{t-1,j}. \quad (6)$$

Thus, given the past, the $x_{t,i} - x_{t-1,i}$ with $z_{t-1,i} = 0$ form a sample from a Poisson

regression, so

$$\begin{aligned}
L_t^{(1)}(\theta) &\propto \prod_{i:z_{t-1,i}=0} \lambda_{t,i}^{x_{t,i}-x_{t-1,i}} \exp(-\lambda_{t,i}) \\
&= \exp \left(\sum_{i:z_{t-1,i}=0} \left[(x_{t,i} - x_{t-1,i}) \left(\theta_0 + \theta_1 \sum_{j \in N_i^x} x_{t-1,j} \right) - \exp \left(\theta_0 + \theta_1 \sum_{j \in N_i^x} x_{t-1,j} \right) \right] \right). \tag{7}
\end{aligned}$$

3.4 Likelihood based on *Ips* spp. colonization

The conditional dependence structure for whether colonization by *Ips* beetles has occurred is assumed to be

$$[y_{t,i}|x_t, (y_{t,j})_{j \neq i}, (w_s)_{s=t-1,t-2,\dots}] \sim [y_{t,i}|x_{t,i}, u_{t,N_i^y}, u_{t-1,N_i^y}, y_{t-1,i}, z_{t-1,i}]. \tag{8}$$

Thus we assume that the conditional distribution of *Ips* spp. colonization at time t depends on turpentine beetle colonization at time t , *Ips* spp. colonization at sites $j \in N_i^y$ at both time $t - 1$ and t , where N_i^y consists of the first and second order neighbors to i (note that N_i^y does not include i). Since it is hypothesized that turpentine beetles predispose red pines to colonization by *Ips* spp., we include in the model a possible relation to the number of turpentine beetle pitch tubes on the tree. Since *Ips* spp. attack different red pines 1–3 times per year and can overwinter near the trees they have colonized, we assume relations among neighboring sites for both time t and $t - 1$ and that a first- and second-order neighborhood would suffice to capture spatial dependence in this study.

The local characteristic $[y_{t,i}|x_{t,i}, u_{t,N_i^y}, u_{t-1,N_i^y}, y_{t-1,i}, z_{t-1,i}]$ is specified as follows. If the tree at site i was dead at time $t - 1$ (i.e. $z_{t-1,i} = 1$) or was colonized by *Ips* spp. at previous times (i.e., $y_{t-1,i} = 1$ or 2), the local characteristic is deterministic with $y_{t,i} = 0$ or 2 , since *Ips* spp. will not colonize a dead tree. *Ips* spp. could theoretically colonize a tree that dies from competitive thinning, i.e., overshadowing and crowding by more dominant neighbors, although in practice the insects would likely find and colonize a weakened tree in advance of tree death, and would colonize only if the subcortical tissue was sufficiently thick. Such trees also contribute little to the ecological dynamics of the system, as they are commonly colonized by competing species of insects against which *Ips* spp. fare poorly. We also disregard the possibility that *Ips* spp. colonize lightning strikes or recent windthrow of live trees, due to the absence of such events observed during our annual surveys. Hence, focusing on colonization of live trees, if the tree at site i was alive at time $t - 1$ (i.e. $z_{t-1,i} = 0$) and was not colonized previously ($y_{t-1,i} = 0$), the local characteristic is assumed to be a logistic regression,

$$[y_{t,i}|x_{t,i}, u_{t,N_i^y}, u_{t-1,N_i^y}, y_{t-1,i} = 0, z_{t-1,i} = 0] \sim \text{Bernoulli}(p_{t,i}) \tag{9}$$

where

$$\text{logit}(p_{t,i}) = \psi_0 + \psi_1 x_{t,i} + \psi_2 \sum_{j \in N_i^y} u_{t-1,j} + \psi_3 \sum_{j \in N_i^y} u_{t,j}. \quad (10)$$

Since $u_{t,i} = y_{t,i}$ in (9), by the Hammersley-Clifford theorem, $L_t^{(2)}(\psi)$ is equal to

$$\frac{\exp\left(\sum_{i: y_{t-1,i} = z_{t-1,i} = 0} \left[\psi_0 + \psi_1 x_{t,i} + \psi_2 \sum_{j \in N_i^y} u_{t-1,j}\right] u_{t,i} + \psi_3 \sum_{i < j: j \in N_i^y} u_{t,i} u_{t,j}\right)}{c(x_t, y_{t-1}, z_{t-1}, \psi)} \quad (11)$$

where $c(x_t, y_{t-1}, z_{t-1}, \psi)$ is a normalizing constant (note that $j \in N_i^y \Leftrightarrow i \in N_j^y$). In other words, given the past, the $u_{t,i}$ with $y_{t,i} = z_{t,i} = 0$ form an autologistic model (Besag, 1974).

3.5 Likelihood based on tree condition

The conditional dependence structure for tree condition is assumed to be

$$[z_{t,i} | x_t, y_t, (z_{t,j})_{j \neq i}, (w_s)_{s=t-1, t-2, \dots}] \sim [z_{t,i} | x_{t,i}, u_{t,i}, z_{t-1, N_i^z}, z_{t-1, i}] \quad (12)$$

where the neighborhood N_i^z consists of the neighbors up to the fifth order. If the tree at site i was dead at time $t-1$ (i.e. $z_{t-1, i} = 1$), the local characteristic is deterministic with $z_{t,i} = 1$, because a dead tree remains dead. But if the tree at site i was alive at time $t-1$ (i.e. $z_{t-1, i} = 0$), the local characteristic is assumed to be a logistic regression,

$$[z_{t,i} | x_{t,i}, u_{t,i}, z_{t-1, N_i^z}, z_{t-1, i} = 0] \sim \text{Bernoulli}(q_{t,i})$$

where

$$\text{logit}(q_{t,i}) = \varphi_0 + \varphi_1 x_{t,i} + \varphi_2 u_{t,i} + \varphi_3 \sum_{j \in N_i^z} z_{t-1, j}. \quad (13)$$

That is, mortality rate of a tree depends on both turpentine beetle colonization and *Ips* spp. colonization. The additional term involving the tree condition at time $t-1$ is a way of accounting for any potential spatial dependence. Again we consider a fairly large neighborhood that consists of neighbors up to the fifth order. Conditional on the past, the $z_{t,i}$ with $z_{t-1, i} = 0$ form a sample from a logistic regressions, so

$$\begin{aligned} L_t^{(3)}(\varphi) &= \prod_{i: z_{t-1, i} = 0} \frac{\exp(z_{t,i} \text{logit}(q_{t,i}))}{1 + \exp(\text{logit}(q_{t,i}))} \\ &= \prod_{i: z_{t-1, i} = 0} \frac{\exp(z_{t,i} (\varphi_0 + \varphi_1 x_{t,i} + \varphi_2 u_{t,i} + \varphi_3 \sum_{j \in N_i^z} z_{t-1, j}))}{1 + \exp(\varphi_0 + \varphi_1 x_{t,i} + \varphi_2 u_{t,i} + \varphi_3 \sum_{j \in N_i^z} z_{t-1, j})}. \end{aligned} \quad (14)$$

4 Bayesian model and posterior simulations

We assume independent improper uniform priors

$$p(\theta) \propto 1, \quad \theta \in \mathbb{R}^2; \quad p(\psi) \propto 1, \quad \psi \in \mathbb{R}^4; \quad p(\varphi) \propto 1, \quad \varphi \in \mathbb{R}^4.$$

Thus θ, ψ, φ are *a posteriori* independent with densities

$$\pi(\theta) \propto L^{(1)}(\theta), \quad \theta \in \mathbb{R}^2; \quad \pi(\psi) \propto L^{(2)}(\psi), \quad \psi \in \mathbb{R}^4; \quad \pi(\varphi) \propto L^{(3)}(\varphi), \quad \varphi \in \mathbb{R}^4. \quad (15)$$

For a discussion of posterior propriety, see Appendix A. For the remaining discussion of MCMC simulations, we assume the reader is familiar with MCMC methods (e.g. Robert and Casella (2004)).

For turpentine beetles, we will simulate from the marginal posterior distribution of θ using a Metropolis within Gibbs algorithm, where we alternate between updating θ_0 and θ_1 . Since the full conditional for $\lambda_0 = \exp(\theta_0)$ is a Gamma distribution with shape parameter $\sum_{t,i} (x_{t,i} - x_{t-1,i})$ and inverse scale parameter $\sum_{t,i} \exp(\theta_1 \sum_{j \in N_i^x} x_{t-1,j})$, where in both cases the sum $\sum_{t,i}$ is over those t, i with $z_{t-1,i} = y_{t-1,i} = 0$, we use a Gibbs update for this component. The full conditional for the other parameter θ_1 is not a standard distribution, so here we use a Metropolis random walk algorithm with a normal proposal distribution, cf. Robert and Casella (2004).

For *Ips* spp., suppose we use a Metropolis-Hastings algorithm to simulate from the marginal posterior distribution of ψ . Let $L_{\text{unnorm}}^{(2)}(\psi; u)$ denote $L^{(2)}$ in (4) but without the unknown normalizing constant

$$c(\psi) = \prod_{t=1}^5 c(x_t, y_{t-1}, z_{t-1}, \psi)$$

from (11); here u denotes the vector of all observed $u_{t,i}$ values. If ψ is the current and ψ' is the proposed parameter values in the Metropolis-Hastings algorithm, then the Hastings ratio depends on the ratio $c(\psi')/c(\psi)$ of unknown normalizing constants. This can be approximated by path sampling (e.g. Gelman and Meng (1998)),

$$\log \frac{c(\psi')}{c(\psi)} \approx \frac{1}{n} \sum_{k=1}^n \left[\frac{d}{ds} \log L_{\text{unnorm}}^{(2)}(\psi(s_k); v_k) \right]. \quad (16)$$

Here we let s_1, \dots, s_n be independent and uniformly distributed on $[0, 1]$, and $\psi(s) = s\psi' + (1-s)\psi$, $0 \leq s \leq 1$ is a line segment. Further, each v_k is a perfect simulation of $u = (u_1, \dots, u_5)$ where u_t given the past follows the autologistic model

(11) with parameter $\psi(s_k)$ (Propp and Wilson, 1996; Møller, 1999). Furthermore, given s_1, \dots, s_n , the perfect simulations v_1, \dots, v_n are independent.

We use a Metropolis random walk algorithm with independent normal proposal distributions for $\psi_0, \psi_1, \psi_2, \psi_3$, where we propose to change all four parameters at the same time, since the main part of the running time of the algorithm is by far used in generating the perfect simulations, and this is the same amount of work whether we are changing one or all four parameters.

In the case of φ , we use a Metropolis within Gibbs algorithm, where we alternate between simulating from the marginal posterior distribution of $\varphi_0, \varphi_1, \varphi_2, \varphi_3$, respectively. Neither of these parameters have standard distributions, so for each parameter we use a Metropolis random walk update with a normally distributed proposal.

When running the Metropolis random walk algorithm for either $\theta_1, \psi, \varphi_0, \varphi_1, \varphi_2$, or φ_3 , the standard deviation of the normal proposal distribution is chosen to reach an average acceptance probability about 0.3 (Roberts et al., 1997).

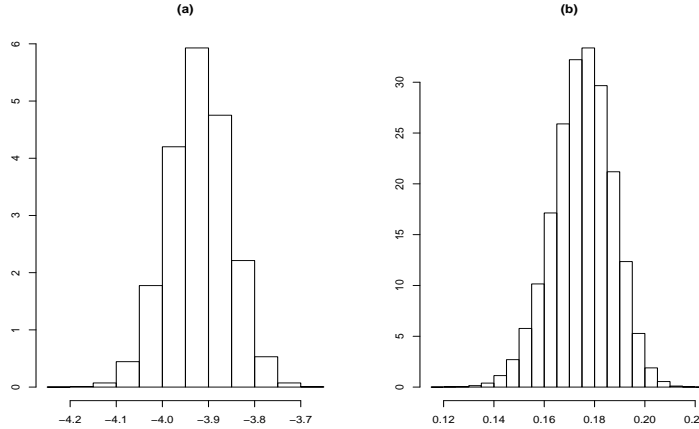
5 Statistical inference and discussion of the ecological questions

5.1 Posterior distributions of the model parameters

For inference of the parameters θ in the turpentine beetle colonization model, Figure 2 gives the posterior distributions based on an MCMC run length of 100,000 with a burn-in length of 1,000. The results suggest that there is a positive relation between the new turpentine beetle colonization and the number of turpentine beetle tubes in the previous year, at not only the same site, but also the sites that are up to the fifth-order neighbors. That is, the more turpentine beetles there were in the previous year on a tree and its neighboring trees, the more new colonization can be expected to occur on this tree in the current year. Here the extent of local temporal dependence is captured by a 1-year lag and that of local spatial dependence by about 5.14 m, which is the distance between a fifth-order neighbor and the site of a tree. We have also fitted a model that has one term for the zero-, first-, second-order neighbors and another term for the third- to fifth-order neighbors. The results there (not shown) suggest that the regression coefficients for the two types of neighborhoods are similar and thus we combine all the neighbors up to the fifth order. This phenomenon is consistent with a hypothesis in which turpentine beetles colonize trees that are being slowly weakened by the spread of a root fungus, such as *L. terebrantis* or *L. procerum*. These fungi are introduced to trees by the beetles and spread via root grafts at a rate of 5m per year, according to our best estimates based on root excavations and fungal isolations (Klepzig

et al., 1991; Erbilgin and Raffa, 2002). This hypothesis is consistent with the work of Erbilgin and Raffa (2003), who found that the probability of tree death falls below 50% at a distance of 5 m from the outer edge of the pocket margin.

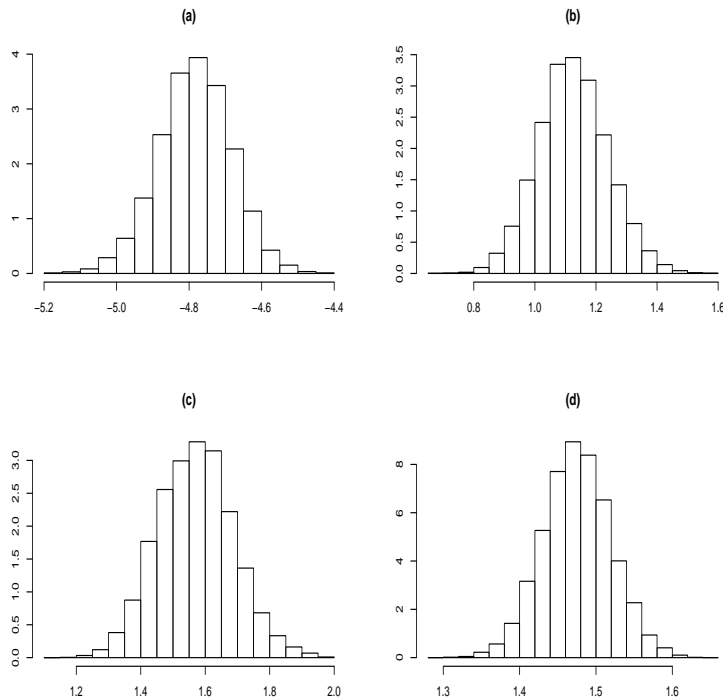
Figure 2: Posterior distribution of (a) θ_0 ; (b) θ_1 in the turpentine beetle colonization model.



For inference of the parameters ψ in the *Ips* spp. colonization model, Figure 3 gives the posterior distributions based on an MCMC run length of 60,000 with a burn-in length of 1,000. For the approximation (16), we use only $n = 10$ perfect simulations, which seems to give a reasonable approximation of the normalizing constant ratio. The results suggest that there is a positive relation between the *Ips* spp. colonization in the current year and the number of turpentine beetle tubes in the same year at the same site, *Ips* spp. colonization in the previous year at the neighboring sites (excluding the same site), and *Ips* spp. colonization in the current year at the neighboring sites (excluding the same site), up to the second-order neighbors. In other words, the more turpentine beetles there are on a tree, the more likely that the tree will be colonized by *Ips* spp. Thus there is strong evidence that turpentine beetles pre-dispose trees to colonization by *Ips* spp. Moreover, there is clear spatial and temporal dependence in the *Ips* spp. colonization. The more trees in the neighborhood that were colonized by *Ips* spp. in the previous year, the more likely that the tree is colonized by *Ips* spp. in the current year. Similarly the more trees in the neighborhood that are colonized by *Ips* spp. in the current year, the more likely that the tree is colonized by *Ips* spp. in the current year. Here the extent of local temporal dependence is captured by a 1-year lag and that of local spatial dependence by about 2.07 m, which is the distance between a second-

order neighbor and the site of the tree. Concentration of *Ips* spp. attacks among nearby trees may occur for three reasons, none of which are mutually exclusive. First, insect brood emerging from a previously colonized tree may preferentially colonize nearby trees. This may occur, for example, if brood adults from late fall overwinter in the duff around the base of their brood tree, and then emerges to colonize nearby trees in the spring. Although little is known about relations between brood tree and overwintering locations, inclement weather and predators exert substantial mortality on bark beetles engaging in host seeking behaviors (Berryman, 1979). Second, localized attacks may occur when high numbers of bark beetles are attracted by aggregation pheromones of a successful attack and begin to attack nearby trees, a phenomena known as “switching” (Geiszler et al., 1980). Third, turpentine beetles, and/or fungal root pathogens, may weaken trees in local neighborhoods and make them more susceptible to attacks and colonizations by *Ips* spp. (Owen, 1985).

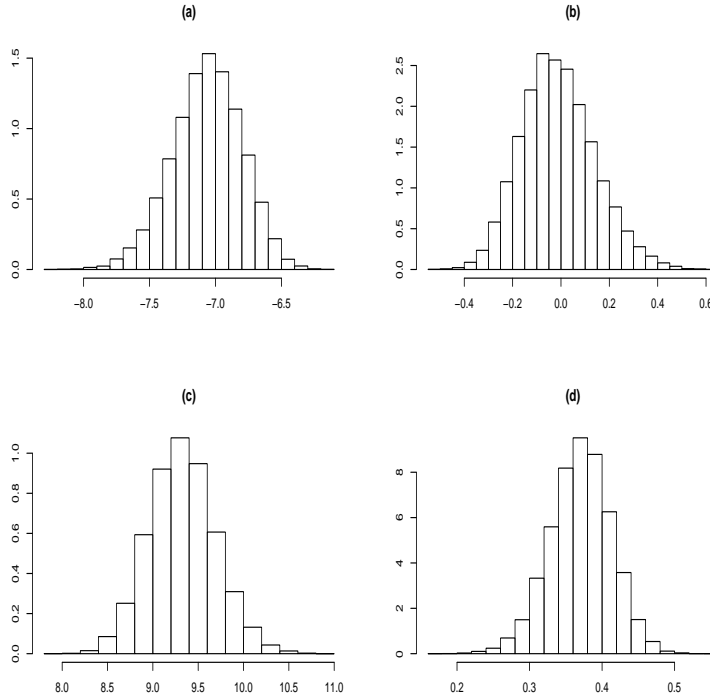
Figure 3: Posterior distribution of (a) ψ_0 ; (b) ψ_1 ; (c) ψ_2 ; (d) ψ_3 in the *Ips* spp. colonization model.



For inference of the parameters φ in the tree condition model, Figure 4 gives

the posterior distributions based on an MCMC run length of 100,000 with a burn-in length of 1,000. The results suggest that there is no evidence of a direct relation between a tree's condition and the number of its turpentine beetle tubes, but there is a strong positive relation between *Ips* spp. colonization and subsequent tree death. That is, the number of turpentine beetles does not directly influence the mortality of tree, but there is a very large increase in the probability that a tree dies after colonized by *Ips* spp. in the same year. This is not surprising, as trees may survive colonization of the root collar by turpentine beetles for more than one year. However, *Ips* spp. utilize aggregation pheromones to attract high numbers of conspecifics that quickly colonize all available subcortical tissue. The water-conducting tissues are mined by the developing larvae, and the tree dies soon thereafter. Furthermore it appears necessary to account for the spatial-temporal dependence among the tree conditions.

Figure 4: Posterior distribution of (a) φ_0 ; (b) φ_1 ; (c) φ_2 ; (d) φ_3 in the tree condition model.



5.2 Empirical and predictive rates of mortality and *Ips* spp. colonization

In this and the next subsection we check important aspects of the model that correspond to the ecological questions of interest, particularly the relations among turpentine beetle colonization, *Ips* spp. colonization, and tree conditions (see Section 1). The model checking is based on posterior predictive distributions obtained by a Monte Carlo sample $(x^{(s)}, u^{(s)}, z^{(s)})$, $s = 1, \dots, S$ where the Monte Carlo sample size is chosen to be $S = 100$. More precisely, since inference is performed conditional on e , given a posterior simulation $(\theta^{(s)}, \psi^{(s)}, \varphi^{(s)})$, we simulate “new data” $(x^{(s)}, u^{(s)}, z^{(s)})$ from the conditional distribution of d given e as specified in Section 3. This is done using the sequential model construction in Section 3, where simulation of x_t and z_t given their relevant past is straightforward (see Sections 3.3 and 3.5), while we use perfect simulation for y_t given the relevant past (see Section 3.4). Note that $x_0^{(s)} = x_0$, $y_0^{(s)} = y_0$, and $z_{-1}^{(s)} = z_{-1}$. The samples $(\theta^{(s)}, \psi^{(s)}, \varphi^{(s)})$, $s = 1, \dots, S$ are chosen such that they are effectively independent posterior simulations. Moreover, we let $(x^{(0)}, y^{(0)}, z^{(0)})$ denote the data.

In this section, we consider the posterior predictive distribution of various statistics related to mortality rates of trees and rates of *Ips* spp. colonization. First, define

$$\begin{aligned} \mathcal{I}_{0,0} &= \{i : z_{-1,i} = 0, x_{0,i} = 0, u_{0,i} = 0\}, & \mathcal{I}_{0,1} &= \{i : z_{-1,i} = 0, x_{0,i} = 0, u_{0,i} = 1\}, \\ \mathcal{I}_{1,0} &= \{i : z_{-1,i} = 0, x_{0,i} > 0, u_{0,i} = 0\}, & \mathcal{I}_{1,1} &= \{i : z_{-1,i} = 0, x_{0,i} > 0, u_{0,i} = 1\}, \end{aligned}$$

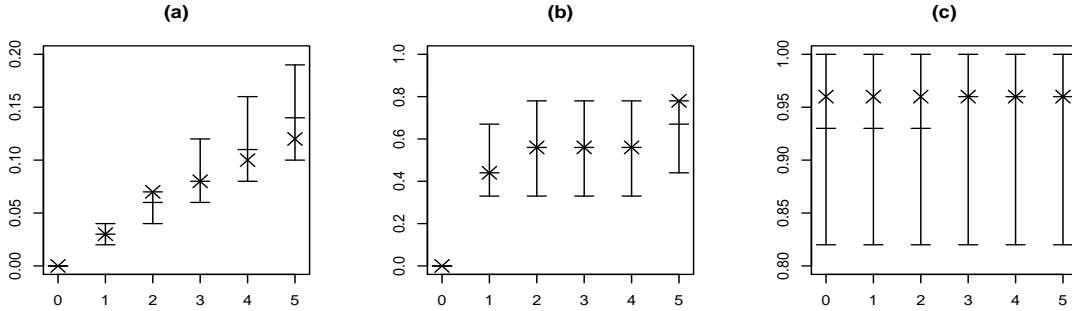
and

$$p_{k,l}^{(s)}(t) = \frac{1}{|\mathcal{I}_{k,l}|} \sum_{i \in \mathcal{I}_{k,l}} \mathbf{1}[z_{t,i}^{(s)} = 1], \quad s = 0, \dots, S, \quad t = 0, \dots, 5, \quad k, l = 0, 1$$

where $|A|$ denotes the cardinality of a finite set A . Then $p_{0,0}^{(0)}(t)$ is the observed tree mortality rate of trees, which were alive at time -1 and had no bark beetle colonization by time 0; $p_{0,1}^{(0)}(t)$ is the observed mortality rate of trees that were colonized by *Ips* spp.; $p_{1,0}^{(0)}(t)$ is the observed mortality rate of trees that were colonized by turpentine beetles; and $p_{1,1}^{(0)}(t)$ is the observed mortality rate of trees that were colonized by both turpentine beetles and *Ips* spp. Figure 5 shows for each value of $(k, l) = (0, 0), (0, 1), (1, 0)$ and $t = 0, \dots, 5$ the observed mortality rate $p_{k,l}^{(0)}(t)$ and the 2.5th, 50th, 97.5th percentiles of the posterior predictive distribution obtained from $p_{k,l}^{(s)}(t)$, $s = 1, \dots, S$. Further, for the case $(k, l) = (1, 1)$ (not shown in Figure 5), the 2.5th, 50th, 97.5th percentiles for the mortality rates are for all times $t = 0, \dots, 5$ given by 0.50, 1.00, and 1.00, respectively, and the corresponding observed values are all 1.00. For all values of (k, l) , the observed rates lie in the

centers of the corresponding predictive distributions. Thus overall there is no evidence against our model. Compared to $p_{0,0}^{(0)}(t)$, which may be interpreted as a kind of observed baseline mortality rate, $p_{0,1}^{(0)}(t)$ increased greatly and the large increase occurred within the same year of *Ips* spp. colonization; $p_{1,0}^{(0)}(t)$ increased at time 1 and the increase leveled off at time 2; and $p_{1,1}^{(0)}(t)$ is nearly 100% within the same year of the colonization. The predictive distributions show a similar behavior. The fact that deaths of trees occur in both the first and the second year after turpentine beetle colonization gives further evidence that turpentine beetles predispose a tree to death rather than killing a tree directly. The result here also supports the theory that *Ips* spp., unlike turpentine beetles, are the ultimate mortality agents of red pines.

Figure 5: Central 95% prediction intervals and medians (indicated by bars) for the tree mortality rates over time $t = 0, \dots, 5$ among those trees that were alive at $t = -1$ and, (a) were not colonized ($x_{i,0} = u_{i,0} = 0$), (b) were colonized by turpentine beetles ($x_{i,0} > 0, u_{i,0} = 0$), and (c) were colonized by *Ips* spp. ($x_{i,0} = 0, u_{i,0} = 1$) at $t = 0$. The corresponding observed tree mortality rates are indicated by crosses. Note the different scales on the y -axes.



Next, let

$$\mathcal{I}_k = \{i : z_{-1,i} = 0, x_{0,i} = k\}, \quad k = 0, 1,$$

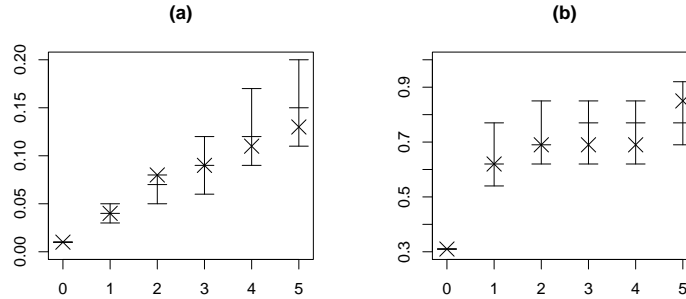
denote the collection of sites where a tree was alive at time -1 and was ($k = 1$) or was not ($k = 0$) colonized by turpentine beetles by time 0, and let

$$p_k^{(s)}(t) = \frac{1}{|\mathcal{I}_k|} \sum_{i \in \mathcal{I}_k} \mathbf{1}[u_{t,i}^{(s)} = 1], \quad s = 0, \dots, S, \quad t = 0, \dots, 5, \quad k = 0, 1.$$

Then $p_k^{(0)}(t)$ is the observed rate of *Ips* spp. colonization of a tree from \mathcal{I}_k by time $t = 0, \dots, 5$. Figure 6 is similar to Figure 5 but concerns $p_k^{(s)}(t)$ for $k = 0, 1$ and

$t = 0, \dots, 5$ Again there is no evidence against our model. Compared to $p_0^{(0)}(t)$, the rates of *Ips* spp. colonization $p_1^{(0)}(t)$ are much higher and leveled off after 2–3 years, which support the theory that turpentine beetles pre-dispose the trees to subsequent colonization and thus kill by *Ips* spp.

Figure 6: Central 95% prediction intervals and medians (indicated by bars) for the rate of *Ips* spp. colonization over time $t = 0, \dots, 5$ among those trees that were alive at $t = -1$ and (a) were not colonized by turpentine beetles ($x_{i,0} = 0$) or (b) were colonized by turpentine beetles ($x_{i,0} > 0$). The corresponding observed rate of *Ips* spp. colonization are indicated by crosses. Note the different scales on the y -axes.



5.3 Checking further aspects of the model

To check whether the model captures the relation between turpentine beetle colonization and *Ips* spp. colonization and between colonization of *Ips* spp. and tree mortality, we consider

$$r_{x,u}^{(s)} = \sum_{t=1}^5 \sum_i (x_{t,i}^{(s)} - x_{t-1,i}^{(s)}) u_{t,i}^{(s)}, \quad r_{u,z}^{(s)} = \sum_{t=1}^5 \sum_i u_{t,i}^{(s)} z_{t,i}^{(s)}, \quad s = 0, \dots, S.$$

Here $r_{x,u}^{(0)}$ summarizes the observed relation between new colonization of turpentine beetles and new colonization of *Ips* spp. in the same year and at the same site, and $r_{u,z}^{(0)}$ summarizes the observed occurrences of *Ips* spp. colonization that is involved

in mortality of trees. Furthermore, for spatial dependence structure, we consider

$$\begin{aligned} v_{x,x}^{(s)}(\delta) &= \sum_{i,j:d(i,j) \in N(\delta)} \mathbf{1}[x_{5,i}^{(s)} > 0, x_{5,j}^{(s)} > 0], \quad s = 0, \dots, S, \quad \delta > 0, \\ v_{y,y}^{(s)}(\delta) &= \sum_{i,j:d(i,j) \in N(\delta)} \mathbf{1}[y_{5,i}^{(s)} > 0, y_{5,j}^{(s)} > 0], \quad s = 0, \dots, S, \quad \delta > 0, \\ v_{z,z}^{(s)}(\delta) &= \sum_{i,j:d(i,j) \in N(\delta)} \mathbf{1}[z_{5,i}^{(s)} = 1, z_{5,j}^{(s)} = 1], \quad s = 0, \dots, S, \quad \delta > 0, \end{aligned}$$

where $d(i, j)$ denotes the Euclidean distance between sites i and j , and $N(\delta) = (\delta - 1, \delta]$ is a half-open interval. That is, $v_{x,x}^{(0)}(\delta)$ ($v_{y,y}^{(0)}(\delta)$, $v_{z,z}^{(0)}(\delta)$) captures the observed spatial relation between turpentine beetle colonization (*Ips* spp. colonization, tree mortality) at two sites that are at least $\delta - 1$ and at most δ apart in distance. Here we focus on cumulative effect of all three variables for simplicity. Finally, for temporal dependence structure, we consider

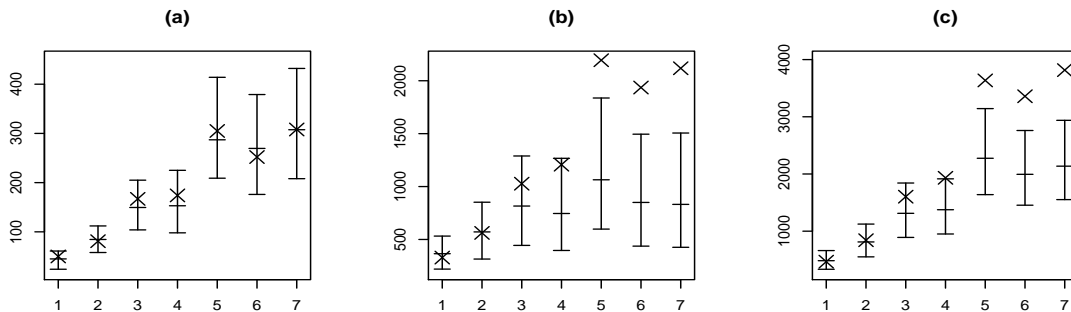
$$\begin{aligned} w_x^{(s)}(t) &= \frac{1}{N} \sum_{i=1}^N \mathbf{1}[x_{t,i}^{(s)} = 0], \\ w_y^{(s)}(t) &= \frac{1}{N} \sum_{i=1}^N \mathbf{1}[y_{t,i}^{(s)} = 0], \\ w_z^{(s)}(t) &= \frac{1}{N} \sum_{i=1}^N \mathbf{1}[z_{t,i}^{(s)} = 0], \end{aligned}$$

where $s = 0, \dots, S$, $t = 0, \dots, 5$ for $w_x(t)$ and $w_y(t)$, while $t = -1, \dots, 5$ for $w_z(t)$, and $N = 2715$. That is, $w_x^{(0)}(t)$ ($w_y^{(0)}(t)$, $w_z^{(0)}(t)$) is the observed proportion of trees that are not colonized by turpentine beetles (that are not colonized by *Ips* spp., that are alive) by time t .

Figures 7 and 8 are similar to Figure 5 but concern the statistics above except $r_{x,u}^{(s)}$ and $r_{u,z}^{(s)}$, where the 2.5%, 50%, 97.5% percentiles are 14.0, 28.0, 149.0 for $r_{x,u}^{(s)}$, and 225.0, 314.5, 409.0 for $r_{u,z}^{(s)}$. Thus the observed values $r_{x,u}^{(0)} = 58$ and $r_{u,z}^{(0)} = 269$ fall well within the central 95% prediction intervals. Our model also adequately captures the spatial dependence for turpentine beetle colonization at all lag distances (see $v_{x,x}^{(s)}(\delta)$ in Figure 7). For *Ips* spp. colonization and tree condition (see $v_{y,y}^{(s)}(\delta)$ and $v_{z,z}^{(s)}(\delta)$ in Figure 7), the spatial dependence is well captured by the model when the lag distances are small. The observed values tend to be larger than what the model predicts, which may be a result of the large cluster of trees that were colonized by *Ips* spp. and/or were dead in the southeastern part of the plantation. Our model furthermore adequately captures the temporal dependence

for *Ips* spp. colonization and tree condition at all time points (see $w_y^{(s)}(t)$ and $w_z^{(s)}(t)$ in Figure 8). But for turpentine beetle colonization (see $w_x^{(s)}(t)$ in Figure 8), the observed values tend to be slightly larger than what the model predicts.

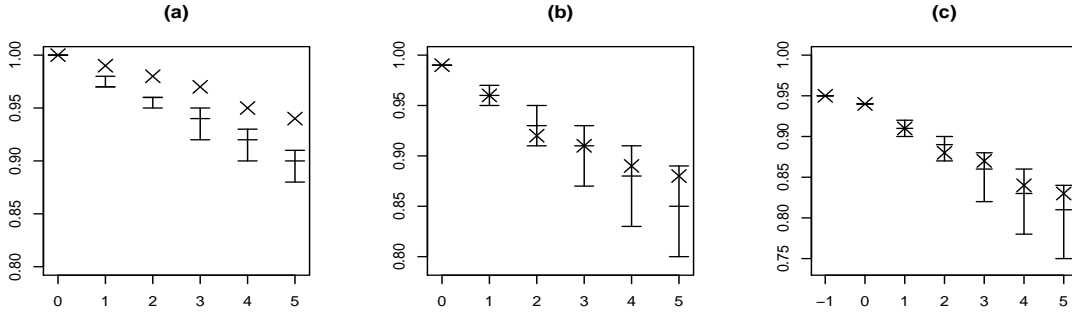
Figure 7: Central 95% prediction intervals and medians (indicated by bars) for (a) $v_{x,x}^{(s)}(\delta)$, (b) $v_{y,y}^{(s)}(\delta)$, and (c) $v_{z,z}^{(s)}(\delta)$. The corresponding observed values are indicated by crosses. Note the different scales on the y -axes.



6 Concluding remarks

In this article, we have examined the effect of two bark beetle groups on the mortality of red pine trees in a Wisconsin plantation. We have constructed spatial-temporal statistical models to quantify the relations among turpentine beetle colonization, *Ips* spp. colonization, and mortality of red pine trees, while accounting for correlation across space and over time. For statistical inference, we have adopted a Bayesian hierarchical model and devised MCMC algorithms for obtaining the posterior distributions of model parameters. Based on the results in Sections 5.2–5.3, our impression is that the spatial-temporal model in Section 3 has adequately captured the relations among the three variables, turpentine beetle colonization, *Ips* spp. colonization, and tree condition. Moreover, our model has often though not always captured adequately the spatial and temporal structure. The data analysis in Section 5 suggests that turpentine beetle colonization is associated with higher likelihood of *Ips* spp. colonization and *Ips* spp. colonization is associated with higher likelihood of red pine tree mortality, whereas there is no direct association between turpentine beetle colonization and red pine tree mortality. There is strong evidence that turpentine beetle colonization does not kill a red pine tree directly, but rather predisposes the tree to subsequent colonization by *Ips* spp.

Figure 8: Central 95% prediction intervals and medians (indicated by bars) for (a) $w_x^{(s)}(t)$, (b) $w_y^{(s)}(t)$, and (c) $w_z^{(s)}(t)$. The corresponding observed values are indicated by crosses. Note the different scales on the y -axes.



The evidence is also strong that *Ips* spp. are the ultimate mortality agents of red pine trees. The modeling approach here is of general utility to systems in which interactions among several species affect overall dynamics, but likewise generate spatial-temporal patterns that can complicate dissection of underlying processes. Such systems are quite likely common in forest ecosystems. Employment of this approach can help managers predict insect and pathogen dynamics as well as direct preventative and remedial measures against inciting rather than merely ultimate agents affecting forest health.

Appendix A

From a practical viewpoint, we would expect our MCMC runs to diverge if an improper posterior distribution had been specified. From a theoretical viewpoint, since the three likelihood functions in (15) are log concave, propriety of the posteriors with uniform improper priors is equivalent to the existence of the maximum likelihood estimate (MLE) based on $L^{(1)}(\theta)$, $L^{(2)}(\psi)$, and $L^{(3)}(\varphi)$, respectively. This can be established as sketched below.

The likelihood functions $L^{(1)}(\theta)$, $L^{(2)}(\psi)$, $L^{(3)}(\varphi)$ in (7), (11), (14) are products of log concave functions $L_t^{(1)}(\theta)$, $L_t^{(2)}(\psi)$, $L_t^{(3)}(\varphi)$, respectively. Therefore, to verify the existence of the MLE based on $L^{(1)}(\theta)$, $L^{(2)}(\psi)$, $L^{(3)}(\varphi)$, it suffices for each $t = 1, \dots, 5$ to verify the existence of the MLE based on $L_t^{(1)}(\theta)$, $L_t^{(2)}(\psi)$, $L_t^{(3)}(\varphi)$, respectively. This can easily be checked in the cases of the Poisson regression $L_t^{(1)}(\theta)$ based on the data x_t and the logistic regression $L^{(3)}(\varphi)$ based on the data

z_t , either by theoretical results (Barndorff-Nielsen, 1978; Jacobsen, 1989) or using software for generalized linear models. Moreover, by (11), $L_t^{(2)}(\psi)$ is of regular exponential family form with canonical statistic

$$s_t^{(2)}(u_t) = \sum_{i: y_{t-1,i}=z_{t-1,i}=0} \left(u_{t,i}, x_{t,i}u_{t,i}, \sum_{j \in N_i^y} u_{t-1,j}u_{t,i}, \sum_{j: j \in N_i^y} u_{t,i}u_{t,j} \right).$$

Consequently, by a well-known result from exponential family theory (Barndorff-Nielsen, 1978), the MLE of ψ based on the data u_t exists if $s_t^{(2)}(u_t)$ belongs to the interior of the convex hull of its support. This condition seems less straightforward to check, so alternatively, MCMC methods for finding the MLE may be applied (Geyer and Thompson, 1992).

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