



Quantifying spatial and temporal variability of spatially correlated disturbances

David E. Hiebeler^{a,*}, Isaac J. Michaud^{a,b}

^a Department of Mathematics and Statistics, University of Maine, Orono, ME 04469, United States

^b Department of Mathematical Sciences, University of New England, Biddeford, ME 04005, United States

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ABSTRACT

We propose three metrics to quantify the spatial and temporal structure of events within spatial dynamical systems. Although the original intention was to develop metrics to separately quantify spatial and temporal variability or clustering, our ultimate conclusion is that it is impossible to completely separate space and time. The spatial structure observed within a system depends on the temporal scale over which the measurements were taken, and the temporal structure observed depends on the spatial scale of measurements. We explore two variations of the basic contact process lattice population model where, instead of individual sites becoming empty independently, larger-scale disturbance events simultaneously affect several sites; these sites may either be arranged within a contiguous block, or sampled from within a larger region. We adjust the rate of such disturbance events in such a way that the per-site disturbance rate is held fixed. Changing the spatial scale of disturbances while controlling the per-site rate induces changes in the temporal structure of disturbances as well (depending on the spatial scale at which it is measured), because the larger-scale disturbances occur less frequently. Analytical results are obtained for our particular model using the hypergeometric distribution, but our spatiotemporal metrics can also be applied numerically to observations of events in simulations or field data to quantify the level of spatial and temporal variation in spatially structured systems. We find in our model that measurements of disturbances at intermediate spatial scales are most useful at indicating the success of the population; measurements at either the micro- (single sites) or macro- (entire landscape) scales miss fundamental features of the system. Although the two versions of our model go extinct for widely different scales of disturbances, our metrics have very similar critical values for population persistence among the two models.

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1. Introduction

The spatial distribution of individuals plays a key role in determining the success of populations, as do the spatial distribution and temporal variability of various resources and other external factors influencing the individuals. For example, the spatial arrangement and temporal variability of suitable habitat containing necessary resources can impact population dynamics, depending on the dispersal strategy of the species of interest (DeWoody et al., 2005; Haugaasen and Peres, 2007; Hiebeler, 2000, 2004, 2007; Johst et al., 2002; Keymer et al., 2000; Lavorel et al., 1994, 1995; Lewontin and Cohen, 1969; Xu et al., 2006). The spatial scale of disturbance events has also been shown to affect population dynamics (Caswell and Etter, 1993; Hiebeler, 2005; Hiebeler and Morin, 2007; Johst and Drechsler, 2003; Kallimanis et al., 2006; Moloney and Levin, 1996) and biodiversity (Banitz et al., 2008).

Large-scale spatial disturbances may be part of an immediate event due to a mechanism such as gap formation in a forest canopy where a single event produces a large gap, or part of a sequence of events occurring over a relatively rapid timescale, such as the formation of a small gap which increases the rate of treefalls nearby which in turn then expand the gap (Kubo et al., 1996; Manrubia and Solé, 1997; Schlicht and Iwasa, 2004). Spatial or temporal environmental variation, or a combination of the two, can also influence the outcome of competitive interactions between multiple species (Chesson, 1985, 1990), while the spatial scales of mixing or other features of a population may affect dynamics, and the resulting dynamics observed depend on the scale at which the population is measured (Chesson, 1991, 1996).

A previous study (Hiebeler, 2005) showed specifically that for a locally dispersing lattice population model with spatially correlated disturbances, i.e. blocks of contiguous sites being simultaneously disturbed, increasing the spatial scale of the disturbances (in such a way that the overall per-site disturbance rate is held constant) reduces the equilibrium density of the population. Although the model was intended to explore the effects of varying purely spatial characteristics of disturbances in the model by keeping the rate of

* Corresponding author. Tel.: +1 207 581 3924.

E-mail address: hiebeler@math.umaine.edu (D.E. Hiebeler).

URL: <http://www.math.umaine.edu/~hiebler> (D.E. Hiebeler).

disturbances fixed, in fact the temporal *variability* of disturbances was intrinsically linked to their spatial scale.

As an example of a system with large-scale features such as those mentioned above, spatio-temporal dynamics of disturbances have been identified as an important feature of modeling the impact of commercial fishing on non-target benthic species (Pascual and Levin, 1999; Thrush and Dayton, 2002). Through the use of trawling, large, contiguous areas of the ocean floor can be disturbed nearly simultaneously with respect to many benthic species life cycle, fragmenting the local environment and altering its suitability for up to 18 months (Tuck et al., 1998). Through the use of fishing restrictions it has been observed that fishing pressure will be transferred from traditional fishing grounds to areas which were previously unfished (Dinmore et al., 2003). Such controls demonstrate a top-down approach to manipulating the temporal and spatial variability of disturbances in order to protect fisheries can cause unforeseen consequences to species which take a long time to regenerate (Duplisea et al., 2002). For species that are less mobile, recovery can be a slow process because areas can only recover through the generation of new members instead of being repopulated by immigration from neighboring areas (Jennings et al., 2001).

Here we develop models and metrics to further investigate the spatial and temporal aspects of variability. By developing quantitative metrics to describe these two facets of variability, we show how the two features cannot be studied in isolation; when studying temporal variability, a spatial scale must be chosen, and when studying spatial variability, a temporal scale must be specified. We derive analytical results for our metrics as applied to the model with correlated disturbances. While it may be possible to similarly derive mathematical results for other population models, the metrics may also be applied more widely to simulation models or empirical data even where analytical results are not feasible.

2. The model and metrics

The continuous-time basic contact process (Harris, 1974) on a square lattice is a patch-occupancy process on an $L \times L$ lattice. Each occupied site reproduces according to a Poisson process at rate ϕ . When a site reproduces, it drops its offspring onto one of the four neighboring sites chosen at random. If the target site is empty, it is colonized (i.e. becomes occupied); if the target site is already occupied, the offspring is wasted. Each site is disturbed at rate μ ; if a disturbed site is occupied, it becomes empty. Disturbance has no long-term effects on a site, so a disturbed site is immediately able to be recolonized by neighboring occupied sites. Note that the model is often specified by instead saying that each occupied site dies at rate μ , which is equivalent. Because of the properties of Poisson processes, sites are disturbed at a total rate of $L^2\mu$ in the entire lattice; the location of a given disturbance event is chosen at random from among all sites in the lattice. Wraparound boundary conditions were used with all simulations in our study.

A modified version of the contact process previously used to study the effects of correlated disturbances (Hiebeler, 2005) is the starting point for the present analysis. That model, subsequently referred to here as the “solid-blocks” model, still takes place on an $L \times L$ lattice, with each site reproducing at rate ϕ and dropping offspring onto a randomly chosen adjacent neighbor. However, rather than disturbances occurring at rate $L^2\mu$ and affecting a single randomly chosen site in the lattice as in the basic contact process, disturbance events now occur at rate $L^2\mu/b^2$; each disturbance event affects a $b \times b$ block of contiguous sites (with wraparound at the lattice edges), whose upper-left corner is chosen at random from the lattice. (We say the disturbance event “targets” that site.) Every occupied site within a disturbance block simultaneously becomes empty. This still causes each individual site to be

disturbed at rate μ according to a Poisson process, as in the basic contact process. Defining a “site event” as an event at a particular site, a reproduction event consists of a single site event, while a disturbance event consists of b^2 simultaneous disturbance site events.

An additional variation of the model, referred to here as the “outer-blocks” model, was used to further explore the effects of spatial and temporal variability in disturbances on a locally dispersing population. In this version, disturbance events still occur at rate $L^2\mu/b^2$. However, each disturbance event affects b^2 sites chosen at random (without replacement) from within a larger $c \times c$ block of contiguous sites. Here, b is referred to as the “inner” block size and c as the “outer” block size, although note that the b^2 sites simultaneously disturbed are not actually arranged in a contiguous block (unless $c = b$, when this model degenerates to the solid-blocks model).

Simulations of these models were implemented as discrete-event simulations, where the times between consecutive events were chosen from exponential probability distributions with appropriate means. Simulations were implemented in the C programming language with the OpenMPI platform (Gabriel et al., 2004) for efficiency. A set of L^2 consecutive site events was defined as a Monte Carlo time step, so that each site on average experienced a single event per time step. The population density (proportion of sites occupied) was recorded after each time step. Simulations were run for a maximum of 5000 time steps. For efficiency, automated tests based on those used by Caswell and Etter (1993) were used to determine if the population density had reached equilibrium so that a simulation could be terminated early. After 200 time steps had elapsed, a linear regression of the population density within a moving window of the previous 100 time steps was performed. When the slope of this fitted line had magnitude less than 0.001, the difference between the minimum and maximum population densities within the moving window was less than 0.1, and at least 30 fitted lines with positive slopes and 30 with negative slopes had been observed, the system was considered to have reached equilibrium. Because the population density continues to fluctuate stochastically at equilibrium, once the simulation had reached 5000 time steps or the above tests had been passed, the model was run for another 50 time steps, and the population density averaged over those steps was recorded as the final equilibrium population density for that simulation.

We develop metrics to measure the temporal and spatial variability or clustering of disturbances in the model. Although the goal was to separately quantify the temporal and spatial variability of disturbances, it’s not possible to consider these two issues separately. To quantify temporal variability, we construct a metric based on the distribution of times between observed events. However, it is also necessary to indicate where these observations are taken, or more precisely, a spatial scale m of the observed region. Let Ψ_i be the time of the i th disturbance site event observed within a fixed $m \times m$ block of sites within the lattice, referred to as the “measurement region.” Define $T_i := \Psi_{i+1} - \Psi_i$ be the inter-event times between site events; note that some of the T_i will be zero, when multiple sites are disturbed at the same time within the measurement region. Letting $E[T]$ and σ_T be the mean and standard deviation of the distribution of T , the coefficient of variation $cv[T] = \sigma_T/E[T]$ is our measure of temporal variability. We used this, rather than simply the variance or standard deviation of T , because it is not affected by rescaling the units of time in the model or by changing the per-site disturbance rate μ .

In Hiebeler (2005), spatial clustering of disturbances was quantified via the value β , defined as the probability that a randomly chosen neighbor of a site being disturbed is also being simultaneously disturbed. In terms of the disturbance block size, $\beta = 1 - 1/b$. The value β was convenient to include in mathematical

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