



The University of Chicago

Understanding Shifts in Wildfire Regimes as Emergent Threshold Phenomena. Author(s): Richard D. Zinck, Mercedes Pascual, and Volker Grimm Source: *The American Naturalist*, Vol. 178, No. 6 (December 2011), pp. E149-E161 Published by: <u>The University of Chicago Press</u> for <u>The American Society of Naturalists</u> Stable URL: <u>http://www.jstor.org/stable/10.1086/662675</u>

Accessed: 07/06/2013 18:01

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

http://www.jstor.org

E-Article

Understanding Shifts in Wildfire Regimes as Emergent Threshold Phenomena

Richard D. Zinck,^{1,2,*} Mercedes Pascual,¹ and Volker Grimm²

1. Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109; and Howard Hughes Medical Institute, Chevy Chase, Maryland 20815; 2. Department of Ecological Modelling, Helmholtz Centre for Environmental Research–UFZ, Permoserstrasse 15, D-04318 Leipzig, Germany

Submitted November 5, 2010; Accepted August 2, 2011; Electronically published October 28, 2011

ABSTRACT: Ecosystems driven by wildfire regimes are characterized by fire size distributions resembling power laws. Existing models produce power laws, but their predicted exponents are too high and fail to capture the exponent's variation with geographic region. Here we present a minimal model of fire dynamics that describes fire spread as a stochastic birth-death process, analogous to stochastic population growth or disease spread and incorporating memory effects from previous fires. The model reproduces multiple regional patterns in fire regimes and allows us to classify different regions in terms of their proximity to a critical threshold. Transitions across this critical threshold imply abrupt and pronounced increases in average fire size. The model predicts that large regions in Canada are currently close to this transition and might be driven beyond the threshold in the future. We illustrate this point by analyzing the time series for large fires (>199 ha) from the Canadian Boreal Plains, found to have shifted from a subcritical regime to a critical regime in the recent past. By contrast to its predecessor, the model also suggests that a critical transition, and not self-organized criticality, underlies forest fire dynamics, with implications for other ecological systems exhibiting power-law-like patterns, in particular for their sensitivity to environmental change and control efforts.

Keywords: forest fire model, wildfire, threshold phenomena, regime shift, climate change, criticality, self-organized criticality, power-law scalings.

Introduction

Wildfires act as key drivers in many terrestrial ecosystems. Changes in wildfire regimes can have significant impacts from local to global scales on patterns of species abundance and succession, as well as on ecosystem services and, via the atmosphere and biogeochemical cycles, on climate itself (Turner and Romme 1994; Whelan 1995; Amiro et al. 2001). It has therefore been of interest to understand the mechanisms controlling wildfire regimes and to predict

* Corresponding author; e-mail: richard@zinck.de.

when and how they will change (Flannigan et al. 2009; Krawchuk et al. 2009).

From a different perspective, wildfire dynamics have been at the heart of the study of criticality and selforganization in nature (Malamud et al. 1998; Pascual et al. 2002; Pascual and Guichard 2005). They have been used as a central metaphor for numerous phenomena such as earthquakes, avalanches, and communicable diseases (Rhodes and Anderson 1996; Turcotte 1999). A characteristic pattern in all these systems is a heavy-tailed, powerlaw-like distribution of event sizes, such as fires and epidemics. These distributions imply the intermittent occurrence of extreme events, such as very large fires, in a sea of events of all sizes, in proportions characterized by the exponent of the approximate power law.

Spanning a vast range of climatic and biotic conditions, fire size distributions resembling power laws have been documented from all over the world, for example, from Australia, China, Italy, and across the United States (Ratz 1996; Malamud et al. 1998, 2005; Ricotta et al. 1999, 2001; Song et al. 2001). Importantly, however, not all fire size distributions are the same; they are all heavy tailed but of different slope over a given range of sizes that can also vary. Although the varying slope of fire size distributions has been highlighted and used to characterize ecoregions across the United States (Malamud et al. 2005), this key pattern remains largely unexplained. The observed gradient in slope (characterized, e.g., by power-law exponents, ranging from about -1.9 to -1.3) corresponds to an increased frequency of large fires relative to smaller ones, from east to west across the United States.

Models addressing wildfire regimes cover a wide range of model types of different complexity (Keane et al. 2004). At one extreme, the best-known minimal model for forest fires (the Drossel-Schwabl model, hereafter DSM; Henley 1989; Drossel and Schwabl 1992) is an extension of the original fire model proposed in the context of self-organized criticality (hereafter SOC; Bak et al. 1988). It has

Am. Nat. 2011. Vol. 178, pp. E149–E161. © 2011 by The University of Chicago. 0003-0147/2011/17806-52597\$15.00. All rights reserved. DOI: 10.1086/662675

been investigated mostly in statistical physics. Large-scale patterns emerge as the system self-organizes from simple rules for the local propagation of fire, the regrowth of vegetation, and the ignition of new fires by sparking events. Self-organization means here that regardless of parameters and initial conditions, the system takes itself to the same state, always generating the same macroscopic patterns in fire size distributions and the average (mean) density of grid cells susceptible to fire (provided the temporal scales of fire propagation and vegetation regrowth are sufficiently separated; Drossel and Schwabl 1992). This appealing property is also the reason why this simple model fails to capture the variation in slope observed in fire size distributions: its robustness implies that wildfire systems are not strongly affected by changes in parameters and, therefore, by differences in the biotic and abiotic environment resulting from environmental change or human control efforts. Despite this clear limitation, including the associated tendency to produce too many large fires, SOC models have demonstrated that a heavy-tailed distribution in fire sizes can, in principle, be explained by a set of simple hypotheses.

At the opposite extreme, very detailed, realistic models from landscape ecology can produce the observed spectrum in the steepness of the fire size distribution (Moritz et al. 2005). Although sophisticated techniques are available, parameters and key mechanisms may be difficult to identify. Hence, we present here an approach of intermediate complexity that maintains the tractability of the minimal DSM but still incorporates the effects of regional characteristics on wildfire regimes in a simple way.

One approach to handle this problem is pattern-oriented modeling (Grimm et al. 2005), in which several patterns in a system are identified and used to select between competing hypotheses. A recent pattern-oriented analysis of more generic, tractable wildfire models of intermediate complexity has shown that they are essentially equivalent to the DSM, generating size distributions that resemble power laws but sharing the inability to produce the variation seen in the exponents of fire size distributions (Zinck and Grimm 2009). Despite this common limitation, these models do produce realistic fire shapes (Zinck and Grimm 2008) and the observed hump-shaped relationship between average annual area burned and landscape-level diversity of succession stages (Zinck and Grimm 2009; Zinck et al. 2010).

The common property shared by these generic wildfire models is a spatial memory of previous fires (Peterson 2002; Zinck and Grimm 2009), such that the flammability of a local patch depends mostly on the time since the last consumption of its fuel and, hence, on the biomass regrowth since the last fire. Thus, these models represent mostly fuel-limited systems. Their inability to produce the whole spectrum of fire size distributions is an indication that not all wildfire systems are dominated by fuel limitation and that the influence of other regional drivers such as the characteristic vegetation, topography, and weather patterns of fire spread is not negligible. Here, we demonstrate how regional differences in these drivers and a spatial memory may account for the variation observed in macroscopic patterns such as fire size distribution.

One advantage of minimal models, due to their level of abstraction, is that they may apply across different systems, and this leads us to the development of the model we present here. There have been some exploratory applications in both directions, from epidemiology to landscape ecology (as, e.g., in O'Neil et al. 1992), in which susceptible-infected-recovered-type models were run on heterogeneous landscapes, and from statistical physics to epidemiology via the metaphor of fire in the context of SOC (Rhodes and Anderson 1996; Rhodes et al. 1997, 1998; Pascual and Guichard 2005).

In the DSM application to epidemics (Rhodes and Anderson 1996), it was found that their observed size distributions are also heavy tailed and that the distributions for different diseases, such as measles and rubella, can exhibit a varying degree of steepness unexplained by the model. One possible solution, suggested by Rhodes et al. (1997), was to change the dimensionality of the underlying transmission network, as the network on which a disease spreads might not be limited to two dimensions. Although this modification does not transfer to wildfire dynamics, a central concept of epidemiology, the idea of a basic reproductive ratio, R_0 , potentially does. The basic reproductive ratio is the average number of infected individuals produced by one individual during its lifetime as infected and therefore differs between diseases. Here, we incorporate this concept into a wildfire model.

We present here a model in which fire spread is represented as a stochastic propagation process-a birthdeath process of burning grid cells-providing a phenomenological representation of the many regional factors, such as weather, topography, and vegetation, that influence its reproductive success. We show that this model, and therefore the two main processes of a stochastic fire spread and an ecological memory of previous fires in the fuel mosaic, can account for the complete variation of exponents observed across the ecoregions of Canada. We demonstrate that this seemingly small modification of existing models leads to fundamentally different predictions from SOC on the sensitivity of wildfire regimes to changes in external drivers. Specifically, this new model suggests the existence of a drastic transition rather than a gradual one from moderately to strongly fire-driven ecosystems. By contrast to SOC, the model implies that ecoregions that are currently close to this transition will be sensitive to



Figure 1: Graphical representation of the control flow of the model. Representation of ignition and regrowth are identical to the Drossel-Schwabl model (with separate timescales). Crucially, the way in which fires spread (burning) is probabilistic; that is, fire does not automatically spread to all susceptible neighbors, as in the classic self-organized criticality fire model. Rather, we use a stochastic birth-death process to model the reproductive dynamics of fire. Its intrinsic, regional spread success is $\sigma = \lambda/\mu$, which corresponds to the basic reproductive ratio of epidemics.

changes in the environment and human interventions affecting fire propagation, such as are expected with climate change. Power-law-like patterns emerge at a specific critical point or threshold and degenerate in a characteristic way as one moves away from it. We show how the qualitative understanding gained from our model can be used to classify wildfire regimes as subcritical, critical, or supercritical and to identify regions that are close to this critical point. We identify such regions for Canada and end with a discussion of other critical phenomena in ecology, especially the epidemic dynamics of infectious diseases.

The Model

Our model is based on a lattice of L^2 sites. The processes of sparking (generating ignition events), burning (stochastic spread of fire among neighboring cells), and spatial reappearance of fuel are marked separately in the algorithmic flowchart (fig. 1). We preserve the treatment of fuel consumption and regrowth of SOC-type models (DSM; Drossel and Schwabl 1992), in which a timedependent flammability emerges at the site level (Zinck and Grimm 2009), but change the way in which fires spread (fig. 1, burning). Fuel reappearance is modeled with a spatial point process. Using a point process, we can relate the expected average area burned and average fire size directly to the parameters of regrowth and sparking frequency by following the analysis for the DSM.

We call p_s the fraction of cells on the lattice that are in state *s* (*s* can be fuel, abbreviated as "t" for "tree" or "e" for "empty"). Fuel reappears spontaneously in empty cells at rate *p*, and ignitions occur spontaneously at the cell level with a probability *f*. A cell can ignite only if it carries fuel; hence *f* corresponds to the rate of sparking events rather than ignitions. Further, we assume that timescales are separated such that $f \ll p$ and $p \ll 1$, which is more biologically plausible, as it guarantees that fuel does not reappear instantly and is not ignited by a spark as soon as it appears. This condition has been identified in the physics literature as necessary to produce heavy-tailed fire size distributions in SOC fire models (Drossel and Schwabl 1992; Grassberger 1993).

In classical (SOC) fire models, fire spread is determined solely by local fuel availability and is fully deterministic (Drossel and Schwabl 1992). If a neighboring cell of a burning cell carries fuel, the fire will spread to it. Our model emphasizes instead the stochastic nature of fire spread, since a burning cell does not necessarily infect its neighbor, even if this neighbor is carrying fuel. We can use the metaphor of disease spread or that of individual reproduction and consider that a burning cell gives birth or reproduces (see table 1 for a comparison). Furthermore, the acquisition of immunity or individual death would correspond to a severe local reduction in combustible material (fuel) necessary to sustain a fire of the same type (crown or ground fire).

Burned area is defined here as the sum of all the areas that actively burned at some time during the fire but are no longer infectious and cannot continue propagating the fire in the current time step. If we consider snapshots of a fire in progress, only a small fraction of the affected area will be actively burning, and this flaming front will occur mostly at the perimeter of the fire. We make this actively burning (and hence potentially infectious or regenerative) area the main variable of our fire spread process. This differs from a previous analysis of fire spread as a stochastic process by Reed and McKelvey (2002), in which the dynamics of the entire fire-affected area (composed of both the actively burning area and the devastated area left behind) is analyzed using a diameter-dependent hazard rate function. A focus on the infective area allows us to treat the development of a large fire as the outcome of a stochastically growing and shrinking population of actively burning areas that leave dead, or burned, areas behind.

As time progresses, the actively burning area N(t) can shrink, grow, or remain the same in size; N(t) refers only to the area that is burning at time *t*. The fate of the cells comprising N(t) depends on many small-scale factors, such as local vegetation and microclimate, fuel humidity, topographical aspects, and current wind direction and speed (Whelan 1995). Extensive theoretical and empirical studies have focused on understanding the role of these factors in combustion spread (Rothermel 1972; Wagner 1977; Turner and Romme 1994). Here, we represent the effects of such variation phenomenologically by introducing transition rates for the probability of the fire front to grow, shrink, or remain the same, given the vegetation, topography, and average weather conditions in the burning season of an ecoregion. These dynamics can formally be mapped to a stochastic birth and death process with perarea rates (as opposed to per capita for populations) of growing (λ), shrinking (μ), or remaining the same (1 – ($\lambda + \mu$)).

A summary of the algorithm is as follows: A fire starts if a spark hits a cell with fuel. All burning cells are kept in a queue. A random number is drawn to decide whether a burning cell extinguishes (with probability $\mu/(\lambda + \mu)$) or whether a direct neighbor of one of the burning cells starts to burn (with probability $\lambda/(\lambda + \mu)$), provided that it has suitable fuel. We call the controlling parameter $\sigma = \lambda/\mu$ the reproductive ratio of fire, or fire spread success. We go through neighbors in the order of the burning cells in the queue. A fire stops once the last burning cell fails to ignite a neighbor. If run long enough (about 10,000 fires), the model reaches a quasi-stationary state in which the density of fuel-carrying cells, p_{t} , fluctuates around a welldefined temporal mean. In the equilibrium state, the amount of fuel expected to appear between two sparks is $(p/f)(1 - \langle p_t \rangle)$. Because sparking events are rare compared with regrowth, we simulate the model by randomly choosing $\theta = p/f$ sites (regardless of whether they are empty or occupied) between sparks and changing their state to fuel (Grassberger 1993). This speeds up the model simulations considerably.

Fire Data

The fire size data used in figure 2 are available from the Canadian Large Fire Database (CLFD; Canadian Forest Service 1997). The CLFD is a compilation of fires larger than 199 ha that have occurred in Canada from 1959 to 1999. We sorted the data by ecozones, which are characterized by similar conditions in geomorphology, soils,

Table 1: Comparison of fire, population, and disease dynamics

System	Cell state	Event	Control parameter		
Population	Alive, dead	Birth, death	Intrinsic growth rate		
Disease	Infectious, immune, dead	Infection, recovery, death	Reproductive ratio R_0		
Fire	Burning, burned, no fuel	Ignition, extinction	Fire spread success σ		

Note: Burning area is part of the population of a fire that ultimately becomes extinct. The burned area is not part of the fire population; rather, it consists of dead ancestors.



Figure 2: Fire size distributions of 12 ecozones from the Canadian Large Fire Database (red circles = fires larger than 199 ha, 1959–1999). We use log equidistant bins and plot on double-logarithmic scales. Each ecozone (location indicated by map) has its own characteristics in topography, weather, and vegetation that influence the fire size distribution and leave a signature in its shape and steepness. The observed variation in the slope when the distribution is approximated by a power law is successfully produced by our model (blue line = R^2 fit is better than 0.98 for all ecoregions), in which fires have a characteristic spread success σ that varies across ecozones (these are ordered in the plots according to the steepness of their corresponding slope); σ is the probabilistic growth rate of actively burning (and hence infectious) areas, which constitutes the fire front. The columns correspond to subcritical (*left*, $\sigma < 1$), close to critical (*center*, $\sigma \approx 1$), and supercritical (*right*, $\sigma > 1$) regimes.

vegetation, and climate. The fire size distribution was visualized in double-logarithmic plots. We used log equidistant bins; the number of fires per bin was normalized by bin size and number of fires in the ecozone. The variability in the data samples is indicated by 200 bootstrap data sets, of which the upper and lower 2.5% were removed to obtain a 95% confidence interval. A bootstrap data set contains the same number of fires as the original data set. Each fire in a bootstrap data set was sampled at random from the original data set.

We also analyze two epidemic time series in the context of the discussion on the potential relevance of the model to other fields and in the context of future directions. We consider for this the size distribution of measles epidemics in a small city before and after vaccination was available. The measles data for Bradford (West Yorkshire, UK) were provided by P. Rohani.

Parameter Estimation

Maximum Likelihood Fits from Simulation

The simulations were run on grids of $L^2 = 500 \times 500$ cells. Once the densities reach a stationary state (after approximately 10,000 fires), 3,000 fires were sampled to obtain the frequency-area distribution for each combination of ($\theta = p/f$, $\sigma = \lambda/\mu$), with θ in 100, 150, ..., 1,500. The values for σ were selected such that $\lambda + \mu = 1$ always, from $\lambda = 0.38$ to 0.99 in 0.01 steps (lower values of λ result in distributions that no longer exhibit a fat tail).

To minimize edge effects, we obtained the average density of susceptible cells from 500 snapshots in the 400×400 lattice center. We learned from exploratory fittings that cell sizes of 30–55 ha lead to better fits. These values are larger, as expected, than those in Zinck and Grimm (2008) and Ratz (1996; 4–12 ha) for similar cellular

Table 2:	Parameter	estimates for	12	ecozones	from	the	Canadian	Large	Fire	Databas	e
----------	-----------	---------------	----	----------	------	-----	----------	-------	------	---------	---

Ecozone	Panel in figure 2	$\sigma \pm$ SD (BP)	$\sigma \pm$ SD (MLE)	$-\log(L)$	ha/cell	θ
Pacific Maritime	1	.7172 ± .0318	.72 ± .0350	-776.56	33	800
Montane Cordillera	2	$.8533 \pm .001$	$.89 \pm .0205$	-5,661.45	46	700
Northern region	3	.8889 ± .0266	$.89 \pm .0150$	-719.38	49	500
Atlantic Maritime	4	$.8848 \pm .0240$	$.89 \pm .0268$	-616.26	37	800
Prairie	5	$.8979 \pm .0225$	$.89 \pm .0148$	-1,050.14	46	800
Hudson Plains	6	$.9635 \pm .0056$	$.96 \pm .0068$	-2,764.99	49	700
Boreal Shield	7	$.9691 \pm .0015$	$.96 \pm .0168$	-3,782.60	49	800
Boreal Plains	8	$.9678 \pm .0030$	$1.00 \pm .0070$	-14,947.22	45	500
Taiga Plains	9	NA	$4.26 \pm .1641$	-11,644.46	48	100
Taiga Shield	10	NA	$4.26 \pm .1562$	-16,237.11	48	100
Boreal Cordillera	11	NA	$49 \pm .1200$	-1,911.54	34	100
Taiga Cordillera	12	NA	49 ± .1431	-7,065.53	34	100

Note: Estimates for the control parameter $\sigma = \lambda/\mu$ are obtained analytically from branching process (BP) theory and by maximum likelihood (ML) fits with likelihood *L*. The ML fits include estimates for cell size and the regrowth parameter $\theta = p/f$. Panels in figure 2 are numbered according to this list of ecozones.

automata models, since those studies based their parameter estimation on the analysis of burn scars in the landscape rather than on fire size distributions and considered only one region (Ontario). According to that data set and models similar to the DSM, the cell of a grid should be on the order of 4–12 ha/cell. The algorithm does not depend on cell size; the best-fit size can, however, have implications for interpretation. The birth-death process can be interpreted on a smaller scale, yet the fit to data from the CLFD performs better using larger values. This may be partially an effect of the minimum fire size recorded in this database, 199 ha.

Because of the large parameter space for the search (over p/f, σ : 28 × 61 = 1,708) and the computational effort in obtaining the fire size distribution (given that at least 20,000 fires need to be simulated per parameter configuration, that the search needs to be repeated for every ecozone, and that the best cell size needs to be found for each of these), we created and used a simulation database to avoid repeated calculations.

We estimated σ , along with its range of uncertainty, for the Canadian ecoregions by searching for the value that has the highest likelihood, given the data. To assess this likelihood, we compared the fire size distributions of the model, as stored in our database, with the empirical distribution. The fire size distribution is obtained by binning the data according to size class (log equally spaced). Hence, we use a multinomial distribution to determine the likelihood of the data, given the model at a particular parameterization. We maximized a log multinomial likelihood to estimate the parameters for which the data are most likely and to obtain their uncertainty:

$$\max_{(\sigma; p/f; \text{ha/cell})} \left(-\log\left(L\right) = \sum_{i} n_{i} \log\left(p_{i}\right) \right), \quad (1)$$

where n_i is the number of fires in bin *i* and p_i is the probability of a fire being sorted into bin *i*, given the parameterization of the model. The results are provided in table 2.

Parameter Estimates by Analytical Approximation

Another way of estimating σ , which applies, however, only to subcritical ($\sigma < 1$) regimes, comes from the theory on birth-death processes. A birth-death process refers here to a homogeneous branching process in which the branching ratio, σ , is related to the average fire size $\langle s \rangle$ (or outbreak size, in the case of disease; Jansen et al. 2003), as

$$\sigma = 1 - \frac{1}{\langle s \rangle}.$$
 (2)

The estimates of σ made in this way are listed in table 2, along with the results from the maximum likelihood method. This approximation has been used by Jansen et al. (2003) to estimate the effective reproductive ratio of diseases when vaccination leads to a low success of transmission (technically, when $R_0 < 1$). Here, we normalized the average fire size by the smallest fire size found in the database. Because this formula breaks down for $\sigma \ge 1$, values near or slightly above criticality will be underestimated, resulting in estimates smaller than 1. We use a moving-window approach, in which σ is estimated at each point in time (when a fire occurred), using 600 prior fires, to detect changes of σ over time. We estimate the variation in σ by using the estimation procedure for 15 bootstrap data sets at each point.

Results

Our model reproduces the entire spectrum of slopes apparent in the fire size distributions of the CLFD (fig. 2). This spectrum is representative of the slopes reported in the United States and from other continents, such as Australia, Italy, and China. The parameter values we report for these ecoregions (table 2) were found by maximum likelihood fitting to our model and from branching process theory.

Although small changes in fire spread success σ usually have very little influence on the average area burned and average fire size, they can lead to distinct and abrupt changes at the critical point ($\sigma = 1$; see fig. 3, *lower left*, *lower right*). The probability of finding a cluster of susceptible cells that spans the entire grid drops abruptly at $\sigma = 1$ (fig. 3, *upper left*). If a spanning cluster is found, which happens only rarely, its area is considerably smaller. The average density of susceptible cells on the lattice has a similarly sharp decrease at $\sigma = 1$ (fig. 3, *upper right*). It drops from almost 1 to $p_t \approx 0.4$, a value also characteristic of the DSM, the classic SOC fire model.

For practical applications, the average fire size (fig. 3, *lower left*) and average area burned (fig. 3, *lower right*) are two important quantities. The average fire size, which remains fairly small for $\sigma \leq 1$, jumps upward at $\sigma = 1$, reaching a plateau (cf. fig. 2, prairies [5] and Hudson Plains [6]). The height of this plateau is determined by the parameter $\theta = p/f$, which is proportional to the number of cells that turn susceptible between two successive fires (on average) and differs between ecozones. The average area burned shows an analogous behavior, with a sharp increase at the same critical value of σ . The value of the plateau it reaches is determined by the parameter p controlling the reappearance of fuel at the cell level.

The three ecoregions closest to the critical point ($\sigma = 1$) are the Hudson Plains, the Boreal Shield, and the Boreal



Figure 3: Model showing critical behavior controlled by σ . The probability of finding a spanning cluster (a connected cluster of fuel that reaches from one end of the lattice to the other) and its weight (relative area) drops sharply at $\sigma = 1$ (*upper left*). This is because the average density of fuel on the lattice, p_i , drops abruptly from about 1 to approximately 0.41 (*upper right*), a value also characteristic of the Drossel-Schwabl model (DSM). For large $\sigma \gg 1$, our model effectively behaves like the DSM. The average fuel density is reduced because fires grow larger as σ increases (*lower left*). At $\sigma = 1$, fires can potentially grow to any size and therefore can consume the entire fuel cluster on which they were ignited more frequently, creating a spatially heterogeneous fuel mosaic. The depicted ecoregions are the Pacific Maritime, Boreal Plains, and Taiga Shield (1, 8, and 10, respectively, in fig. 2). Consequently, the average area burned also jumps at this critical value of σ (*lower right*). The respective values of the plateau reached for the average fire size and the average area burned are determined by the area that turns susceptible between fires. Thus, they are controlled by the second parameter in the model, $\theta = p/f$.

E156 The American Naturalist

Plains (fig. 2; table 2). The Boreal Plains lie closest to the critical point. Visual inspection of their time series (fig. 4, *upper left, upper right*) shows an increase in the size of the largest fires after 1978. To quantify this conjecture, also suggested by change in the size distribution (fig. 4, *upper right*) and in the average fire size (pre-1980: 3,278 ha; post-1980: 9,066 ha), we estimated σ by using the analytical estimate (which is suitable for subcritical regimes) for five different sections in the time series, containing 270 fires each. We used 10,000 bootstrap data sets for each of those sections to approximate the variability in this estimate. The results show a strong indication of an increase in fire spread success σ around the year 1980, leading from a subcritical regime to a regime poised at criticality.

This is confirmed by estimates obtained with the maximum likelihood approach, which places the Boreal Plains at the critical transition after 1980. To quantify the statistical significance of this change, we need to assess how likely the observation of such a jump is in time series produced by our model when there is no variation in the underlying σ for both subcritical and critical regimes. In both cases, the observation of such a jump without a change in σ is very low ($p_{(\sigma=0.93)} = 0.068$, $p_{(\sigma=0.96)} = 0.035$, $p_{(\sigma=1)} = 0.0062$). It is therefore very likely that the Boreal Plains have experienced a change from a subcritical regime to the edge of a critical one in recent decades, presumably around 1980.

Figure 5 shows the size distributions of measles outbreaks in Bradford before and after vaccination. For the data collected before vaccination became available (1944–1968), the size distribution is clearly heavy tailed and similar to the distributions seen in supercritical fire regimes. The introduction of vaccination has reduced outbreak sizes (by orders of magnitude) and has led to a steeper distribution (which is no longer heavy tailed).

Discussion

Because of the high degree of abstraction and the commonalities between systems that exhibit transmission or propagation behavior, the forest fire model known as DSM has previously been applied to the dynamics of both wild-



Figure 4: The Boreal Plains have a fire reproduction ratio near criticality $\sigma \approx 1$. Visual inspection of the time series suggests that the fire regime may have intensified over time (*upper left*). This is confirmed by estimates of σ (based on the 600 earlier fires at each point), which increase considerably and take the system from subcritical to closer to critical (around fire 800 or 1980, *lower left*). By splitting the data set at 1980, we obtain size distributions with a higher slope for the later period (2, *upper right*) and whose corresponding average fire size triples from 3,278 (pre-1980, 1) to 9,066 (post-1980, 2) ha. The maximum likelihood estimate of σ for the pre-1980 data is $\sigma = 0.96$ and reaches the critical value of $\sigma = 1$ for the post-1980 data (*lower right*). The likelihood of observing such a jump in estimated σ without an actual change in the parameter is small (with *P* values between .03 and .08, depending on the choice of σ).



Figure 5: Outbreak sizes for communicable diseases in small, isolated communities are known to exhibit heavy-tailed distributions similar to those of fires (Rhodes and Anderson 1996; Rhodes et al. 1998; Cuddington and Beisner 2005). This is illustrated here for measles in Bradford. Not surprisingly, the value of σ estimated for our model indicates that measles spread was supercritical before the introduction of vaccination in 1968. The relevance of forest fire–type models to the epidemic dynamics of infectious diseases, including potentially those in larger cities for the postvaccination era, has been previously proposed; one such city was shown to exhibit a heavy-tailed distribution, with a lower exponent, however, than that predicted by such earlier models (Rhodes et al. 1998). Following work on postvaccination measles in London considered outbreak size distributions based on the stochastic dynamics of birth-death processes (Jansen et al. 2003). Our model is able to account for the change in the slope with vaccination and to consider both types of dynamics, supercritical and subcritical, in a single framework. The introduction of vaccination changes the distribution of epidemic sizes by reducing its tail and decreasing its slope, with the disappearance of the very large epidemics, as illustrated here for Bradford (for years with vaccination levels larger than 70%). Correspondingly, the dynamics switch from supercritical to subcritical (prevaccination, postvaccination, respectively), with a clear change in σ from above 1 to below 1. In wildfire systems, vaccination corresponds to large-scale fuel treatments such as prescribed burning and mechanical fuel reduction.

fires and epidemics. However, the appealing properties of robustness and self-organization in this model are also its weaknesses. They are only partially observed in the specific systems, as reflected in the inability of the model to capture the variation in the slope (and associated shape) of the size distribution of events, whether these are fires or epidemics in the real world.

We presented here an extension of this model that retains its simplicity by subsuming in a phenomenological way several of the many factors that can locally affect the propagation of fire. Future extensions could consider, for example, the role of spotting or seasonality more explicitly. The model incorporates a basic concept from epidemiology, the reproductive ratio of an infectious disease, or R_0 . Thus, fire in our model behaves like a living entity or infectious agent that can reproduce (in area) by spreading into adjacent fuel and also die and fail to propagate, with both processes ruled stochastically by probabilities. We show that the variation in the statistical, macroscale pattern of observed fire size distributions can be explained by differences in the local basic reproductive ratio of fire, given by the ratio of these probabilities. The full variation of exponents in the heavy-tailed distributions results from this birth-death process of fire acting together with the regeneration of the underlying forest landscape, whose extent at any given time reflects the history or memory of previous fires.

By making the seemingly small modification to the DSM and specifically treating the propagation of fire as a stochastic process rather than a deterministic one, we arrive at a fundamentally different view from SOC with regard to the resilience of wildfire ecosystems. Namely, the system does not take itself (self-organize) to a critical state with the same power-law patterns regardless of parameters. The state of the system and its statistical properties depend instead on the value of a parameter (the local reproductive ratio). Power-law-like patterns arise at a critical value of this parameter, at which the system exhibits threshold behavior in a number of important quantities, including the average fire size. Technically, the system exhibits a critical phase transition. This has fundamental implications for the sensitivity of wildfire systems to environmental change or control strategies. Small changes in the parameters underlying fire propagation may have a great effect on the

fire regime (fire sizes and area burned). If SOC were the full story, such changes would not have a significant effect, as the system would self-organize back to the previous state. If our model applies and some wildfire systems are close to a phase transition, then small changes may suddenly and drastically alter their dynamics, whereas they would have little effect in regions far from this point. Another recent study by Puevo et al. (2010) concluded that Amazonian savanna and tropical rainforest fires do not display SOC and suggested external drivers such as weather fluctuations as a source of power-law-like distributions. In our model, external factors may well influence the reproductive success of fire, but strong external forcing is not necessary to explain the variation in size distributions and the absence of SOC in some fire ecosystems (which we identify as subcritical).

Our model suggests that the slope of the fire size distribution (and an estimate of the local reproductive ratio close to 1) provides a signature of how close an ecoregion is to the critical point. There is ongoing debate on whether fire size distributions are best described by power laws or other functions (Reed and McKelvey 2002; Malamud et al. 2005; Newman 2005; Pueyo 2007; Clauset et al. 2009). From our analysis of the data from Canada and the fit of our model to the data, it is unlikely that fire size distributions are power laws in the mathematical sense, although they might be described by them to a sufficient degree for statistical purposes. The fire size distributions of supercritical regimes are relatively flat, since there is a greater number of large fires. Among the empirical fire data, these distributions resemble those of the DSM most (which has been shown not to produce a power law; Grassberger 2002). Thus, as expected, in the limit of a large reproductive ratio, our model effectively behaves like the DSM. Fire size distributions near the critical point ($\sigma =$ 1) are somewhat steeper and should theoretically follow a power law (a technical point regarding the existence of a phase transition that should be further addressed). As we move away from the critical point toward subcritical values of the reproductive ratio, for ecoregions in which fire spread is not very successful, the pattern gets steeper and steeper and degenerates, increasingly losing its resemblance to a power law.

This interpretation of the variation in the slopes of fire size distributions led us to identify the Boreal Plains as the ecoregion closest to the critical point among the regions considered for Canada. The patterns of its time series led us to conjecture that there had been a change from a subcritical regime to a critical regime around 1980, with a sharp increase in the average fire size from 3,278 to 9,066 ha. This jump is indicated not only by the average fire size but also by our temporal estimates of the reproductive number of fire spread in the region.

This approach based on the reproductive success of fire provides an inexpensive tool to monitor fire-prone ecoregions and possible change in their susceptibility to control or environmental drivers. Our model predicts that the effectiveness of control efforts, such as prescribed burning and fire suppression, will vary with reproductive success (and hence between ecoregions). Regions with supercritical values in fire spread success ($\sigma \geq 1$) are dominated by fires that spread aggressively and do not stop for reasons other than heavy environmental forcing or the absolute depletion of fuel in their path (Moritz 1997, 2003). In these regions, the average fire size would be limited mainly by the amount of fuel that rebuilds between fires (controlled by $\theta = p/f$, as in the DSM). This amount can be reduced by prescribed burning and mechanical fuel reduction (Stephens et al. 2009), but fires may still spread even in treated stands (Turner and Romme 1994; Bessie and Johnson 1995). We therefore expect fire suppression to have limited effect in this regime, which may also explain part of the controversy over the effectiveness of suppression efforts in boreal forests (Johnson et al. 2001; Bridge et al. 2005; Cumming 2005). By contrast, in subcritical regions ($\sigma < 1$) the average fire size is small because fire does not spread well. Hence, we expect fire suppression to be more effective in influencing the fate of a fire, while prescribed burning will be less necessary. Gradual changes in vegetation, as expected under global change, may affect the average fire spread success sufficiently to push a subcritical system into a critical or supercritical regime with a rapid and pronounced increase in average area burned. This suggests that monitoring fire spread success and change in vegetation composition (with significant differences in the flammability among tree species, depending, e.g., on the type and amount of resin) in areas where fire spread success is close to critical might contribute to effective mitigation. We expect the prediction of susceptibility made by our approach to be most useful in combination with predictions made by an ensemble of different models based on different approaches, such as mechanistic models that couple wildfire and climate (e.g., Krawchuk et al. 2009). Although we have presented one way to monitor such change when a relatively long time series of fire events is available, other statistical approaches to parameterize the model should also be investigated in future work. For example, high-resolution spatiotemporal data on the propagation of fires could be used to fit the stochastic model via Markov chain Monte Carlo approaches. The supercritical regime will be most challenging, and statistical efforts from propagation patterns should be complemented with empirical studies on the local regrowth of fuel.

Mitigation activities that target the fuel composition correspond to vaccination in models of communicable disease spread (reducing $\theta = p/f$). Although vaccination has not resulted in the eradication of measles, it has substantially changed the dynamics of disease (in terms not just of overall number of cases but also of dominant frequencies, coherence of temporal cycles, and spatial synchrony; Rohani et al. 1999; Earn et al. 2000). In terms of epidemic size distributions, extreme outbreaks have become rarer, leading to a breakdown of the power-law-like patterns (Rhodes et al. 1998; Jansen et al. 2003). As already mentioned, SOC-type models had been applied before to infectious diseases in small, isolated populations for the prevaccination era, for example, in islands, with the observation that epidemic size distributions resemble power laws. The exponents of such distributions were shown to vary for different diseases, and at the other extreme, for the postvaccination era, the exponent of one such distribution for a large city was noted as lower (Rhodes et al. 1998). More recently, birth-death processes were applied to explain the shape of the distributions in large cities, where the dynamics of the disease would become increasingly stochastic with vaccination (Jansen et al. 2003). Interestingly, our model provides one single framework to understand the whole spectrum of observations, with vaccination taking the dynamics from supercritical to subcritical. This is illustrated here with a preliminary analysis of infectious disease data based on our model (fig. 5).

This similarity between forest fire models and epidemiological models reflects the fact that the spread of both disease and fire can be described as a birth and death, or branching, process. Hence, in both disease and fire ecology, the existence of a power-law distribution with exponent -1.5 may indicate a critical state in which small modifications can lead to rapid change. This suggests that further future research across these disciplines might be fruitful, as also supported by previous findings on epidemics as critical phenomena (Rhodes and Anderson 1996; Jansen et al. 2003). It also highlights the importance of branching processes in general, which may turn out to be, together with a memory of previous events, the central principle behind the forest fire metaphor in complex systems.

The strength of our model, its simplicity, comes at the cost of not incorporating detailed submodels. It remains an open question how the control parameter σ emerges from the interaction of multiple small-scale factors within a particular ecoregion and whether hysteresis is involved in the transition (Scheffer et al. 2001). However, the fact that our model is able to explain the differences in the fire size distributions underscores that the spatial memory of former fires and the stochasticity of fire spread are two essential elements of the dynamics on which more mechanistic models can be built. We also have assumed that there is no interaction between the wildfire regime and

other large-scale disturbances, such as massive insect outbreaks and diebacks (Turner 2005).

To close, we note that several ecological systems other than those related to wildfires and whose dynamics involve local interactions have been observed to display patterns resembling power laws, including agroecosystems for the patterns of ant nests and arid ecosystems for the dynamics of vegetation cover (Vandermeer and Perfecto 2006; Kefi et al. 2007; Scanlon et al. 2007). Theoretical studies of models for the spatiotemporal and stochastic dynamics of predators and prey have also shown very similar patterns (Pascual et al. 2002; Roy et al. 2003; Pascual and Guichard 2005). It is interesting to consider that a main difference between all these phenomena and the fire dynamics described here is the lack of a separation of the timescales of the underlying processes. Thus, one intriguing possibility is that within the context of branching processes and a local memory of past events, these different ecological systems could be investigated by considering a continuum in the relationship between the timescales of propagation, regrowth, and external drivers. Beyond ecology and epidemiology, current developments in statistical physics and neurobiology are shifting conceptual ideas related to SOC toward a class of dynamics capable of explaining a broader set of patterns in nature, including approximate scalings that resemble power laws (Bonachela and Muñoz 2009; Levina et al. 2009; Bonachela et al. 2010). The name of self-organized quasi criticality has emerged (Bonachela and Muñoz 2009). Interestingly, central features of the dynamics, especially phase transitions of a percolation type with a broad scaling region and a hovering (but not strict self-organization) of the systems around the critical point, have important commonalities with the properties of the forest fire model presented here and with robust critical systems with no apparent separation of timescales (Roy et al. 2003; Pascual and Guichard 2005). These connections should be explored further, as they raise the intriguing possibility of a fundamental type of dynamics that would underlie many different patterns in nature and is ultimately related to the most basic processes of biology. These are on one side, the birth-death processes underlying transmission of an infectious state, and on the other side is a memory of previous infections that render the system immune or refractory locally and introduce a nonlinear feedback in the overall dynamics. Importantly, these dynamics are related to the general concept of phase transitions, which also raises the possibility that threshold phenomena with substantial sensitivity to environmental change are much more common than SOC would have implied.

Acknowledgments

This work would not have been possible without the open access to data over the Internet (in particular to the Canadian Large Fire Database and the data collected by B. T. Grenfell). We also thank T. Bedford, J. Calabrese, and M. Roy for useful discussions on statistical matters and two reviewers for their careful comments on the manuscript. This work was supported by the European Commission (FP6, New and Emerging Science and Technology PATRES [Pattern Resilience] project, contract n043268). M.P. is an investigator of the Howard Hughes Medical Institute.

Literature Cited

- Amiro, B., B. Stocks, M. Alexander, M. Flannigan, and B. Wotton. 2001. Fire, climate change, carbon and fuel management in the Canadian boreal forest. International Journal of Wildland Fire 10: 405–413.
- Bak, P., C. Tang, and K. Wiesenfeld. 1988. Self-organized criticality. Physical Review A 38:364–374.
- Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76:747–762.
- Bonachela, J. A., and M. A. Muñoz. 2009. Self-organization without conservation: true or just apparent scale-invariance? Journal of Statistical Mechanics: Theory and Experiment 2009:P09009.
- Bonachela, J. A., S. de Franciscis, J. J. Torres, and M. A. Muñoz. 2010. Self-organization without conservation: are neuronal avalanches generically critical? Journal of Statistical Mechanics: Theory and Experiment 2010:P02015.
- Bridge, S. R. J., K. Miyanishi, and E. A. Johnson. 2005. A critical evaluation of fire suppression effects in the boreal forest of Ontario. Forest Science 51:41–50.
- Canadian Forest Service. 1997. Canadian large fire database. http:// fire.cfs.nrcan.gc.ca/research/climatechange/lfdbe.htm.
- Clauset, A., C. R. Shalizi, and M. E. J. Newman. 2009. Power-law distributions in empirical data. SIAM Review 51:661–703.
- Cuddington, K., and B. Beisner. 2005. Ecological paradigms lost: routes of theory change. Elsevier Academic, Burlington, MA.
- Cumming, S. G. 2005. Effective fire suppression in boreal forests. Canadian Journal of Forest Research 35:772–786.
- Drossel, B., and F. Schwabl. 1992. Self-organized critical forest-fire model. Physical Review Letters 69:1629.
- Earn, D. J., P. Rohani, B. M. Bolker, and B. T. Grenfell. 2000. A simple model for complex dynamical transitions in epidemics. Science 287:667–670.
- Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15:549–560.
- Grassberger, P. 1993. On a self-organized critical forest-fire model. Journal of Physics A 26:2081–2089.
- 2002. Critical behaviour of the Drossel-Schwabl forest fire model. New Journal of Physics 4:17.
- Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H. Thulke, J. Weiner, T. Wiegand, and D. L. DeAngelis. 2005.

Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991.

- Henley, C. L. 1989. Self-organized percolation: a simpler model. Bulletin of the American Physical Society 34:838.
- Jansen, V. A. A., N. Stollenwerk, H. J. Jensen, M. E. Ramsay, W. J. Edmunds, and C. J. Rhodes. 2003. Measles outbreaks in a population with declining vaccine uptake. Science 301:804.
- Johnson, E. A., K. Miyanishi, and S. R. J. Bridge. 2001. Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. Conservation Biology 15:1554–1557.
- Keane, R. E., G. J. Cary, I. D. Davies, M. D. Flannigan, R. H. Gardner, S. Lavorel, J. M. Lenihan, C. Li, and T. S. Rupp. 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecological Modelling 179:3–27.
- Kefi, S., M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. El Aich, and P. C. de Ruiter. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213–217.
- Krawchuk, M. A., M. A. Moritz, M.-A. Parisien, J. V. Dorn, and K. Hayhoe. 2009. Global pyrogeography: the current and future distribution of wildfire. PLoS ONE 4:e5102.
- Levina, A., J. M. Herrmann, and T. Geisel. 2009. Phase transitions towards criticality in a neural system with adaptive interactions. Physical Review Letters 102:118110.
- Malamud, B. D., G. Morein, and D. L. Turcotte. 1998. Forest fires: an example of self-organized critical behavior. Science 281:1840– 1842.
- Malamud, B. D., J. D. A. Millington, and G. L. W. Perry. 2005. Characterizing wildfire regimes in the United States. Proceedings of the National Academy of Sciences of the USA 102:4694–4699.
- Moritz, M. A. 1997. Analyzing extreme disturbance events: fire in Los Padres National Forest. Ecological Applications 7:1252–1262.
 ——. 2003. Spatiotemporal analysis of controls on shrubland fire regimes: age dependency and fire hazard. Ecology 84:351–361.
- Moritz, M. A., M. E. Morais, L. A. Summerell, J. M. Carlson, and J. Doyle. 2005. Wildfires, complexity, and highly optimized tolerance. Proceedings of the National Academy of Sciences of the USA 102: 17912–17917.
- Newman, M. 2005. Power laws, Pareto distributions and Zipf's law. Contemporary Physics 46:323–351.
- O'Neil, R. V., R. H. Gardner, M. G. Turner, and W. H. Romme. 1992. Epidemiology theory and disturbance spread on landscapes. Landscape Ecology 7:19–26.
- Pascual, M., and F. Guichard. 2005. Criticality and disturbance in spatial ecological systems. Trends in Ecology & Evolution 20:88– 95.
- Pascual, M., M. Roy, F. Guichard, and G. Flierl. 2002. Cluster size distributions: signatures of self-organization in spatial ecologies. Philosophical Transactions of the Royal Society B: Biological Sciences 357:657–666.
- Peterson, G. D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems 5:329–338.
- Pueyo, S. 2007. Self-organised criticality and the response of wildland fires to climate change. Climatic Change 82:131–161.
- Pueyo, S., P. de Alencastro Graça, R. Barbosa, R. Cots, E. Cardona, and P. Fearnside. 2010. Testing for criticality in ecosystem dynamics: the case of Amazonian rainforest and savanna fire. Ecology Letters 13:793–802.
- Ratz, A. 1996. A generic forest fire model: spatial patterns in forest fire ecosystems. PhD thesis. Phillips-Universität, Marburg.

- Reed, W. J., and K. S. McKelvey. 2002. Power-law behaviour and parametric models for the size-distribution of forest fires. Ecological Modelling 150:239–254.
- Rhodes, C. J., and R. M. Anderson. 1996. Power laws governing epidemics in isolated populations. Nature 381:600–602.
- Rhodes, C. J., H. J. Jensen, and R. M. Anderson. 1997. On the critical behaviour of simple epidemics. Proceedings of the Royal Society B: Biological Sciences 264:1639–1646.
- Rhodes, C. J., A. R. Butler, and R. M. Anderson. 1998. Epidemiology of communicable disease in small populations. Journal of Molecular Medicine 76:111–116.
- Ricotta, C., G. Avena, and M. Marchetti. 1999. The flaming sandpile: self-organized criticality and wildfires. Ecological Modelling 119: 73–77.
- Ricotta, C., M. Arianoutsou, R. Dıaz-Delgado, B. Duguy, F. Lloret, E. Maroudi, S. Mazzoleni, et al. 2001. Self-organized criticality of wildfires ecologically revisited. Ecological Modelling 141:307–311.
- Rohani, P., D. J. Earn, and B. T. Grenfell. 1999. Opposite patterns of synchrony in sympatric disease metapopulations. Science 286: 968–971.
- Rothermel, R. 1972. A mathematical model for predicting fire spread in wildland fuels. Research paper INT-115. U.S. Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Roy, M., M. Pascual, and A. Franc. 2003. Broad scaling region in a spatial ecological system. Complexity 8:19–27.
- Scanlon, T. M., K. K. Caylor, S. A. Levin, and I. Rodriguez-Iturbe. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. Nature 449:209–212.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

- Song, W., F. Weicheng, W. Binghong, and Z. Jianjun. 2001. Selforganized criticality of forest fire in China. Ecological Modelling 145:61–68.
- Stephens, S. L., J. J. Moghaddas, C. Edminster, C. E. Fiedler, S. Haase, M. Harrington, J. E. Keeley, et al. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19:305–320.
- Turcotte, D. L. 1999. Applications of statistical mechanics to natural hazards and landforms. Physica A 274:294–299.
- Turner, M. G. 2005. Landscape ecology: what is the state of the science? Annual Review of Ecology, Evolution, and Systematics 36: 319–344.
- Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9:59–77.
- Vandermeer, J., and I. Perfecto. 2006. A keystone mutualism drives pattern in a power function. Science 311:1000–1002.
- Wagner, C. V. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23–34.
- Whelan, R. J. 1995. The ecology of fire. Cambridge University Press, Cambridge.
- Zinck, R. D., and V. Grimm. 2008. More realistic than anticipated: a classical forest fire model from statistical physics captures real fire shapes. Open Ecology Journal 1:8–13.
- ———. 2009. Unifying wildfire models from ecology and statistical physics. American Naturalist 174:E170–E185.
- Zinck, R. D., K. Johst, and V. Grimm. 2010. Wildfire, landscape diversity and the Drossel-Schwabl model. Ecological Modelling 221:98–105.

Associate Editor: Daniel Roelke Editor: Judith L. Bronstein