

Tree Mortality Following Boreal Forest Fires Reveals Scale-Dependant Interactions Between Community Structure and Fire Intensity

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ABSTRACT

Fire disturbance patterns influence forest communities at a range of spatial scales. Forest community structure may also influence pre disturbance patterns, because tree species vary in their fuel value and in their tolerance to pre damage. However, the influence of community structure on pre disturbance likely depends on latent ecological differences between pres and on the spatial scale at which patterns are observed. Using data on pre intensity, community structure, and post-pre tree survival in four systematically sampled boreal forest pres, we tested the hypotheses that: (1) patterns in post-pre tree survival reflect interactions between pre intensity and community structure; (2) these relationships change with the spatial scale of observation. To test the first hypothesis, we used information theoretic methods to compare eight generalized linear mixed effects models describing the influence of community structure and pre intensity on tree survival in a 500 m² sample plot,

accounting for latent pre-to-pre differences in response. To test the scaling hypothesis, we reaveraged the data at nine successively larger spatial resolutions up to approximately 2 km², at each resolution tracking the parameter values of the best model. When fit to the plot-level data, the dominant feature of the best model was a strong intensity-survival correlation which varied from pre to pre, and depended on plot-level community structure. In some pres, community structure and survival became more tightly coupled at larger scales, whereas pre intensity became less important. These results support the view that pre disturbance patterns are influenced by cross-scale interactions between community structure and pre intensity.

Key words: boreal forest; community structure; pre intensity; mixed effects model; tree survival; scaling.

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INTRODUCTION

Wildfires play an important role in forest ecosystems, generating disturbance patterns that influence community structure at a range of spatial scales (van Wagner 1988; Perera and Baldwin

2000; Morissette and others 2002; Harper and others 2004). Conversely, forest community structure may also affect fire disturbance patterns. For one thing, variability in community structure drives changes in fire intensity and rate of spread, because tree species vary in their properties as fuel (Byram 1959). Prevailing meteorological conditions influence fuel loading differently for different tree species so community structure also mediates some of the relationship between fire behavior and weather (Forestry Canada Fire Danger Group 1992). Finally, tree species vary in their fire tolerance (Regelbrugge and Conard 1993; Hely and others 2003) so that variation in fire disturbance patterns may reflect the divergent responses of different communities to the same fire behavior.

Fire disturbance patterns, represented here as post-fire survival rates, thus represent an intricate confluence of weather, fuel distributions, and species-specific tolerances to fire damage (Byram 1959; Whelan 1995). One way to untangle the interacting effects of these variables is to contrast the effects of fire intensity, which is influenced by weather and tree fuel characteristics, with community structure, which influences tree fuel characteristics and tolerance to fire damage (for example, Regelbrugge and Conard 1993; Hely and others 2003). However, estimating statistical parameters on intensity-species interactions has been hindered by the variability in post-fire survival data (Perera and others 2009).

Some of this variability may result from the fact that interactions between fire intensity and community structure are embedded in the system at multiple spatial scales. By this we mean that small-scale processes, such as tree-to-tree differences in fire tolerance or fuel value, may both influence, and be influenced by, larger-scale patterns, such as landscape-scale variation in community structure or weather. These cross-scale interactions (*sensu* Peters and others 2007) may create nonlinear dynamics and feedback loops (Peters and others 2004), and can lead to complex pattern formation (Malamud and others 1998; Benavent-Corai and others 2007). In general, it is challenging to examine how pattern-process relationships change across scales of observation (but see Peters and others 2004) because the necessary analytical framework is just emerging (for example, Peters and others 2007). But fire disturbance patterns may be a good candidate for such an analysis because variability in fire disturbance patterns increases nonlinearly with the scale of observation (Haeussler and Bergeron 2004; Peters and others 2004).

Here we analyze patterns in tree survival in four systematically sampled boreal forest fires to (1) test the hypothesis that fire intensity and community structure interact in determining post-fire tree survival, at the scale of a 500 m² sample plot and (2) explore how relationships between survival, intensity, and community structure change across spatial scales. The first goal is accomplished by identifying a set of generalized linear mixed effects models (GLMMs) describing competing hypotheses for intensity-species interactions, and comparing the likelihood of these models given the data. We attempt progress on the second goal by spatially averaging the data at different resolutions up to approximately 2 km², refitting the best GLMM, and recording the parameter values at each scale. We predicted that if cross-scale interactions between fire intensity and community structure were important in determining post-fire tree survival patterns, then this would be evident by changes in the parameter values of a GLMM fit at different scales.

MATERIALS AND METHODS

Study Site

The fires we studied occurred during the summer of 2005 in the boreal forest of Ontario. The boreal forest is primarily composed of coniferous and mixedwood forest types dominated by black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*). The most prevalent natural disturbances are forest fires and insect epidemics (Perera and Baldwin 2000). Anthropogenic disturbance by logging is also common—the majority of the boreal forest in Ontario was harvested during the twentieth century so that nearly 40% of the 30 million ha managed by the Ontario Ministry of Natural Resources (OMNR) is less than 60 years old (Perera and Baldwin 2000).

A total of 1,045 fires were reported in boreal Ontario during 2005, covering approximately 38,000 ha or 1% of the total area of the forest (Perera and others 2009). From these, we selected 11 fires based on their accessibility by air and the completeness of available data, including the shape of the fire, details of fire suppression activities, and pre-burn forest cover data including disturbance history. More information on tree survival in these 11 fires can be found in Perera and others (2009).

We chose the four most similar fires from the set of 11 for use in this study (hereafter referenced by their OMNR fire codes: NIP-020, THU-030,

THU-031, and THU-067). These Pres occurred in the same region of the boreal forest and so had similar terrain and species composition (Figure 1). They also occurred during similar Pre weather. When analyzing random effects of sample Pre on intensity-survival relationships, the fact that the four Pres were similar enhanced our confidence that the random effects we observed were not due to systematic differences between the Pres, such as large-scale differences in terrain or species composition.

Data Collection

Raw data on tree survival was obtained by interpreting high-resolution aerial photographs of the Pres taken in September 2005 (183 months post-Pre). The photographs were taken from an altitude of approximately 100 m using an automated stereo system consisting of two cameras mounted 6.1 m apart on a boom carried on the underside of a helicopter. The focal length was 100 mm and the photos were captured on ASA color portrait 70 mm film.

The subject of each photo was a circular sample plot, 12.6 m in radius, with an area approximately 500 m². These plots were placed systematically approximately 300 m apart throughout the entire Pre, with areas affected by prior anthropogenic disturbance (for example, logging) or Pre suppression

excluded. This resulted in 467 sample plots which systematically sampled 6734, 429, 1429, and 2325 ha of burned forest in NIP-020, THU-030, THU-031, and THU-067, respectively. The sampling grid of plots covered 49%, 88%, 86%, and 42% of the total area of each respective Pre.

The photos were interpreted using stereo images to give estimates of the number of live and dead trees (hereafter trees and snags) in each plot after the Pre. We visited 50 of the study plots on foot and directly counted the trees and snags. Photo-estimates were well correlated with actual abundance ($r^2 = 0.82$ and 0.89 for trees and snags, respectively). Survival in each plot was then estimated from the interpreted data as the number of trees divided by the total number of trees and snags.

Fire intensity—the amount of energy generated per second by a 1-m section of the Pre front (kW/m)—in each plot was obtained from Smith and others (2008). The authors estimated Pre intensity in our study Pres by categorizing the degree of Pre branch consumption, also known as the crown fraction burned (CFB), for snags in the photos. Fire behavior can be classified on a continuum ranging from slow-moving low-intensity surface Pres, to fast-moving high-intensity crown Pres (Whelan 1995). By virtue of their different fuel-consumption patterns—surface Pres are fueled primarily by the duff layer of the soil whereas crown Pres con-

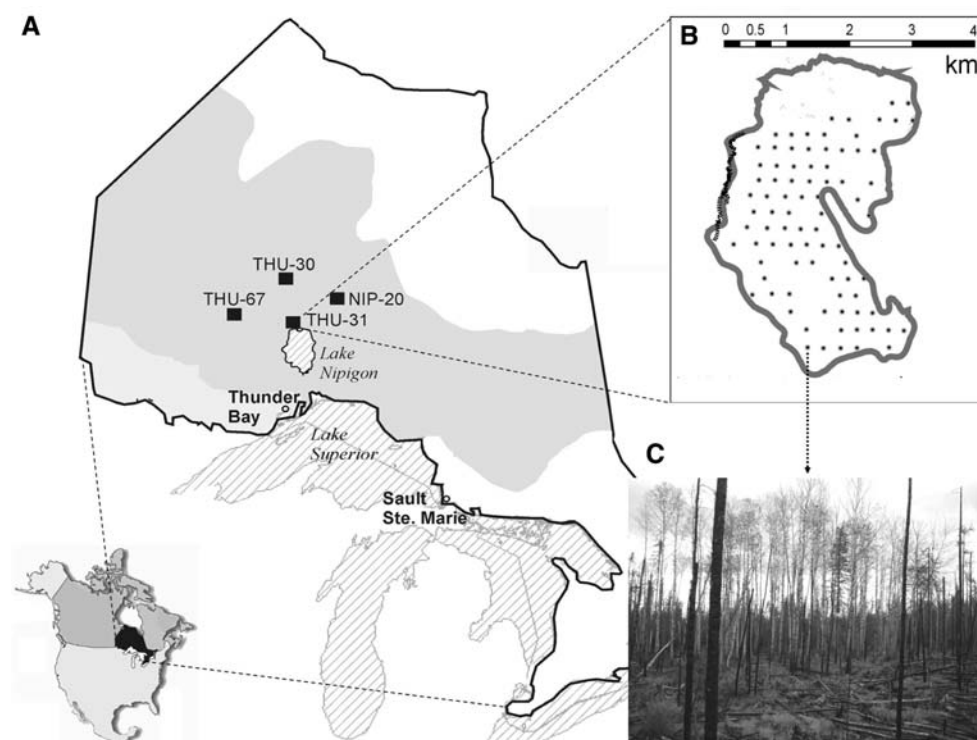


Figure 1. (A) A map of the study site shows the location of the four Pres in the boreal forest of Ontario, (B) the layout of the sample plots within a Pre, and (C) a photo of one of the sample plots taken while groundtruthing the aerial survival estimates.

sume tree branches as their primary fuel. Each type of fire behavior exhibits a characteristic pattern of CFB and fire intensity. The Canadian Forest Fire Behavior Prediction System (FBP), which is a primary tool for forest fire research, identifies canonical fire behaviors and associated CFB and intensity levels (Forestry Canada Fire Danger Group 1992; Taylor and others 1996; Table 1). Creeping surface fires have an average intensity of approximately 10 kW/m and do not usually consume tree branches. Surface fires have an average intensity of approximately 500 kW/m and consume some branches, leaving the majority intact. As fire intensity increases to approximately 2000 kW/m fire behavior shifts critically and begins to occasionally engulf entire trees, destroying the majority of the branch structure. Fires with intensities beyond 4000 kW/m travel primarily through the canopy layer, consuming all pine branch structure. Smith and others (2008) used this information with the FBP system, and its field guide for fire managers (Taylor and others 1996) to estimate fire intensity in the sample plots based on observed CFB. This method examines only the physical condition of snags in a plot and so can be independent of survival, which involves enumerating tree-snag ratios.

Canopy species composition in each plot came from provincial forest resource information (FRI) data (OMNR 2000). FRI data represents canopy species composition as the percentage of the overstory of a stand that is composed of each species.

Analysis

Percent cover data on canopy species, such as the FRI data, can be challenging to interpret as independent variables in statistical models because the proportional abundances of each species are correlated. The correlation results first from the constraint that the proportions sum to 1, so that if some species are abundant others must be rare. It also probably reflects community dynamics: to the extent that community structure is not random,

but rather represents a characteristic ecological trajectory, the proportional abundance of one species depends ecologically on that of the others.

We used principal component analysis (PCA; Jolliffe 2002) on the proportional abundances in each plot to make weighted averages of the FRI data that were statistically independent of one another. As well as being orthogonal, respective PC axes capture from the original data the most variance possible in a single dimension.

Because the PC axes are orthogonal, we can interpret linear models that use the PC axes as input variables. However, these axes do not necessarily have biological meaning. By including multiple PC axes in the analysis, we aimed to capture variation in community structure *per se*, without regard to the biological significance of each individual PC axis.

Before doing the PCA on the FRI data, we removed species whose overall average contribution to the canopy was less than 5%, to prevent the PCA from being biased toward rare species. We thus performed PCA on raw proportional abundances of *P. mariana*, *P. banksiana*, *P. tremuloides*, and *B. papyrifera* (Figure 2). PCA was done using the function `prcomp` in the software package R (version 2.8.1; R Development Core Team 2008) without scaling or centering the data. We used the first three PC axes, PC1, PC2, and PC3, in subsequent analyses.

To test for interactions between fire intensity and species composition while accounting for random variation between fires, we identified eight statistical models that varied in how species composition and fire intensity interacted, and in how random fire effects were incorporated (Table 2). The models were fit with GLMMs (Pinheiro and Bates 2000) using survival as the dependent variable with a logit link. For the independent variables, we identified four potential equations for including species composition and crossed these with two different types of random effects, giving the total of eight candidate models. Species composition in the models was either absent, represented as only PC1, or as the first three PC axes, including two-way

Table 1. Relating Observed Branch Destruction on Fire-Killed Trees with Average Intensity Based on the Canadian Fire Behavior Prediction System (Forestry Canada Fire Danger Group 1992) Using the Method of Smith and others (2008)

Fire intensity, kW/m	Expected fire behavior	Crown fraction burned
10	Creeping surface fire	All pine branches present
500	Surface fire	Majority of pine branches present
2000	Surface fire with intermittent crowning	Majority of pine branches absent
4000	Continuous crown fire	Fine branches completely absent

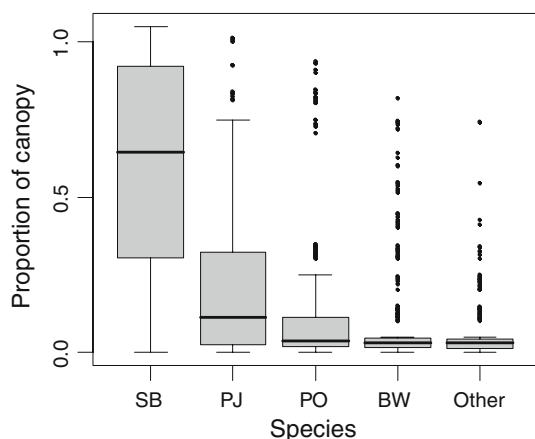


Figure 2. Proportional contribution of each species to the overstory of the study plots from FRI data. FRI data has a precision of 0.1 so to distinguish outliers from one another the data for this figure were “jittered” by adding a random number to each value from a uniform distribution with minimum 0 and maximum 0.05. From left to right, the species codes represent black spruce (*P. mariana*), jack pine (*P. banksiana*), trembling aspen (*P. tremuloides*), and white birch (*B. papyrifera*).

interactions between each PC axes and pre intensity. Where 3 PC axes were included we also fit the model without intensity-species interactions. We explored two different types of random effects. In models 1-4, the intercept of the model equation included a random component that varied from pre to pre. In models 5-8, both the intercept and the intensity-survival slope had random components.

We used Akaike’s Information Criterion (AIC) to select the best model from this set. Contrasting the AIC values of the first four models with the latter four assessed the hypothesis that the shape of the influence of pre intensity on survival varied randomly from pre to pre, whereas contrasts among the

first four models and among the last four examined the role of community structure under two respective types of random effects. Models were fit using the lme4 package in R (Bates and others 2008).

To test whether the intensity-species interactions observed at the spatial scale of a sample plot held at other scales, we aggregated the data over nearby plots and refit the best model using the average survival, pre intensity, and species composition of the aggregate data. This procedure was done at nine respective spatial scales by aggregating each sample plot with its *n* nearest neighbors (*n* = 1, 2, ..., 9). At each level of aggregation, we summed the number of trees and snags in each neighborhood before recalculating survival, and averaged the pre intensity and PCA scores of the plots in each neighborhood. We thus changed the spatial resolution of the data while keeping the underlying relationships between intensity, community structure, and survival intact. We predicted that if cross-scale interactions between pre intensity and community structure were important in determining survival, then the coefficients of the best-fitting model would change significantly across spatial resolutions. Before fitting the model at each scale, we standardized all the independent variables to be between 0 and 1 to allow direct comparison of the model coefficients between variables and across scales.

Because the same plot appeared in multiple aggregates at each scale, the observations at a given scale are not independent and the estimated standard errors of the model coefficients are erroneously small. This complicates testing statistical significance by standard methods (for example, using the standard errors to produce confidence intervals for the parameters). Instead, we bootstrapped null-distributions of the model coefficients by repeatedly aggregating plots without regard to

Table 2. Structure of the Eight General Linear Mixed Effects Models We Tested, Their Degrees of Freedom, Negative Log Likelihood, AIC, and the Difference from the AIC of the Best-Fitting Model

Model	Equation	Random effects	Df	-log (L)	AIC	ΔAIC
1	Intensity	Fire	3	2726.5	5459.1	190.9
2	Intensity * PC1	Fire	5	2664.1	5338.2	70
3	Intensity + PC1 + PC2 + PC3	Fire	6	2702.2	5416.5	148.3
4	Intensity * (PC1 + PC2 + PC3)	Fire	9	2644.7	5307.4	39.2
5	Intensity * (PC1 + PC2 + PC3)	Intensity × Fire	11	2623.1	5268.2	0
6	Intensity + PC1 + PC2 + PC3	Intensity × Fire	8	2646.0	5308	39.8
7	Intensity * PC1	Intensity × Fire	7	2633.7	5281.4	13.2
8	Intensity	Intensity × Fire	5	2664.8	5339.7	71.5

For two factors A and B, the notation A * B = A + B + A × B with any implied duplicate terms removed. The best model of the set according to AIC is Bold.

their spatial location. By contrasting the model coefficients obtained during the spatial analysis against these null-distributions, we tested the null-hypotheses that changes in the parameter values across scales were due simply to aggregating the data, rather than to latent spatial structure in the relationships.

The null-distributions we used contained 1000 coefficients for each variable and spatial scale. We interpreted the coefficients of the scaling analysis as statistically significant if they were less than the 5th (or greater than the 95th) percentile of the null-distribution. We performed this analysis separately on each fire to avoid considering the scaling properties of random effects.

RESULTS

Model 5, which featured respective two-way interactions between fire intensity and each of the three orthogonal measures of community structure, had the highest likelihood and the lowest AIC value (Table 2). In addition to a multidimensional dependence on community structure, this model described a survival-intensity relationship that depended on latent differences between fires (Table 3).

The strongest pattern in the fit of this model to the data was the relationship between survival and fire intensity, although the shape of the relationship was different in different fires, particularly at low fire intensities (Figure 3). Where fire intensity was moderate, the model also suggested higher survival rates in plots whose canopy composition

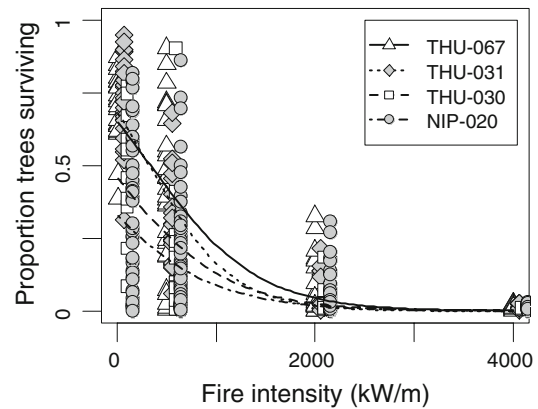


Figure 3. Tree survival as a function of fire intensity. Data points show intensity and survival in 467 sample plots laid approximately 300 m apart in four boreal forest fires which occurred from June to August 2005. Curves show the predictions of the best mixed effects model for this data. The fixed effects in this model were fire intensity, three orthogonal measures of plot canopy species composition, and two-way interactions between intensity and species composition. An interaction between study fire and fire intensity was included as a random effect. Intensity data were jittered to make the figure easier to read.

ranked low on the PC1 axis (Figure 4). Together, the 3 PC axes captured 90% of the variation present in the original data (with rare species were removed) with PC1, PC2, and PC3 capturing 53%, 21%, and 16%, respectively. Each PC axis was more strongly correlated with one canopy species. Specifically, PC1, PC2, and PC3 were most strongly

Table 3. Summary of the Best-Fitting Mixed Effects Model

Term	Estimate	SE	P
<i>Fixed effects</i>			
Intercept	0.2918	0.3067	0.3414
Intensity	-0.0024	0.0002	<0.0001**
PC1	-0.2039	0.1011	0.0436*
PC2	-0.2070	0.1043	0.0472*
PC3	-0.4488	0.1302	0.0006**
Intensity × PC1	0.0008	0.0002	0.0003**
Intensity × PC2	-0.0002	0.0002	0.3883
Intensity × PC3	0.0007	0.0003	0.0255*
Term			SD
<i>Random effects</i>			
Intercept			0.598218
Intensity			0.000302

*P < 0.05.
**P < 0.001.

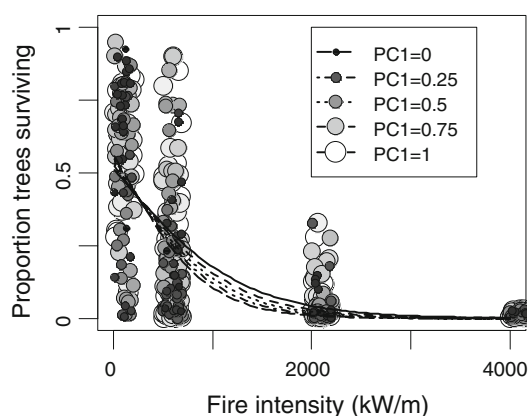


Figure 4. Tree survival in the sample plots as a function of fire intensity and PC1, which was the first of three orthogonal measures of canopy species composition derived from PCA of canopy cover data for each plot. Curves show the statistically significant interaction between fire intensity and PC1 in determining tree survival rates, as predicted by the best-fitting mixed effects model. Intensity data were jittered to make the figure easier to read.

related to *P. mariana*, *P. banksiana*, and *P. tremuloides*, respectively (Table 4).

There were varying levels of spatial autocorrelation in the independent variables, with species composition showing spatial dependence on the order of 1 km, whereas fire intensity showed negligible spatial autocorrelation. An exponential spatial autocorrelation function fit the data well (Figure 5). PC2, in particular, showed high spatial autocorrelation at distances up to 1 km. During the scaling analysis, where fire intensity, species composition, and tree survival were averaged over spatial neighborhoods of increasing size in each respective fire, the relationship between survival and species composition changed significantly in NIP-020, THU-031, and THU-030 (Figure 6), but not in THU-067. Specifically, in all fires except THU-067, species composition became more strongly correlated with survival at intermediate scales. In contrast, the correlation between fire

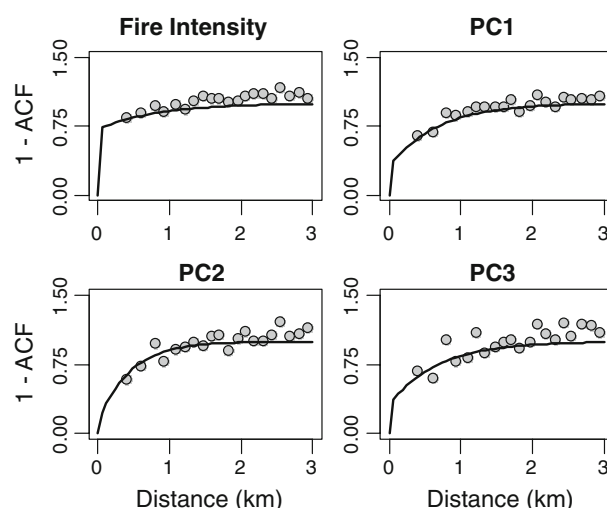


Figure 5. Spatial autocorrelation functions (ACF) for fire intensity and community structure. Points show the empirical semivariogram of each variable, which estimates the function $1 - ACF$. Solid lines show the results of fitting each variable with an exponential spatial ACF. ACFs were estimated using functions in the nlme package for R (Pinheiro and Bates 2000).

intensity and survival diminished as the scale of observation increased.

As we reaveraged the data and refit the model at successively larger spatial scales, we tested the null-hypothesis that changes in parameter values were due to the effects of this aggregation alone, rather than the spatial structure of the data. In all fires but THU-067, the correlations between survival and community structure evident at intermediate scales were improbable ($P < 0.1$) given this null-hypothesis. In contrast, the parameters of the intensity-survival relationship were always between the 5th and 95th percentiles of the null-distribution for each scale, indicating that intensity-survival relationships observed at larger scales could probably be attributed simply to averaging a pattern generated at the plot level.

Table 4. Principal Component Analysis on the Community Composition of the Sample Plots, Showing the Weight Given to Each Species for Each PC Axis

Species	PC1 (0.53)	PC2 (0.21)	PC3 (0.16)
<i>Picea mariana</i>	0.98	-0.21	-0.01
<i>Pinus banksiana</i>	0.20	0.95	-0.25
<i>Populus tremuloides</i>	0.05	0.23	0.88
<i>Betula papyrifera</i>	0.03	0.08	0.40

Parentetical numbers in the column head refer to the proportion of the variability in the original data explained by each PC axis.

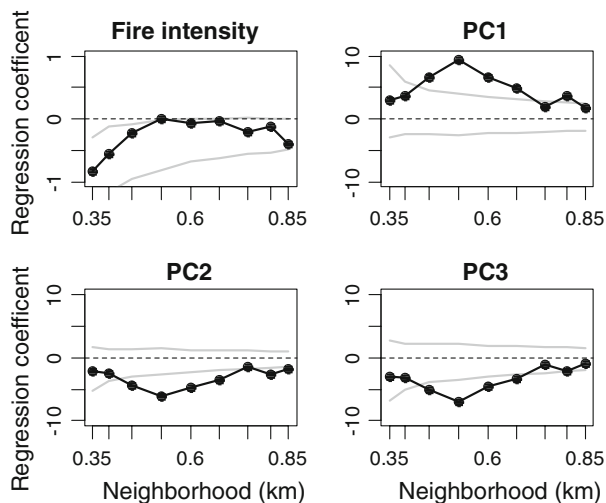


Figure 6. Regression coefficients at different spatial scales for the relationship between survival and each independent variable in THU-030. The points show the coefficients obtained by aggregating survival, fire intensity, and the principal components of species composition in each plot with its n nearest neighbors ($n = 1, 2, \dots, 9$) and refitting the model using the averages of each variable over each spatial aggregate. Null-distributions controlling for the effect of aggregation alone were obtained by repeating the procedure 1000 times, but aggregating over random plots selected without regard to their spatial location. Gray lines follow the estimated 5% and 95% quantiles of the null-distribution. The horizontal axis of the plots is the average radius of spatial neighborhood used in the aggregations.

DISCUSSION

Forest fires are important in structuring boreal forest ecosystems at a range of spatial scales (van Wagner 1988; Perera and Baldwin 2000; Morissette and others 2002; Harper and others 2004). Tree survival is an important aspect of fire disturbance that has been correlated with many variables including soil moisture, fire size, and weather patterns (for example, Perera and others 2009). Fire intensity and species composition are two variables whose role in determining tree survival is particularly well-supported (Moreno and Oechel 1993; Regelbrugge and Conard 1993; Haeussler and Bergeron 2004; Harper and others 2004), yet interactions between these variables remain enigmatic. For example, Regelbrugge and Conard (1993) and Hely and others (2003) found that the effects of fire damage varied by species, whereas Franklin and others (2006) found that variation in species composition did not contribute to survival probability after a high-intensity fire.

We collected data on post-fire tree survival, fire intensity, and species composition by systematic

sampling four fires that occurred in the boreal forest of Ontario in 2005. We found that at the scale of a sample plot (approximately 500 m²) species composition and fire intensity interacted to determine tree survival. At a mechanistic level, this supports the hypotheses that (1) species-specific physiological differences in fire tolerance can drive correlations between community structure and fire disturbance patterns and (2) species-specific contributions to the types of fuel a fire encounters may drive similar correlations indirectly by influencing fire behavior (for example, Hely and others 2003).

We used PCA to produce three orthogonal measures of species composition that captured 90% of the variation in the original data, once rare species were removed. The advantage of this approach is the ability to consider multiple independent aspects of community structure. Looking at community structure from different angles may be the key to elucidating generalities in its influence on survival patterns. The disadvantage of this approach is that the PC axes are challenging to interpret biologically, so although we can say that community structure plays a role in determining how fire intensity influences tree survival, we cannot attribute this to the properties of particular species or functional groups.

Spatial autocorrelation—the dependence of a measurement on the values of its neighbors—is another aspect of the data we examined. The PC axes all had higher levels of spatial autocorrelation than fire intensity. However, because our measure of fire intensity had a low resolution, we cannot infer the properties of fire behavior from this observation. Community structure is spatially autocorrelated in part because seed dispersal links the successional trajectories of neighboring stands (for example, Nathan and Muller-Landau 2000), and because the edaphic conditions which influence the relative competitive ability of different species vary at large spatial scales (Perera and Baldwin 2000).

In addition to spatial autocorrelation, we found that the relationship between species composition and survival changed with the spatial scale of observation in some fires. This suggests that tree survival can be influenced by canopy species composition simultaneously at the scale of plot and at the scale of several plots. Biologically, the pattern in Figure 6 may signify cross-scale interactions (*sensu* Peters and others 2007) where survival probability at small scales is influenced by local process (that is, fire intensity and species composition in a plot), but also large-scale patterns (that is, the spatial distribution of community structure

among neighboring plots). For example, survival in a stand with community structure x (an arbitrary measure of community structure), where the average community structure in the surrounding landscape is also x , may have different ecological characteristics than if the stand is surrounded by community structure y . These differences may cause divergent fire behaviors and disturbance patterns. One way to see cross-scale interactions therefore is as creating latent differences between similar realizations of small-scale processes, due to the larger spatial or temporal context in which those processes occur. Statistically, this point of view suggests combining mixed effects models to analyze observations with latent differences between groups with spatial analyses to explore the dependence of observations on their neighbors.

Understanding how pattern-process relationships change across scales is a defining problem in ecology (Levin 1992). Fire disturbance patterns, as measured by tree survival, provide a good example of cross-scale interactions, exhibiting interactions between intensity and community structure that change with the spatial scale of observation.

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