

# A spatiotemporal Ripley's *K*-function to analyze interactions between spruce budworm and fire in British Columbia, Canada

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**Abstract:** In this paper, we extend traditional methods of spatial statistics to study spatiotemporal correlations between two different point processes. After introducing the methodology, we apply this analysis to a particular case study of interest in ecology, the interaction between damage by a particular forest pest (western spruce budworm (*Choristoneura occidentalis*)) and forest fires. Our analysis, which covers parts of British Columbia in the 26-year period from 1970 to 1995, indicates that areas affected by budworm infestation have a significantly decreased risk of forest fire for the 7 years following the infestation. Conversely, forest fires decrease the risk of infestation for at least 6 years after the fire. These temporal correlations extend over a spatial range of at least 25 km. Our study rejects the common assumption that insect infestation necessarily results in increased fire risk. This case study illustrates the utility of point process modeling and spatial statistics to understanding ecosystem dynamics extending over both space and time.

**Résumé :** Dans cet article, les auteurs adaptent les méthodes traditionnelles de statistiques spatiales pour étudier les corrélations spatiotemporelles entre deux processus ponctuels différents. Après avoir présenté la méthodologie, les auteurs l'appliquent à une étude de cas spécifique qui présente un intérêt pour l'écologie, soit l'interaction entre les dommages causés par un ravageur forestier en particulier (la tordeuse occidentale de l'épinette (*Choristoneura occidentalis*)) et les incendies de forêt. Leur analyse, qui couvre une partie de la Colombie-Britannique durant la période de 26 ans allant de 1970 à 1995, indique que les risques d'incendie étaient significativement plus faibles dans les zones affectées par la tordeuse durant les 7 années qui ont suivi une infestation. À l'inverse, les risques d'infestation ont diminué pendant au moins 6 ans après un incendie de forêt. Ces corrélations temporelles s'étendent sur au moins 25 km. Leur étude rejette la conviction implicite que les infestations d'insectes augmentent nécessairement les risques d'incendie. Cette étude de cas illustre l'utilité de la modélisation des processus ponctuels et des statistiques spatiales pour comprendre la dynamique des écosystèmes dans le temps et l'espace.

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## Introduction

Throughout history, insect outbreaks and forest fires have proven themselves to be powerful agents of forest disturbance and mortality. In 2004, in the United States alone, almost 10 million acres of forest (USDA 2005) was damaged or destroyed by insect pests or pathogens and another 6.8 million acres of forest (National Interagency Fire Center 2008) was lost to forest fires despite widespread programs to control insect outbreaks and to manage forest fires. It is often stated in the literature that insect outbreaks and forest fires are nonindependent forms of disturbance. The suggestions are that insect outbreaks may leave forests more or less vulnerable to forest fires (Knight 1987; Despain 1990; Péch 1993; Kulakowski et al. 2003), that forest fires may "immunize" forests against certain insect outbreaks while

leaving trees vulnerable to others (Veblen et al. 1994; Bebi et al. 2003; Kulakowski et al. 2003; McHugh et al. 2003), and that two-way interactions between forest fires and insect outbreaks may act synergistically to determine forest composition (Schmid and Hinds 1974; McCullough et al. 1998). Since both the sign and the magnitude of potential correlations are still under debate and the mechanisms by which forest fires and insect outbreaks interact are complex, it is important to study the empirical spatiotemporal correlations of actual disturbances. In doing so, we can determine the net interaction between these two disturbance modes and, from this, draw conclusions about the dominant mechanisms mediating these interactions. Quantitative studies of the spatiotemporal dynamics between insect damage and forest fires (e.g., Fleming et al. 2002) have, however, been few owing to a shortage of spatially explicit, large-scale data sets and techniques with which to analyze such data.

It is important to distinguish between two different types of interactions between multiple "contagious" disturbance phenomena. When a specific tree is affected by more than one disturbance type over a period of time, the extent of disturbance interaction depends on the specific biological and ecological response of that tree. In this case, the interaction between the two disturbances is mediated by changes in the local structure and composition of the ecosystem. At larger scales, the extent of disturbance interaction depends

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on both changes in the local state of the ecosystem and the spatial geometry of the disturbed landscape. Whereas traditional long-term plot experiments can explore local-scale interaction between disturbances, understanding the landscape-level interaction requires analysis of the spatiotemporal dynamics of the disturbance processes. In this analysis, we develop a technique to study landscape-level interactions between two contagious disturbance processes by extending a traditional estimate of second-order properties, Ripley's cross- $K$ -function  $K_{12}(s)$  (Cressie 1993) to a space-time cross- $K$ -function  $K_{12}(s, t)$ . In addition, we modify the expressions for  $K_{12}(s, t)$  and its variance  $V_{12}(s, t)$  to account for the directionality inherent in having two different point processes interacting in time.

### Description of the data

The data used in this analysis were drawn from the British Columbia Natural Disturbance Database compiled by the Canadian Forest Service. The western spruce budworm (*Choristoneura occidentalis*) is a major forest pest in British Columbia and at times has been the most destructive forest defoliator in western North America (Furnish and Carolin 1977). Its primary hosts are Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), although it has a number of secondary hosts such as Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western larch (*Larix occidentalis* Nutt.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The western spruce budworm larvae will feed on older growth from previous seasons but prefer new growth, damaging expanding needles and developing cones (Fellin and Dewey 1982). Successive years of severe defoliation can cause decreased growth, deformity, and ultimately mortality. Because the western spruce budworm feeds on specific host species, in British Columbia the western spruce budworm is primarily confined to the Interior Douglas-Fir biogeoclimatic zone. To minimize heterogeneity in disturbance risk, we therefore limit the spatial scope of our analysis to the region illustrated in Fig. 1A. This study region, which roughly co-

incides with the Interior Douglas-Fir zone, represents the area that experienced repeated western spruce budworm infestation during the 26 years under study. Figure 1 shows the 26-year data set of western spruce budworm damage and forest fires used in this analysis. In the period examined, 1970–1995, there were 13 622 fires events and 6822 recorded regions of budworm infestation, affecting up to 0.30% and 17.2%, respectively, of the study region in any given year. Both fire and insect damage databases included disturbances as small as 0.1 ha, so although our database is missing very small disturbances that may be overlooked by aerial survey, we do capture the vast majority of the area affected by either of these two disturbances.

While the effects of insect damage and fire occur on the scale of individual trees, the original data were composed of polygons of the fraction of infected trees and the locations and sizes of fires. The individual-based nature of the two disturbance processes was reconstructed in the following way. Trees were assumed to be located randomly (i.e., placed according to a Poisson process) on the landscape with an average density of 100 trees/ha. The number of insect-damaged trees was calculated by multiplying the tree density by the fraction of damaged trees within each polygon. The spatial extent of each fire was then reconstructed assuming a circular burn centered on the reported fire location. Each point location (affected tree) was indexed by its position ( $x, y$ ) and the year ( $t$ ) in which the disturbance occurred. In addition to using a Poisson process, we also evaluated other methods of reconstructing the point process nature of the disturbances, such as assigning points on a grid within the original polygons at a range of size scales. Similar results were obtained from these analyses.

### Spatiotemporal model

One commonly used method of estimating whether a single stochastic process is clustered in space and time is Ripley's  $K$ -function (Ripley 1976, 1977) defined as

$$[1] \quad K(s, t) = \frac{1}{\lambda} E[\text{no. of further events occurring within distance } s \text{ and time } t \text{ of an arbitrary event}]$$

where the number of events ( $N$ ) and the area ( $A$ ) may be used, under the assumptions of homogeneity, to estimate the intensity of the point process  $\lambda = N/A$ . Unlike the Knox test for spatial correlation, Ripley's  $K$ -function allows us to examine space-time clustering over a range of spatial and temporal scales. Specifically, we define a space-time cross- $K$ -function as

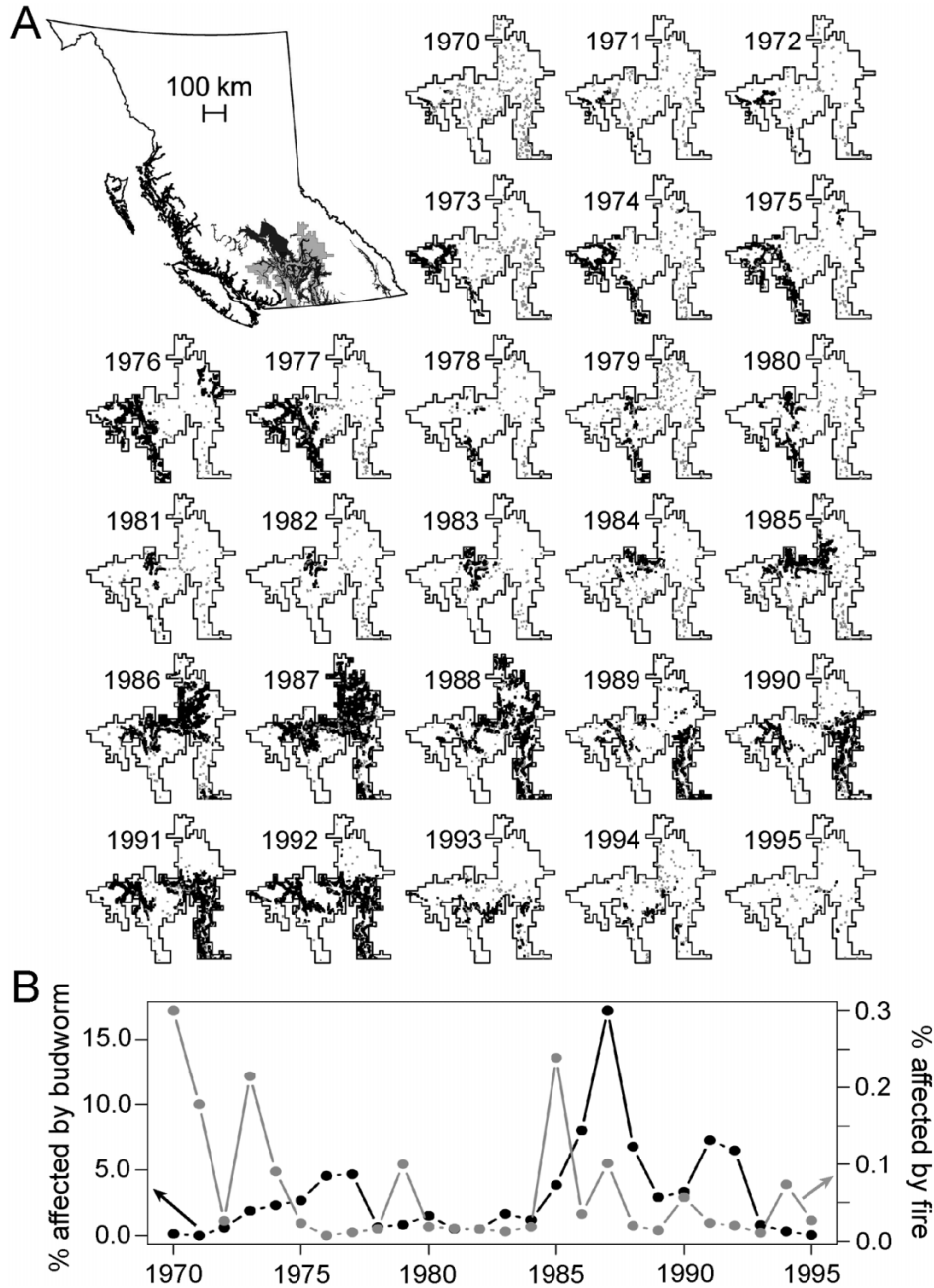
$$[2] \quad K_{bf}(s, t) = \frac{1}{\lambda_f} E[\text{no. of further fire events occurring within } (s, t) \text{ of a given budworm event}]$$

where  $\lambda_f \sim N_f/A$  represents the intensity of the fire point process. The converse function  $K_{fb}(s, t)$  is defined analogously throughout. Directionality is inferred by considering only those point pairs that occur in a particular sequence. For example, in calculating eq. 2, we consider only those point pairs for which a fire event occurred  $t$  years following a budworm infestation event. In this case,  $K_{bf}(s, t) \neq K_{fb}(s, t)$ , and therefore, you need all  $N_f \times N_b$  functions to completely describe the second-order proper-

ties of the process. Note that this function may be estimated using a weighted average of the more traditional bivariate  $K$ -function  $K_{bf}(s)$  (as estimated by the `k12hat` function in the R package "splancs" (R Development Core Team 2005)), where the insect point process and the fire point process are drawn from different years with a given lag time.

Rather than analyzing the raw cross-correlations, we calculated the derived function

**Fig. 1.** (A) Interior Douglas-Fir zone overlaid with the fire (shaded) and western spruce budworm (solid) disturbance data for the period 1970–1995. Upper left represents the Interior Douglas-Fir biogeoclimatic zone (solid) and the study region (shaded) within the province of British Columbia. (B) Time series plot of the percentage of the study region affected by forest fires (shaded circles) and western spruce budworm (solid circles) during the period 1970–1995.



$$[3] \quad D_{0,bf}(s, t) = \frac{K_{bf}(s, t) - K_{bf}(s) \bullet K_{bf}(t)}{K_{bf}(s) \bullet K_{bf}(t)}$$

where  $K_{bf}(s)$  and  $K_{bf}(t)$  are the cross- $K$ -functions in pure space or pure time, respectively. This function has been used by a number of authors in the analysis of geographical epidemiology (e.g., see Diggle et al. 1995; Gatrell et al. 1996). In this context,  $D_{0,bf}(s, t)$  may be interpreted as representing the increased risk of a fire event owing to a budworm activity event at spatial distance  $s$  and time lag  $t$  and represents the portion of the total space–time correlation

that remains after correcting for purely spatial and purely temporal correlations.

A nice feature of the  $D_{0,bf}$  function (eq. 3) is that it eliminates correlations between the two processes arising from purely spatial covariates, such as elevational gradients, and purely temporal covariates, such as weather-related increases in fire frequency and insect outbreak frequency (e.g., the Moran effect). In doing so, we isolate the effect of only those processes that are correlated in both space and time. While purely spatial or purely temporal correlations may exist owing to a variety of unknown temporal or spatial heter-

ogeneities, as discussed by Diggle et al. (1995), the statistical tests used in this analysis isolate the effect of only those processes that are correlated in both space and time and remain valid even if the underlying process is nonstationary. The results presented below are based on calculations using a reweighting edge-correction method in which point pairs falling outside the boundary are estimated from analogous areas inside the boundary (Cressie 1993). Estimating  $D_{0,bf}(s, t)$  and  $D_{o,bf}(s, t)$  using a buffer edge-correction method gave similar results.

The size of the data set and the computational requirements of the calculation (which scale roughly as  $N_f \times N_b$ ) prohibit the simultaneous estimation of  $D_{0,bf}(s, t)$  and its statistical significance using our entire data set. One approach would be to divide the spatial region under consideration into subregions and to calculate  $D_{0,bf}(s, t)$  separately on each subregion (see Diggle 2003). This was not an option in this analysis because subregional calculations would have limited the spatial scale of our analysis and the complex geometry of our space would have allowed only a very small number of replicates. Instead, we take advantage of the fact that Ripley's  $K$ -function is invariant to random thinning (Cressie 1993; Diggle 2003) and estimate  $D_{0,bf}(s, t)$  using a random subsampling (Monte Carlo) approach in which 0.05% of the original fire and budworm data sets are randomly selected and used to estimate  $D_{0,bf}(s, t)$ . Five hundred replicates were considered sufficient for testing hypotheses at the 1% level (Diggle 2003) and sufficient convergence was achieved with this sample size. Our final estimate of  $D_{0,bf}(s, t)$  was taken as the mean of the 500 subsample estimates, with confidence limits derived from the 2.5 and 97.5 percentiles of the subsample distribution.

To generate a null distribution against which our estimates of  $D_{0,bf}(s, t)$  would be assessed, we needed to consider which "benchmark" would be the most appropriate for assessing no spatiotemporal correlation (Diggle 2003). In this context, the most appropriate null distribution was that generated by a randomization of the year labels for one of the two point processes (in this case, the fire process was randomized). In other words, for our estimate of  $D_{0,bf}(s, t)$  to be considered statistically significant, it must be an extreme value relative to what would be expected if the timing of events were permuted so as to eliminate the kind of spatiotemporal correlations that we are looking for in our analysis. Therefore, for each of these 500 subsamples, we randomly permuted the year labels for the fire data set and reestimated  $D_{0,bf}(s, t)$ . The final result of our calculations is an empirical distribution of  $D_{0,bf}(s, t)$  (generated from 500 subsampled estimates) and a null distribution of  $D_{0,bf}(s, t)$  (generated from 500 subsampled and year-permuted estimates). The statistical significance of our results is derived from differences between these two distributions.

Although the strong interdependence between values of  $D_{0,bf}(s, t)$  at different  $s$  and  $t$  makes formal analytical significance testing difficult, another approach would be to compare our estimates against a null model of zero space-time interaction. If two processes are space-time independent, ~95% of the  $R_{bf}(s, t)$  values should lie within  $\pm 2$ , where  $R_{bf}(s, t)$  is given by

$$[4] \quad R_{bf}(s, t) = \frac{D_{0,bf}(s, t)[K_{bf}(s) \bullet K_{bf}(t)]}{\sqrt{V_{bf}(s, t)}}$$

$R_{bf}(s, t)$  is analogous to the standardized residuals of the  $K_{bf}(s, t)$  function once purely spatial and purely temporal correlations have been accounted for (Diggle et al. 1995).  $V_{bf}(s, t)$  is the variance of  $D_{0,bf}(s, t)$  under the null hypothesis of zero space-time interaction and can be calculated analytically (Lynch 2006). A predominance of  $R_{bf}(s, t)$  values whose absolute value is larger than 2 indicates spatiotemporal interactions that are statistically significant (Diggle et al. 1995). Although both procedures (subsampling and analytical calculation of  $R_{bf}(s, t)$ ) give similar results, we have presented only the subsampling results here. Details on the analytical calculation may be found in Lynch (2006).

## Results

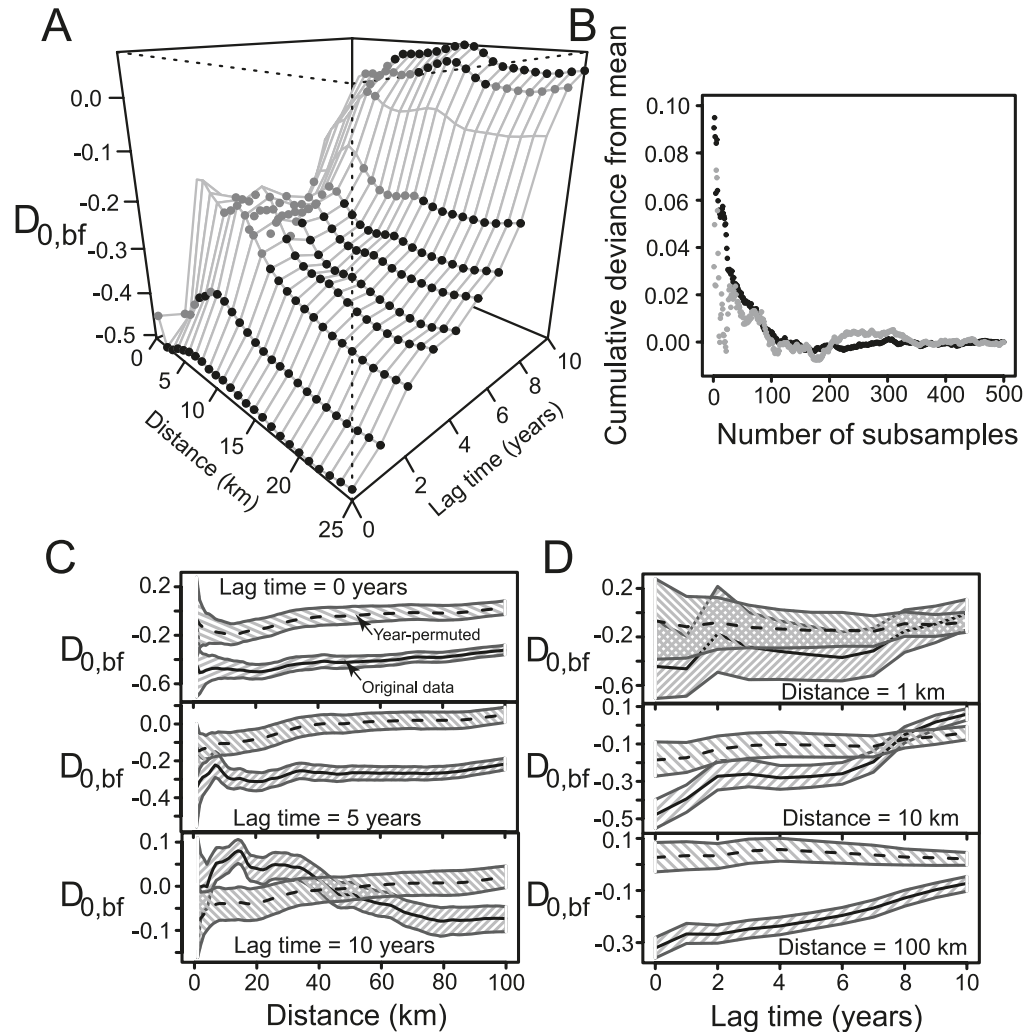
The results of our analysis are plotted in Figs. 2 and 3. Figure 2A shows  $D_{0,bf}(s, t)$ , the additional risk of forest fire following *C. occidentalis* activity. The grid surface represents all points, and solid and shaded circles represent different levels of statistical significance. Solid points are those for which there was no overlap in the 95% confidence intervals of the original and label-permuted estimates of  $D_{0,bf}(s, t)$ , i.e., at least 95% of the subsamples gave an estimate of  $D_{0,bf}(s, t)$  that was statistically significant ( $p \leq 0.025$ ) when compared against the null (label-permuted) distribution. Shaded points represent those for which the mean value of  $D_{0,bf}(s, t)$  for the original data set fell outside the 95% confidence interval for the label-permuted estimations, i.e., the mean estimate of  $D_{0,bf}(s, t)$  across all 500 samples was statistically significant ( $p \leq 0.025$ ) when compared against the null (label-permuted) distribution. Figure 2B shows the convergence of the estimate of  $D_{0,bf}(s, t)$  as the number of subsamples increases for two different points on the surface of Fig. 2A. Figures 2C and 2D show cross sections of the spatiotemporal correlations at different lag times and distances, respectively. The confidence intervals illustrated in Figs. 2C and 2D are formed by the 2.5 and 97.5 percentiles of the distributions for  $D_{0,bf}(s, t)$ , both for the original data and for the year-permuted data. Note that in the top panel of Fig. 2C, the lag 0 confidence intervals overlap but the mean of distribution for the original data is outside the confidence interval of the null (year-permuted) envelope and the corresponding point in Fig. 2A (distance = 1 km, lag = 0 years) is shaded. In contrast, the same panel shows that by 20 km, there is no overlap between the two confidence intervals and the corresponding point in Fig. 2A (distance = 20 km, lag = 0 years) is solid.

We see that budworm outbreaks lead to a significantly decreased risk of forest fire. In the immediate vicinity of a spruce budworm outbreak, the risk of fire during the first year following the outbreak is reduced by ~50%. This reduction in fire risk decreases steadily over the next 5–10 years following the budworm damage and also declines with increasing distance from the infection center but remains significant to at least 100 km, the longest length scale considered in this study.

Figure 3 is identical in layout to Fig. 2 and shows the effect of forest fire on future risk of *C. occidentalis* damage.



**Fig. 2.** (A)  $D_{0,bf}(s, t)$  indicating increased ( $D_{0,bf} > 0$ ) or decreased ( $D_{0,bf} < 0$ ) risk of forest fire following western spruce budworm infestation. Points on the surface plot indicate different levels of statistical significance as explained in the text. (B) Difference between the mean after a given number of subsamples have been averaged and the final mean achieved after 500 subsamples for two different points in the range of space and time considered (solid circles, distance = 20 km, lag time = 1 year; shaded circles, distance = 80 km, lag time = 7 years). (C) Cross sections of the  $D_{0,bf}(s, t)$  distributions for lags of 0 years (top panel), 5 years (middle panel), and 10 years (bottom panel). Both the original data (solid line, mean; right hatching, 95% confidence envelope) and the year-permuted data (broken line, mean; left hatching, 95% confidence envelope) are shown to illustrate the sampling distributions used to assess statistical significance. Areas where the confidence envelopes overlap are cross-hatched. (D) Cross sections of the  $D_{0,bf}(s, t)$  distributions for distances of 1 km (top panel), 10 km (middle panel), and 100 km (bottom panel).



In the same year of a fire, there is a large (25%) but not statistically significant increase in the risk of *C. occidentalis* infestation in areas within 1 km of the fire. (The lack of statistical significance is due in part to the large variance for very small values of  $s$ ; the sample size of fire and insect points within a distance  $s$  shrinks as  $s \rightarrow 0$ .) All other distances show a statistically significant decreased risk of *C. occidentalis* infestation for 6 years following fire. The most pronounced effect is 2 years following fire in which areas within 25 km of the fire show up to a 47% decreased risk of *C. occidentalis* infestation. The risk of budworm damage recovers slowly in the period 2–6 years following fire, although this recovery is not uniform across all spatial distances.

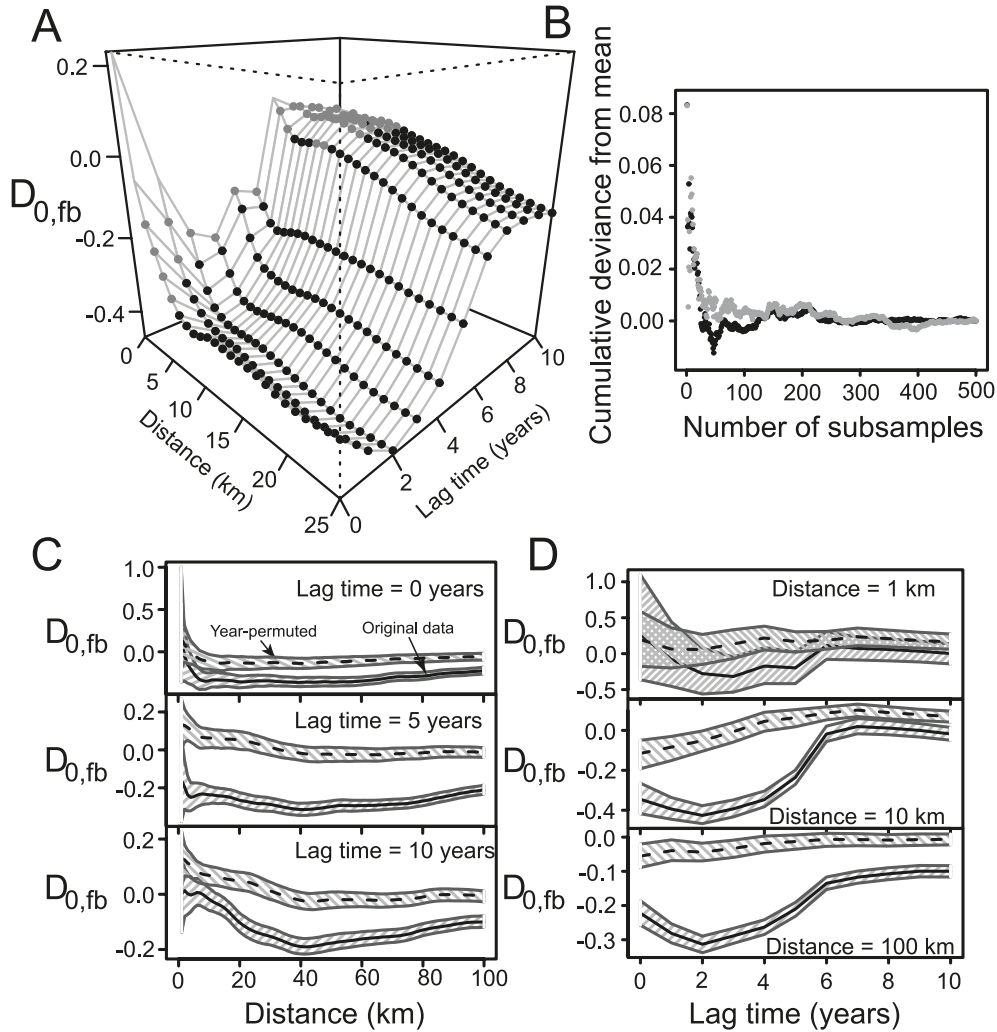
Because the date of budworm damage were resolved only

to the level of year, it is impossible to say whether, for lag = 0, budworm damage or fire actually came first. In this case, the space–time  $K_{12}(s, t)$  coincides with the more traditional cross- $K$ -function  $K_{12}(s)$ , and it is difficult to draw conclusions about the temporal order (and subsequently the causality) of the interaction. Nevertheless, in both cases, the lag = 0 results corresponds closely to the overall trends in the space–time surface and it is reasonable to assign some biological significance to these lag = 0 correlations (some, but not all, of which are statistically significant).

## Discussion

Analyzing the empirical data on actual fire and insect outbreaks enables us to determine the net effect of these com-

**Fig. 3.** (A)  $D_{0,fb}(s, t)$  indicating increased ( $D_{0,fb} > 0$ ) or decreased ( $D_{0,fb} < 0$ ) risk of western spruce budworm outbreak following a forest fire. (B) Difference between the mean after a given number of subsamples have been averaged and the final mean achieved after 500 subsamples for two different points in the range of space and time considered (solid circles, distance = 20 km, lag time = 1 year; shaded circles, distance = 80 km, lag time = 7 years). (C) Cross sections of the  $D_{0,fb}(s, t)$  distributions for lags of 0 years (top panel), 5 years (middle panel), and 10 years (bottom panel). Both the original data (solid line, mean; right hatching, 95% confidence envelope) and the year-permuted data (broken line, mean; left hatching, 95% confidence envelope) are shown to illustrate the sampling distributions used to assess statistical significance. Areas where the confidence envelopes overlap are cross-hatched. (D) Cross sections of the  $D_{0,fb}(s, t)$  distributions for distances of 1 km (top panel), 10 km (middle panel), and 100 km (bottom panel).



peting factors on the probability of fire. While additional field studies will be required to study the balance between the altered risks of surface and canopy fires due to insect activity in this system, our analysis suggests that the net affect, on average, is that *C. occidentalis* outbreaks decrease forest fire risk in the 5–10 years following an outbreak. The results shown in Fig. 2 directly contradict the common assumption that insect damage necessarily increases the risk of forest fire (McCullough et al. 1998; Dale 2001; O’Driscoll 2004; Robbins 2004). While studies suggest that this may be the case for certain insects in particular forests (e.g., jack pine budworm (*Choristoneura pinus*) in jack pine (*Pinus banksiana* Lamb.) forests (McCullough et al. 1998)), the overall situation is more complex. Previous studies have suggested several mechanisms by which insect damage may promote

or inhibit fires via changes in the vertical distribution of fine fuels within the canopy and changes in the light, temperature, and humidity conditions within the forest (Knight 1987; Reid 1989; Despain 1990; Kulakowski et al. 2003). For example, insect-related damage can lead to extensive patches of dead needles within the forest canopy. If these remain in the overstory, the resulting matrix of fine, dry fuels may increase the risk of a stand-replacing canopy fire (Knight 1987; McCullough et al. 1998). On the other hand, if dead needles quickly fall off the trees, fuel in the canopy layer may decrease, reducing the risk of canopy fire (Despain 1990). Similarly, insect activity can alter the occurrence of surface fires. If needle drop occurs owing to insect activity and dead needles accumulate on the forest floor, this increases the availability of dry surface fuels,

promoting the occurrence of surface fires (McCullough et al. 1998). Conversely, defoliation following insect activity can lead to an opening of the canopy that promotes growth of understory herbs and other ground cover (Reid 1989), and the resulting increase in understory moisture may lead to a decreased risk of surface fires following insect defoliation (Kulakowski et al. 2003).

Figure 3 shows that, except in the immediate spatiotemporal vicinity of a fire, fire is associated with a decreased risk of budworm activity for at least 6 years. Budworm activity at all spatial distances slowly recovers over that 6-year period, although by the seventh year after fire, budworm activity in the immediate vicinity of the fire (<8 km) is insignificant (e.g., Fig. 3C, top), while budworm activity at farther distances remains significantly depressed for at least 10 years following fire (e.g., Fig. 3C, bottom). The largest decrease in budworm activity is at a distance of ~40 km from the fire, and the differential impact at 40 km versus 0 km increases over time since fire. One hypothesis to explain these complex spatiotemporal patterns would be a gradual rearrangement of the budworm activity in space and time in response to postfire conditions. Although the years immediately following a fire may present budworm with limited opportunity for infestation, the 7-year period over which activity resumes would be consistent with the time required for insect infestation on young trees established following fire-related mortality. In addition, increasing budworm infestation on young trees may actually redistribute budworms in the region, leading to a decreased risk in neighboring areas. These hypotheses need further investigation, but this approach allows us to identify both long-term and short-term spatiotemporal correlations between forest fires and subsequent insect outbreaks.

Although not statistically significant in this analysis, the distance = zero increase in *C. occidentalis* infestation risk in summers of high forest fire activity is consistent with the overall shape of the curve in that region and may indicate biologically significant local responses to fire that deserve further investigation. One often-cited possibility is that trees that are damaged but not killed by a forest fire may be less able to defend themselves against insect infestation and may act as epicenters for outbreak that then spread into surrounding healthy forest (Knight 1987; McCullough et al. 1998; Dale 2001). However, these studies have focused on interactions between bark beetles and forest fires, and there are several reasons to suggest that weakened tree defenses are unlikely to play a major role in precipitating outbreaks of western spruce budworm. Previous work has demonstrated that the primary mechanisms of Douglas-fir resistance to *C. occidentalis* are high growth rate and late bud burst phenology as opposed to chemical defenses via secondary compounds (Chen et al. 2001, 2002), and studies of the closely related spruce budworm (*Choristoneura fumiferana*) suggest that outbreaks are not initiated by a single epicenter but occur in synchrony over large areas (Royama 1984).

A second explanation for why fires may promote insect outbreaks is that forest fires perturb the balance between *C. occidentalis* and its predators or parasites. It is believed that predation on *C. occidentalis* larvae by ants and birds is effective in regulating budworm populations at endemic levels but is ineffective once populations have reached outbreak

levels (Torgersen and Campbell 1982; Campbell et al. 1983; Torgersen et al. 1990). If the ecosystem disruption of a forest fire allows *C. occidentalis* to escape from its predators long enough to reach outbreak levels, this may account for the increased risk of insect outbreak during a particularly active fire season. This may occur because of postfire changes in diet selection among birds known to feed on both seeds, which become more prevalent following a forest fire, and *C. occidentalis* larvae. (Of the five bird species known to feed on *C. occidentalis* (*Hesperiphona vespertina*, *Spinus pinus*, *Spizella passerina*, *Junco hyemalis*, and *Piranga ludoviciana*), four also feed on seeds (Torgersen and Campbell 1982).) Finally, although it is reasonable to suspect that external environmental drivers are associated independently with increased insect and fire activity, the results suggest otherwise. As discussed previously, the  $D_0$  function represents an increase in risk associated with spatiotemporal interactions above and beyond those that are purely spatial or temporal in nature. External environmental fluctuations would not contribute to peaks or valleys in  $D_0$ . Secondly, we see that insect and fire activity are generally negatively correlated within a given summer (i.e., the lag = 0 correlations are mostly negative), which suggests that budworm activity and forest fires are not simply correlated as would be expected if both were independently promoted by external drivers such as drought.

## Conclusion

The interactions between fires and *C. occidentalis* outbreaks found in this study have important implications for the management of forests in western North America. In particular, future climate change and shifting policies regarding fire suppression are likely to have significant consequences for insect populations, forest fires, and their interactions, and an improved understanding of these complex feedbacks has been cited as a research priority (Ayles and Lombardero 2000). While our analysis has focused exclusively on the interaction between *C. occidentalis* and forest fires, our approach provides a general method for exploring space–time interactions among different modes of disturbance wherever long-term, spatially explicit historical records are available.

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