



Predisposition to bark beetle attack by root herbivores and associated pathogens: Roles in forest decline, gap formation, and persistence of endemic bark beetle populations

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ABSTRACT

Bark beetles are largely known for their ability to undergo intermittent population eruptions that transform entire landscapes and pose significant economic hardships. However, most species do not undergo outbreaks, and eruptive species usually exert only minor disturbances. Understanding the dynamics of tree-killing noneruptive species can provide insights into how beetles persist at low densities, and how some spatiotemporal patterns of host predisposition may more likely favor breaching eruptive thresholds than others. Elucidating mechanisms behind low-density populations is challenging, however, due to the requirement of long-term monitoring and high degrees of spatial and temporal covariance. We censused more than 2700 trees annually over 7 years, and at the end of 17 years, in a mature red pine plantation. Trees were measured for the presence of bark beetles and wood borers that breed within the primary stem, root weevils that breed in root collars, and bark beetles that breed in basal stems. We quantify the sequence of events that drive this decline syndrome, with the primary emergent pattern being an interaction between below- and above-ground herbivores and their fungal symbionts. This interaction results in an expanding forest gap, with subsequent colonization by early-successional vegetation. Spatial position strongly affects the likelihood of tree mortality. A red pine is initially very likely to avoid attack by tree-killing *Ips* beetles, but attack becomes increasingly likely as the belowground complex spreads to neighboring trees and eventually make trees susceptible. This system is largely internally driven, as there are strong gap edge, but not stand-edge, effects. Additional stressors, such as drought, can provide an intermittent source of susceptible trees to *Ips* beetles, and elevated temperature slightly accentuates this effect. New gaps can arise from such trees as they subsequently become epicenters for the full complex of organisms associated with this decline, but this is not common. As *Ips* populations rise, there is some element of positive feedback, in that the proportion of killed trees that were not first colonized by root organisms increases. This positive feedback is very weak, however, and we propose the slope between beetle population density and reliance on host stress as a quantitative distinction along a gradient from noneruptive through eruptive species. Almost all trees colonized by *Ips* were subsequently colonized by wood borers, likely a source of negative feedback. We discuss implications to our overall understanding of cross-scale interactions, between-guild interactions, forest declines, and eruptive thresholds.

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1. Introduction

The ability of bark beetles to undergo largescale outbreaks and transform landscapes is widely recognized, and has been the attention of intense study (Coulson, 1979; Romme et al., 1986;

Veblen et al., 1994). However, the dynamics by which populations of some beetle species transition from noneruptive to eruptive conditions, and the extent to which these dynamics reflect within-stand versus migratory processes, are not well understood, and pose some fundamental questions about population dynamics and forest disturbance (Okland et al., 2005; Friedenberget al., 2007). One approach to better understanding these dynamics, and the overall role of bark beetles in forest ecosystems, is through improved knowledge of tree-killing species that do not undergo

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landscape eruptions. Such species may provide a valuable conceptual bridge between the majority of bark beetle species that never attack live trees and those few that kill vast acreages following extended periods during which they persist at barely detectable levels. These categories of tree-killing beetles also pose different challenges to forest management, as species such as the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, often go long periods without having much impact and then suddenly cause largescale losses, while others, such as many *Ips* species, typically exert more chronic damage (Fettig et al., 2007). Such categories are actually gradations, as species such as the fir engraver, *Scolytus ventralis* LeConte, and Douglas fir beetle, *Dendroctonus pseudotsugae* Hopkins, show intermediate behaviors along this continuum.

A key distinction between eruptive versus noneruptive dynamics appears to involve whether bark beetles can generate self-perpetuating dynamics, specifically whether positive feedbacks arising from their ability to coordinate mass attacks (Wood, 1982) can outweigh negative feedbacks arising from host tree resistance, resource availability, natural enemies and adverse weather (Reeve, 1997; Bohlmann et al., 2000; Safranyik and Carroll, 2006). This has often been described as threshold separating population densities at which negative versus positive feedbacks predominate (Berryman, 1976; Mawby et al., 1989). A local population's impetus to surpass this threshold can arise from elevated temperatures that reduce mortality and shorten generation time (Bentz et al., 1991; Hicke et al., 2006), or from widespread physiological stresses that may compromise tree defenses (Koricheva et al., 1998; Safranyik and Carroll, 2006).

We currently know little about the spatiotemporal patterns of external drivers that influence host susceptibility, and how they may affect beetle population responses. However, such spatiotemporal patterns could influence whether beetle populations simply rise and fall as underlying stresses vary, or suddenly surpass an eruptive threshold beyond which they become less reliant on external drivers. Likewise, we know less about potential chronic sources of reduced resistance to bark beetles than acute stressors such as severe drought (Breshears et al., 2005), lightning (Coulson et al., 1983) and defoliation (Wallin and Raffa, 2001). Root herbivory may pose such an underlying chronic stress that influences the behavior, population dynamics and impacts of bark beetles (Owen et al., 2005).

A chronic decline and mortality syndrome is currently affecting mature red pines in the Great Lakes region of North America (Klepzig et al., 1991). A zone of tree mortality spreads from an epicenter, and no or very few living pines remain in these gaps. Trees along the margins show reduced radial and crown growth, but those further into the stand show no symptoms. This epicenter expands as more trees die, and trees along the new margin become symptomatic. We have observed no consistent abiotic differences between declining and asymptomatic stands, despite evaluating a wide range of factors (Klepzig et al., 1991; Erbilgin and Raffa, 2003).

Declining stands generally have higher populations of root- and basal-stem-colonizing beetles than asymptomatic stands (Klepzig et al., 1991; Erbilgin and Raffa, 2003). This complex of phloem feeding insects and their microbial associates partitions the belowground resource based on host morphology and physiology. Adults of the pine root collar weevil, *Hylobius radialis* Buchanan, oviposit below the soil and the larvae feed and develop within the root collars of live trees. The red turpentine beetle, *Dendroctonus valens* LeConte, breeds in either live or dead trees. Adults enter slightly above the soil line, and the larvae develop in the basal stem, root collar and primary roots. Both species are closely associated (71–80%) with *Leptographium* fungi, of which they are moderately efficient vectors (Klepzig et al., 1991). Root grafts link almost all trees in these stands, and *Leptographium* grow through

these connections (Klepzig et al., 1991; Erbilgin and Raffa, 2003). The main stems are colonized by bark beetles in the genus *Ips*, primarily *Ips pini* (Say) and, to a lesser extent, *I. grandicollis* (Eichhoff). The *Ips* species are closely associated with and are efficient vectors of the fungus *Ophiostoma ips* (Kopper et al., 2004). Several species of *Monochamus* wood borers, primarily *M. titillator* (F.), also colonize the main stem. They develop in the phloem as early instar larvae, and then progress into the sapwood where the later instars complete development.

Pinus resinosa respond actively to attacks by root- and stem-colonizing insects and their symbionts (Raffa and Smalley, 1995; Klepzig et al., 1996). Trees rapidly increase their concentrations of phenolics, monoterpenes, and diterpene acids at the point of attack. The resulting concentrations are highly toxic and repellent to the beetles and inhibitory to their associated fungi (Wallin and Raffa, 2000; Raffa et al., 2005). However, many of these same compounds are attractive to members of this complex at low concentrations (Rieske and Raffa, 1991; Raffa et al., 2005).

Based on these observations, we propose the following model. Root- and basal-stem-colonizing beetles enter selected trees and vector *Leptographium* fungi. These organisms do not kill mature trees, but compromise their ability to resist *Ips*-*Ophiostoma* attacks in the main stem. *Leptographium* spread through root grafts, leading to subsequent attacks by *Ips* spp. in neighboring trees, and consequently to a radial pattern of decline and mortality. As trees die, they open the canopy and create conditions amenable to early-successional vegetation.

The purpose of this research was to test two components of this model, the sequence of colonization events within trees, and the spatiotemporal pattern of host infestation and mortality at the stand level. Our overall objective is to generate stand-level information to interface with prior individual-tree and between-stand data on this system. We hope that this will provide a better understanding of the structures of eruptive thresholds and the role of host-mediated transitions in between-guild insect–fungal interactions in disturbance and gap dynamics.

2. Methods

2.1. Spatially explicit evaluations of tree condition and insect colonization

The study site consisted of a *P. resinosa* plantation that was established on a 2 m × 2 m grid in 1963 on sandy soil in Sauk Co, Wisconsin, USA. We mapped this stand in 1986, and made annual observations of all 2715 trees from 1986 to 1992. Observations were made in mid-autumn to early winter, after annual periods of peak insect activity were complete. We catalogued each tree as (a) live or dead, based on foliar coloration, (b) colonized (and if so the number of attacks) or not colonized by *D. valens* (turpentine beetle), based on resin tubes and frass at the base of the tree, (c) colonized or not colonized by *Ips* spp. (pine engravers), based on emergence holes and boring frass on the bottom 3 m of the main stem, and (d) colonized or not colonized by *Monochamus* spp. (wood borers), based on oviposition scars and boring frass on the bottom 3 m of the main stem. We also catalogued a subsample of trees as (e) colonized or not colonized by *Hylobius* spp. (root weevils), based on root injury and resinosis in an excavated area around the root collar. After 1992, only dead trees were recorded on an annual basis until 1995, until a complete census was again taken in 2002.

2.2. Vegetation sampling

At the beginning of the study, the site contained a small gap where red pine trees had died and fallen over. There were no other

trees in this gap. After 10 years, we censused all trees greater than 12.5 mm DBH in this gap. We recorded diameter and species of each tree, and height of those equal to or greater than 3 m.

2.3. Statistical analysis of sequence and distribution patterns of insect colonization and tree mortality

We modeled tree mortality in relation to turpentine beetle, pine engraver, and root weevil colonization and pine engraver colonization in relation to turpentine beetle and root weevil colonization using logistic regression. Likewise, we modeled wood borer colonization in relation to turpentine beetle, root weevil, and pine engraver colonization using logistic regression. We modeled turpentine beetle colonization in relation to root weevil colonization using Poisson regression, as these responses were counts of the number of pitch tubes on a tree rather than presence/absence data. When models contained a term for root weevils, a subset of the data was used, i.e., those trees that were sampled for root weevils by excavating the root collars. The other variables were measured on all trees in all years.

To account for temporal autocorrelation, a 1-year lag was incorporated in the models (i.e., probability of an event based on the events in year prior). To account for spatial autocorrelation, spatial lags based on two neighborhood structures in the previous year were considered. The first neighborhood covariate was defined by summing 0/1 responses in the nearest surrounding square of trees (i.e., potential total of 8, unless on an edge). For example, if analyzing the effect of pine engravers, a first-order spatial covariate would have a value of two for a given tree if the trees immediately to the right and left contained pine engravers but neighbors were otherwise uninfested. The second neighborhood covariate was defined by the sum of 0/1 responses of trees that were two trees removed from the measured tree (potential total of 16).

To examine edge effects, we modeled tree mortality in relation to two variables defining two potential sources of edge effects: the boundary of the plantation under study, and the boundary along the gap formed by dead trees. Logistic regression was performed while accounting for spatial-temporal autocorrelation in a similar manner as before.

Statistical inference of the model parameters was made via maximum likelihood. For all models, we used backward elimination with Akaike's information criterion (AIC) (Akaike, 1973) to guide variable selection. Whenever the second neighborhood was selected, the first neighborhood was included in the model regardless of its statistical significance, for ease of interpretation. If the best model determined in this manner contained the two neighborhoods as covariates, we further compared it with the model that combined the two types of neighborhood into one large neighborhood for dimension reduction and for ease of graphical presentation. The comparison was made based on AIC such that the model with the lowest AIC values was deemed the final best model.

2.4. Weather modeling of population trends and spatiotemporal sequence

Daily temperature interpolation values for Spring Green, Wisconsin (3 km from the study site; 43.1805° N, -90.1534° W) were obtained from Daymet US Data Center (<http://www.daymet.org>) from 1987 to 1995 (Thornton et al., 1997). Values included temperature minimum, maximum, and means, as well as measures of precipitation. Six different seasons were defined depending on known phenologies of the system (e.g., when *Ips* begin flying or when drought stress begins to accumulate; Aukema et al., 2005). For each of these seasons, summary weather variables were created such as total precipitation, number of days with no

rain, average and maximum temperatures, and heating days (sum of the daily maximum temperatures).

We examined the effects of these weather variables on measures of tree mortality, such as number of total dead trees in the plantation, or along the edge, with year being the unit of replication, using multiple regressions. Backward elimination procedures were used to remove candidate variables until all remaining variables were significant at $\alpha = 0.05$. We also used regression to examine the effects of weather variables (as defined above) on the percentage of trees killed within the plantation that were beyond the gap edge using simple linear regression. Inspections of graphs between the candidate variables guided model choices, such as transformations of the predictor and/or response to satisfy assumptions of homoscedasticity and normality of residuals.

3. Results

3.1. Gap progression

At the beginning of the study in 1986, a small gap measuring only 10.9 m wide by 14.6 m across had appeared in the plantation where red pine had died and fallen (Fig. 1A). Around this gap, were approximately 50 more standing dead trees. By 2002, a 10-fold increase in mortality had occurred (Fig. 1B). The gap had expanded to approximately 75 m in diameter, with no living pines persisting in the center.

3.2. Sequence of insect colonization and tree mortality

The probability of tree death was most highly correlated with trees having pine engravers, and increased with the number of dead trees in the surrounding two square rings of neighbors (Table 1). If a tree had pine engravers, there was a greater than 80% chance of death within a year (Fig. 2A). Trees without any neighboring dead trees were unlikely to die. The probability of death increased to over 50% once more than 16 of the nearest 23 trees were dead even if the tree was not infested by pine engravers.

Turpentine beetles were most likely to infest trees that were near trees colonized by root weevils and/or other turpentine

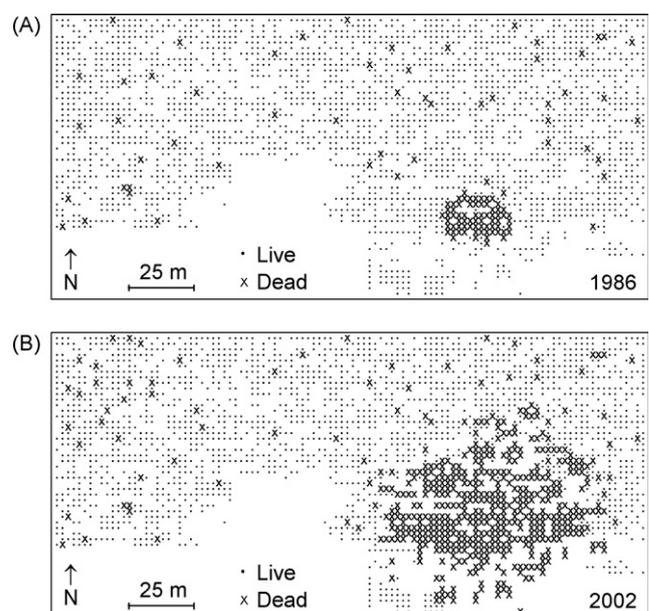


Fig. 1. Stem map in (A) 1986 and (B) 2002 of the red pine stand near Spring Green, Wisconsin, USA. A small number of live trees ($n = 226$) in the western portion of the plot are omitted for graphing purposes.

Table 1

Spatiotemporal models of tree death and insect activity in a red pine plantation, 1986–1992. Model equations should be read from left to right. Standard errors of coefficient estimates are in parentheses. Terms in italics are statistically significant ($p < 0.05$).

Response	Intercept	Root weevils ^a	Turpentine beetles	Pine engravers	Tree mortality	Spatial neighborhoods			AIC
						1st	2nd	Both	
Full dataset									
Tree mortality	-7.070 (0.266)		-0.043 (0.142)	9.255 (0.365)		0.056 (0.174)	0.556 (0.100)		401.98
Tree mortality	-7.072 (0.266)			9.235 (0.357)		0.056 (0.173)	0.554 (0.100)		400.06
Tree mortality	-7.03 (0.262)			9.230 (0.354)				0.372 (0.041)	401.75
Pine engravers	-4.206 (0.075)		0.627 (0.064)			0.715 (0.105)	0.859 (0.063)		2246.7
Pine engravers	-4.204 (0.075)		0.629 (0.064)					0.810 (0.039)	2245.6
Wood borers	-7.608 (0.388)		0.348 (0.090)	3.935 (0.219)	3.898 (0.422)	0.051 (0.165)	0.124 (0.102)		768.88
Wood borers	-7.609 (0.389)		0.349 (0.089)	3.936 (0.219)	3.900 (0.422)			0.099 (0.065)	766.98
Wood borers	-7.604 (0.389)		0.355 (0.089)	3.935 (0.219)	3.977 (0.418)				767.22
Subsample (only trees examined for root weevils)									
Tree mortality	-4.899 (0.379)	0.139 (0.451)	-0.080 (0.124)	6.933 (0.443)		0.194 (0.195)	0.337 (0.112)		229.83
Tree mortality	-4.895 (0.357)			6.932 (0.424)		0.192 (0.193)	0.332 (0.111)		226.41
Tree mortality	-4.891 (0.357)			6.946 (0.424)				0.284 (0.058)	224.67
Pine engravers	-2.274 (0.128)	1.005 (0.173)	0.181 (0.064)			0.345 (0.114)	0.463 (0.070)		911.7
Pine engravers	-2.270 (0.127)	1.005 (0.173)	0.182 (0.064)					0.424 (0.045)	910.26
Turpentine beetles	-2.181 (0.107)	1.179 (0.138)				0.053 (0.033)	0.051 (0.023)		1276.7
Turpentine beetles	-2.181 (0.107)	1.178 (0.138)						0.052 (0.015)	1274.7
Wood borers	-6.405 (0.723)	0.492 (0.288)	0.131 (0.090)	2.430 (0.289)	4.331 (0.741)	-0.073 (0.176)	0.040 (0.108)		443.85
Wood borers	-6.402 (0.722)	0.482 (0.287)	0.131 (0.090)	2.434 (0.283)	4.334 (0.736)				440.08

^a Models incorporating a covariate for the presence of root-boring weevils were fit to a subset of the data that included only trees examined for presence/absence of these insects (see Section 2).

beetles (Fig. 2B). These spatial effects were not as pronounced as for tree mortality, however. If a tree had root weevils, and all of its neighboring trees had at least turpentine beetle attack, then the likelihood that it would be colonized by turpentine beetles reached 50%.

The probability that a tree would be attacked by pine engravers increased with the number of turpentine beetles colonizing it (Fig. 2C). This likelihood increased with the number of trees colonized by pine engravers within the immediate area (Fig. 2C). For example, in the absence of neighboring pine engravers, the likelihood that a tree would be colonized by pine engravers reached 70% when eight turpentine beetles were present in the basal stem. Pine engraver activity in the surrounding trees increased the likelihood of pine engraver colonization. If 10 or more of 23 trees in the surrounding locality contained evidence of pine engraver activity, there was almost a 100% chance that a tree would be colonized by pine engravers.

When pine engraver activity was examined on a subset of the data including trees sampled for root weevils, a similar pattern ensued. The presence of root weevils increased the likelihood of colonization by pine engravers, and appeared to do so even more than turpentine beetles did (Fig. 2D). A tree being colonized by root weevils increased the likelihood of pine engraver colonization by approximately 15%. This effect was overridden, however, as more trees in the surrounding neighborhood were colonized by pine engravers. That is, once 10–15 neighboring trees contained pine engravers, the likelihood of a tree being colonized by pine

engravers reaches 100%, regardless of whether root weevils were present or not.

Wood borers were almost entirely found in dead trees, and they were never found in live trees without other insect activity (Fig. 2E). The biggest predictor of wood borer presence was colonization by pine engravers. Sixty to 100% of trees with pine engraver activity contained wood borers, and this likelihood increased with the number of turpentine beetles in the tree also.

To examine the extent to which high population sizes of pine engravers might reduce their reliance on root infection for tree-killing behavior, we regressed the proportion of killed trees that were located on the gap margin (i.e., a surrogate of dead trees with prior root infection) against the number of killed trees (i.e., a surrogate of *Ips* spp. population size). The results indicate a significant inverse relationship, but with a relatively weak slope (Fig. 3). Thus, the reliance of *Ips* spp. on prior colonization by root or basal-stem insects is only slightly affected by *Ips* spp. population density.

3.3. Effects of spatial location and edge on tree mortality

We fit additional models of tree death excluding the insect complex, thereby solely examining the role of spatial location in tree mortality (Fig. 4). The relationship between probability of tree death and incidence of neighboring dead trees is sigmoidal regardless of whether the tree is located on an edge or within the study plantation. The space between the two planes differs,

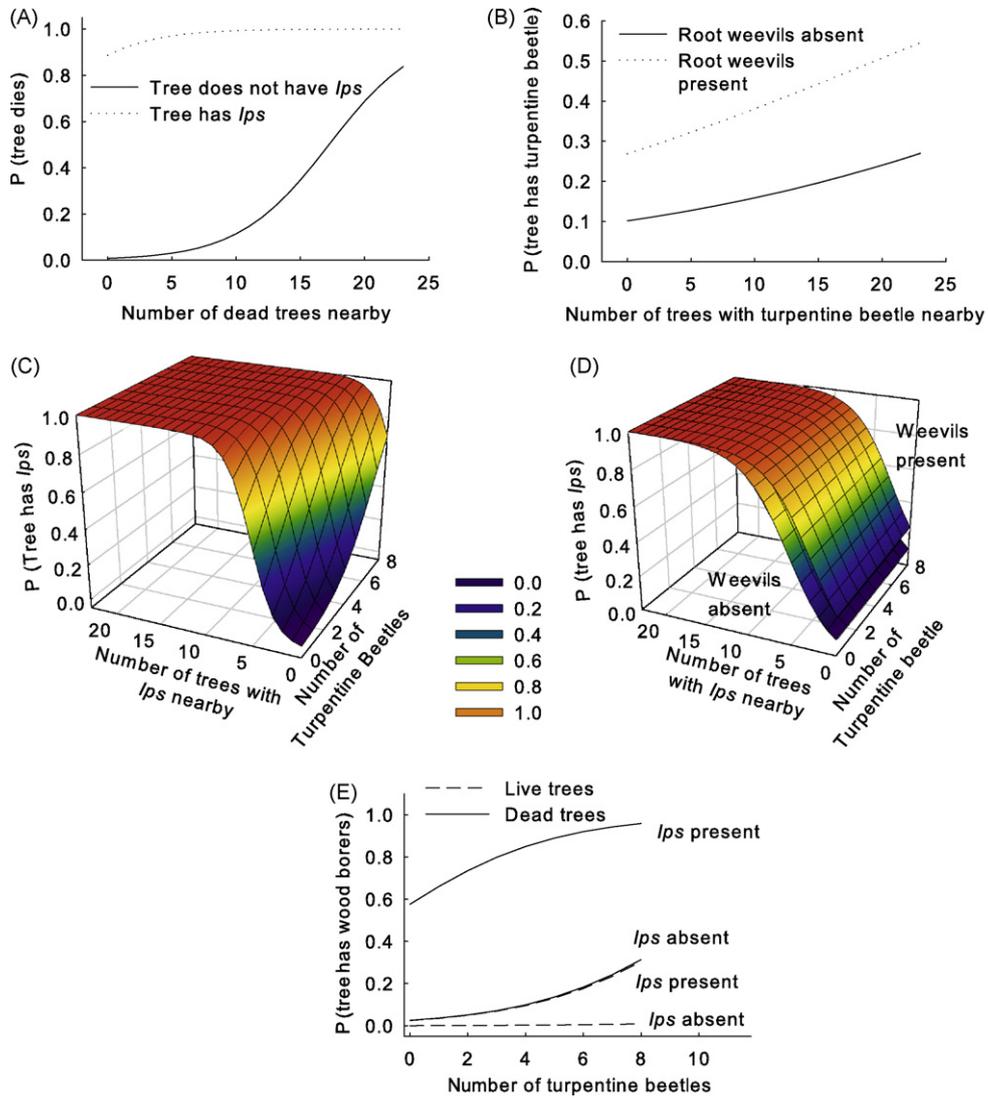


Fig. 2. Probability curves for events attributed to biological agents or tree death in a red pine plantation (see Table 1; $n = 2,715$ trees mapped from 1986 to 1992). (A) Probability that a tree dies as a function of the number of dead trees nearby, in the presence/absence of pine engravers (*Ips* spp.). (B) Probability that a given tree has turpentine beetles given neighboring trees with turpentine beetles and the presence/absence of root weevils. (C and D) Probability that a tree has *Ips* spp. as a function of neighboring trees with *Ips* spp. and the number of turpentine beetles. The complete dataset is utilized in C, while a subset of data examining the likelihood of *Ips* as a function of the presence/absence of root weevils is used in D. (E) Probability that a tree has wood borers as a function of the number of turpentine beetles and the presence/absence of *Ips* spp. in live/dead trees.

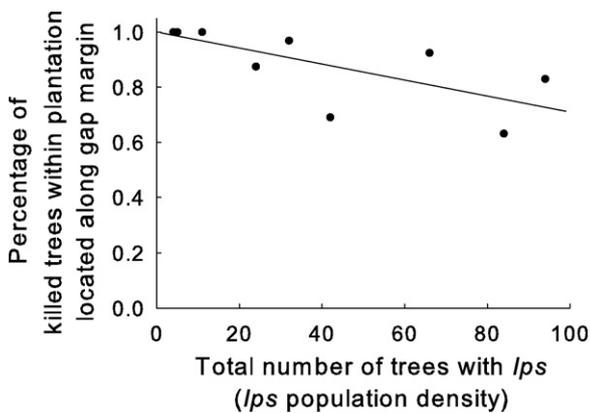


Fig. 3. Percentage of trees along the gap killed by *Ips* as a function of the total number of trees with *Ips*, 1987–1995. Almost all trees along the gap are infested with *Leptographium*, root weevils, and/or turpentine beetles (Erbilgin and Raffa, 2003). Equation is $y = 1 - 0.0029x$; $F_{1,8} = 19.29$, $p < 0.0023$; $R^2 = 0.707$.

however, depending on how the edge is defined (i.e., forest gap or plantation). Location on the edge of the plantation had no effect. That is, there is no difference between likelihood of death when surrounded by dead neighbors when located on the edge of the plantation versus inside the plantation (Fig. 4A). Table 2 displays a logistic regression model for this plane, and the coefficient estimate for ‘edge’ is not significant when defined by plantation edge. In contrast, when the edge caused by an apparent gap inside the plantation is evaluated, there is a strong effect. The probability of death when surrounded by dead neighbors is up to 17% higher when the tree is on the edge of this gap (i.e., space between planes in Fig. 4B). The corresponding ‘gap edge’ coefficient is statistically significant in the best-fitting corresponding model in Table 2.

3.4. Weather effects on tree mortality

Drought appears to increase the likelihood of a tree being attacked and killed by *I. pini*, regardless of whether the trees are located along the gap edge or further into the plantation. *P. resinosa*

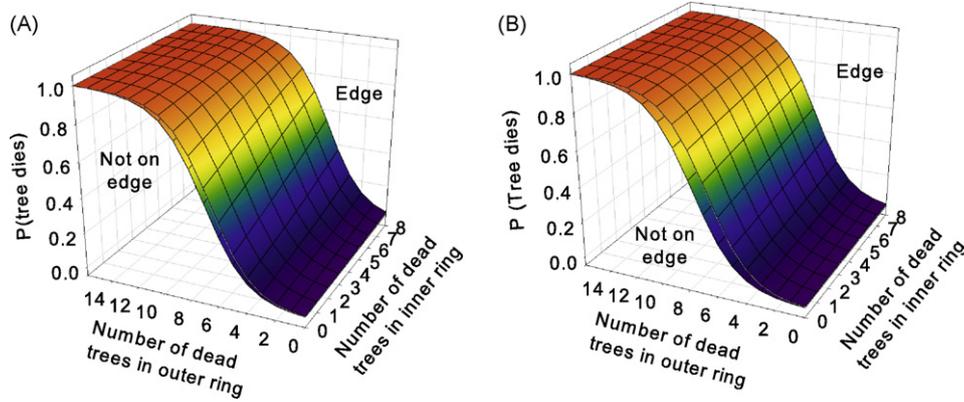


Fig. 4. Probability that a tree dies as a function of proximate dead trees. Axes indicate the number of dead trees in nearest surrounding ring and second nearest surrounding ring (i.e., first and second order neighborhoods). The overlaid planes in each figure indicate trees located/not located on the edge of the study area (A), and the edge of the gap (B).

Table 2

Effect of location of a tree on an edge, defined by study area versus gap, on tree mortality in a red pine plantation, 1986–1992. Model equations should be read from left to right. Standard errors of coefficient estimates are in parentheses. Terms in italics are statistically significant ($p < 0.05$).

Response	Intercept	Edge defined by		Spatial neighborhoods			AIC value
		Study area	Pocket gap	1st	2nd	Both	
Tree mortality	-4.473 (0.079)	-0.330 (0.239)		<i>0.148</i> (0.064)	<i>0.690</i> (0.037)		2540.1
Tree mortality	-4.431 (0.078)	-0.342 (0.238)				<i>0.509</i> (0.021)	2573.8
Tree mortality	-4.501 (0.076)		<i>0.685</i> (0.241)	<i>0.070</i> (0.070)	<i>0.676</i> (0.037)		2534.4
Tree mortality	-4.461 (0.075)		<i>0.276</i> (0.234)			<i>0.494</i> (0.026)	2574.7

mortality increases when the total amount of precipitation between June and August is low. For example, the total number of dead trees can be modeled $\text{sqrt}(y) = 10.48 - 0.16x$, where x is the sum of daily precipitation in cm ($F_{1,14} = 18.96$, $p = 0.0006612$; adjusted $R^2 = 0.5448$). Similarly, the number of dead pines located each year on the margin of the plantation can be modeled $\text{sqrt}(y) = 9.73 - 0.14x$ ($F_{1,14} = 18.48$, $p = 0.0007359$; adjusted $R^2 = 0.5381$).

These models can be slightly improved by incorporating temperature. The total number of dead trees could be explained by a similar model $\text{sqrt}(y) = -6.11831 - 0.08832x_1 + 0.79469x_2$, where x_1 is the total precipitation between April and August and x_2 is the average daily temperature in Celsius ($F_{2,13} = 10.14$,

$p = 0.002217$; adjusted $R^2 = 0.5494$). Similarly, the total number of dead trees in the gap increased with decreasing precipitation and increasing temperatures between April and August, $\text{sqrt}(y) = -5.21807 - 0.07509x_1 + 0.70465x_2$, although the temperature coefficient is not statistically significant ($p = 0.0510$) ($F_{2,13} = 8.194$, $p = 0.004983$; adjusted $R^2 = 0.4896$).

Overall, the percentage of trees killed that had predisposing factors such as prior root or basal stem infestation, based on their locations along a gap edge, increased in an exponential fashion from 80% to 100% as the plantation received upwards of 55 cm of spring and summer rain (Fig. 5). That is, under drought conditions, approximately 20% of the dying trees were located within the plantation in areas away from the forming gap, and hence were unlikely to be infested with root pathogens.

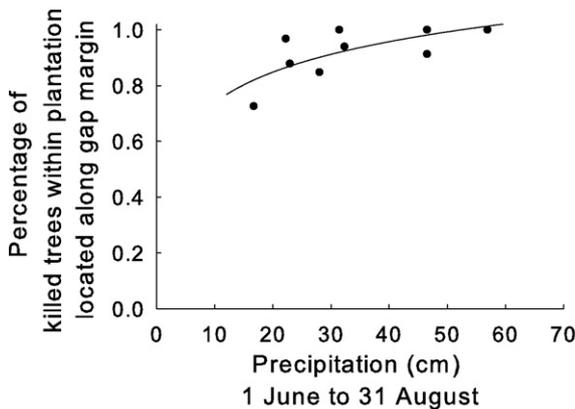


Fig. 5. Effect of summer precipitation (1 June–31 August) on the percentage of trees killed within the plantation that were along the gap edge (i.e., are infested with *Leptographium*, root weevils, and/or turpentine beetles), 1987–1995. Equation is $y = 0.377 + 0.157 \log(x)$; $F_{1,7} = 6.55$, $p < 0.0376$; $R^2 = 0.483$.

3.5. Vegetational succession following gap formation

We monitored the expanding ring of mortality to pines over 15 years, even after annual population censusing of pine trees was ceased. Following death, pines typically fell into the gap from wind disturbance within 3 years. We noted substantial, rapid establishment of broad-leaved vegetation such as grasses, forbs, and deciduous trees in the gap. After 10 years, the most common trees were *Acer negundo* L., *Quercus rubra* L., and *Prunus serotina* Ehrh (Table 3). Ten years after the beginning of this study, most of the gap had a canopy above 3 m in height.

4. Discussion

These results are consistent with the model that interactions among below- and above-ground herbivores, specifically root-colonizing weevils, basal-stem-colonizing bark beetles, upper stem-colonizing bark beetles, and their microbial associates, result

Table 3

Trees and shrubs in a gap resulting from conifer mortality due to interactions between below- and above-ground herbivores. Data were collected in 1996. No deciduous trees were present 10 years earlier at start of study.

Species	Diameter (mm)				Height ^a (m)			
	n	Mean	SE	Range	n	Mean	SE	Max
<i>Acer negundo</i> L.	91	34	2	16–86	53	4.81	0.15	7.56
<i>Celtis occidentalis</i> L.	1	56	na	na	1	5.00	na	5.00
<i>Fraxinus nigra</i> Marsh.	3	30	6	23–45	1	4.70	na	4.70
<i>Populus tremuloides</i> Michx.	3	19	1	16–20	0	na	na	na
<i>Prunus serotina</i> Ehrh.	27	30	2	16–68	16	4.62	0.25	6.68
<i>Quercus alba</i> L.	4	18	1	17–20	0	na	na	na
<i>Quercus bicolor</i> Willd.	4	25	4	16–36	2	3.29	0.29	3.58
<i>Quercus rubra</i> L.	54	33	2	15–90	29	4.32	0.19	6.78

^a Subset of trees greater than or equal to 3 m in height.

in tree mortality and gap formation in stands of *P. resinosa*. The strong effect of edge along the inner gap but not exterior to the plantation (Fig. 4) suggests that internal processes are more important drivers than insect immigration.

The upper stem-colonizing bark beetles, primarily *I. pini*, are the primary causal agents of tree death. That is, all trees successfully colonized by pine engravers are ultimately killed, and trees not colonized by pine engravers are very unlikely to die, even if colonized by root- and basal-stem insects (Fig. 2A). However, root- and basal-stem insects, particularly the pine root collar weevil, *H. radialis*, and the solitary bark beetle, *D. valens*, and their associated fungi almost always precede colonization by *Ips* spp. (Fig. 2C and D). Once they do so, the likelihood of tree death becomes very high, strongly supporting the view that root infestation compromises host resistance to stem-colonizing beetles. Almost all trees colonized by *Ips* spp. are subsequently colonized by wood boring beetles (Fig. 2E), but we found no evidence that these species are important agents of tree mortality in this system (Table 1). Because their galleries overrun those of *Ips* spp., they are likely competitors and facultative predators that exert negative feedback on the bark beetles (Schenck and Benjamin, 1969; Dodds et al., 2001).

The processes described here do not appear unique to red pine, but rather may affect other coniferous systems (Witcosky et al., 1986; Eckhardt et al., 2004) and be important contributors to forest declines (Manion and Lachance, 1992). Declines are often multi-causal, with the various agents exhibiting strong spatio-temporal covariation (Minorsky, 2003; Wardle et al., 2004), so their delineation poses special challenges from both mechanistic and epidemiological perspectives (Rasmussen et al., 2007; Zhu et al., 2008). Similarly, interactions between below- and above-ground herbivory are widely recognized as important yet poorly understood drivers of terrestrial ecosystems at multiple levels of scale (Foggo and Speight, 1993; Maron, 1998; Strong et al., 1999; Bonello et al., 2001; Bardgett et al., 1998; Vanderputten and Peters, 1997), so continual observations over long time series can improve our understanding of underlying complex dynamics.

The sequence of sublethal root herbivory, fungal establishment, and lethal upper stem colonization highlights the importance of spatiotemporal patterns in herbivory (Logan et al., 1998; Bjørnstad et al., 1999; Aukema et al., 2006; Haynes et al., 2009), and hence the need to incorporate these patterns into models of plant defense. Whether a coniferous tree can be colonized by bark beetles is strongly influenced by its constitutive and induced defensive chemistry, which in vigorous trees can interrupt all phases of the colonization sequence (Franceschi et al., 2005). The proximity to killed trees is likewise an important driver, however. Because fungi vectored by root herbivores can grow through root grafts into neighboring trees (Klepzig et al., 1991), and these root weevils are more likely to walk to neighboring trees than fly to distant ones (Rieske and Raffa, 1990), even initially well-defended *P. resinosa* have little chance of surviving for many years (Fig. 4).

Thus, inherent defense physiology, spatial context, and their interaction are all important in host tree survival, providing further support for the view that cross-scale interactions are often critical drivers in forest ecosystems (Peters et al., 2004; Raffa et al., 2008).

These results can hopefully contribute to our understanding of the population dynamics of tree-killing bark beetles. In this system, root- and basal-stem herbivores and their fungal symbionts provide the most reliable source of stress due to their ubiquity and microbial symbioses. However, *Ips* spp. appear to respond to a variety of substitutable stress agents on their hosts, as the proportion of attacks that occurred on uninfected trees increased during drought years (Fig. 5). This was particularly apparent during the severe drought of 1988, when scattered trees throughout the stand were killed. Interestingly, very few of those killed trees became foci of new gaps, but instead the *Ips* spp. population returned to its reliance on belowground herbivores along the gap perimeter after the drought subsided. In contrast, one small cluster of trees neighboring our study site was killed by *Ips* spp. during this drought. These trees were then colonized by root herbivores that breed in dead trees, apparently *Hylobius pales* (Herbst) and *Pachylobius picivorus* (Germar) which vector those *Leptographium* fungi vectored by *H. radialis* and *D. valens* (Klepzig et al., 1991), and subsequently adjoining trees were colonized by *D. valens* and *H. radialis*. This epicenter developed into a continually spreading gap that corresponds to the patterns of below- and above-ground herbivory described here, is now larger than the original gap at the beginning of this study, and persists to date.

The inverse relationship with low slope between the proportion of trees killed without prior root infection and pine engraver population size (Fig. 3) suggests that pine engravers are generating positive feedback, but only weakly so. It seems likely that some other species, particularly those that undergo landscape-scale eruptions, would generate much steeper inverse slopes under analogous evaluation, and that many other species would generate no significant relationship. We propose this as an objective criterion to replace subjective terms currently used to categorize bark beetles, such as “aggressive”. This could be useful because it cannot always be assumed that mortality to large numbers of killed trees indicates self-perpetuating dynamics (Raffa et al., 2008). It is currently not clear what ecological and evolutionary factors have been selected for various degrees of behavioral plasticity in bark beetles (Wallin and Raffa, 2004). However, the patterns in this system suggest that bark beetles tracking an agent of tree stress that is highly predictable in space and time are likewise highly predictable to natural enemies such as predators and competitors (Figs. 2 and 3). Thus interactions between underlying predisposers to and natural enemies of bark beetles could affect the likelihood of population release (Raffa et al., 2005).

These results suggest several questions for future research. Specifically, what physiological changes do root- and basal-stem-

colonizing beetles cause in the subcortical stem tissues of mature trees, and how are these changes perceived by bark beetles? What attributes of tree physiology favor initial establishment by root- and basal-stem-colonizing beetles and their fungal associates? Can the onset and progression of this decline be reduced by cultural techniques such as mixed species- and age-planting, pest-management tactics aimed at reducing *D. valens* and *H. radialis* populations, or severing root grafts to halt the inter-tree growth of *Leptographium*? Answering these questions will improve our ability to utilize species that exert relatively slow but chronic mortality in comparative studies with species that exert intermittent landscape-scale disturbances.

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References

- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csadki, F. (Eds.), 2nd International Symposium on Information Theory, Akademiai Kiado, Budapest, pp. 267–281.
- Aukema, B.H., Clayton, M.K., Raffa, K.F., 2005. Modeling flight activity and population dynamics of the pine engraver, *Ips pini*, in the Great Lakes region: effects of weather and predators over short time scales. *Popul. Ecol.* 47, 61–69.
- Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., Taylor, S.W., 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* 29, 427–441.
- Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biol. Biochem.* 30, 1867–1878.
- Bentz, B.J., Logan, J.A., Amman, G.D., 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera, Scolytidae) and simulation of its phenology. *Can. Ent.* 123, 1083–1094.
- Berryman, A.A., 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environ. Ent.* 5, 1225–1233.
- Bjørnstad, O.N., Ims, R.A., Lambin, X., 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol. Evol.* 14, 427–432.
- Bohlmann, J., Gershenzon, J., Augbourg, S., 2000. Biochemical, molecular genetic, and evolutionary aspects of defense-related terpenoids in conifers. *Res. Adv. Phytochem.* 34, 109–149.
- Bonello, P., Gordon, T.R., Storer, A.J., 2001. Systemic induced resistance in Monterey pine. *Forest Pathol.* 31, 99–106.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 102, 15144–15148.
- Coulson, R.N., 1979. Population dynamics of bark beetles. *Ann. Rev. Entomol.* 24, 417–447.
- Coulson, R.N., Hennier, P.B., Flamm, R.O., Rykiel, E.J., Hu, L.C., Payne, T.L., 1983. The role of lightning in the epidemiology of the southern pine-beetle. *Zeitschrift für angewandte Entomologie* 96, 182–193.
- Dodds, K.J., Graber, C., Stephen, F.M., 2001. Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). *Environ. Ent.* 30, 17–22.
- Eckhardt, L.G., Goyer, R.A., Klepzig, K.D., Jones, J.P., 2004. Interactions of *Hylastes* species (Coleoptera: Scolytidae) with *Leptographium* species associated with loblolly pine decline. *Econ. Ent.* 97, 468–474.
- Erbilgin, N., Raffa, K.F., 2003. Spatial analysis of forest gaps resulting from bark beetle colonization of red pines experiencing belowground herbivory and infection. *Forest Ecol. Manage.* 177, 145–153.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *Forest Ecol. Manage.* 238, 24–53.
- Foggo, A., Speight, M.R., 1993. Root damage and water stress - treatments affecting the exploitation of the buds of common ash *Fraxinus excelsior* L., by larvae of the ash bud moth *Faxinella bjerck* (Lep, Yponomeutidae). *Oecologia* 96, 134–138.
- Franceschi, V.R., Krokene, P., Christiansen, E., Krekling, T., 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol.* 167, 353–375.
- Friedenberg, N.A., Powell, J.A., Ayres, M.P., 2007. Synchrony's double edge: transient dynamics and the Allee effect in stage structured populations. *Ecol. Lett.* 10, 564–573.
- Haynes, K.J., Liebhold, A.M., Johnson, D.M., 2009. Spatial analysis of harmonic oscillation of gypsy moth outbreak intensity. *Oecologia* 159, 249–256.
- Hicke, J.A., Logan, J.A., Powell, J., Ojima, D.S., 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *J. Geophys. Res. Biogeosci.* 111, G02019.
- Klepzig, K.D., Raffa, K.F., Smalley, E.B., 1991. Association of insect-fungal complexes with Red Pine Decline in Wisconsin. *Forest Sci.* 37, 1119–1139.
- Klepzig, K.D., Smalley, E.B., Raffa, K.F., 1996. Combined chemical defenses against an insect-fungal complex. *J. Chem. Ecol.* 22, 1367–1388.
- Kopper, B.J., Klepzig, K.D., Raffa, K.F., 2004. Components of antagonism and mutualism in *Ips pini*-fungal interactions: relationship to a life history of colonizing highly stressed and dead trees. *Environ. Ent.* 33, 28–34.
- Koricheva, J., Larsson, S., Haukioja, E., 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Ann. Rev. Ent.* 43, 195–216.
- Logan, J.A., White, P., Bentz, B.J., Powell, J.A., 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theor. Popul. Biol.* 53, 236–255.
- Manion, P.D., Lachance D., 1992. Forest Decline Concepts. A. *Phytopathol. Soc. Press.* St. Paul, Minnesota.
- Maron, J.L., 1998. Insect herbivory above- and belowground - individual and joint effects on plant fitness. *Ecology* 79, 1281–1293.
- Mawby, W.D., Hain, F.P., Doggett, C.A., 1989. Endemic and epidemic populations of southern pine beetle: implications of the two-phase model for forest managers. *Forest Sci.* 35, 1075–1087.
- Minorsky, P.V., 2003. The decline of sugar maples (*Acer saccharum*). *Plant Physiol.* 133, 441–442.
- Okland, B., Liebhold, A.M., Bjørnstad, O.N., Erbilgin, N., Krokene, P., 2005. Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? *Oecologia* 146, 365–372.
- Owen, D.R., Wood, D.L., Parmeter, J.R., 2005. Association between *Dendroctonus valens* and black stain root disease on ponderosa pine in the Sierra Nevada of California. *Can. Ent.* 137, 367–375.
- Peters, D.P.C., Pielke, R.A., Bestelmeyer, B.T., Allen, C.D., Munson-Mcgee, S., Havstad, K.M., 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proc. Natl. Acad. Sci. U.S.A.* 101, 15130–15135.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58, 501–517.
- Raffa, K.F., Aukema, B.H., Erbilgin, N., Klepzig, K.D., Wallin, K.F., 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. *Rec. Adv. Phytochem.* 39, 80–118.
- Raffa, K.F., Smalley, E.B., 1995. Interaction of pre-attack and induced monoterpene concentrations in conifer defense against bark beetle-microbial complexes. *Oecologia* 102, 285–295.
- Rasmussen, J.G., Møller, J., Aukema, B.H., Raffa, K.F., Zhu, J., 2007. Continuous time modelling of dynamical spatial lattice data observed at sparsely distributed times. *J. R. Stat. Soc. B* 69, 701–713.
- Reeve, J.D., 1997. Predation and bark beetle dynamics. *Oecologia* 112, 48–54.
- Rieske, L.K., Raffa, K.F., 1990. Dispersal patterns and mark-recapture estimates of two pine root weevil species *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae), in Christmas tree plantations. *Environ. Ent.* 19, 1829–1836.
- Rieske, L.K., Raffa, K.F., 1991. Effect of varying ethanol and turpentine levels on attraction of two pine root weevil species *Hylobius pales* and *Pachylobius picivorus* (Coleoptera: Curculionidae). *Environ. Ent.* 20, 48–52.
- Romme, W.H., Knight, D.H., Yavitt, J.B., 1986. Mountain pine beetle outbreaks in the Rocky Mountains - regulators of primary productivity. *Am. Nat.* 127, 484–494.
- Safranyik, L., Carroll, A.L., 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L., Wilson, B. (Eds.), *The Mountain Pine Beetle: A Synthesis of its Biology, Management and Impacts on Lodgepole Pine*. Canadian Forest Service, Pacific Forestry Centre, Natural Resources Canada, Victoria, BC, pp. 3–66.
- Schenk, J.A., Benjamin, D.M., 1969. Notes on the biology of *Ips pini* in Central Wisconsin Jack pine forests. *Ann. Entomol. Soc. Am.* 62, 480–485.
- Strong, D.R., Whipple, A.V., Child, A.L., Dennis, B., 1999. Model selection for a subterranean trophic cascade: root-feeding caterpillars and entomopathogenic nematodes. *Ecology* 80, 2750–2761.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251.
- Vanderputten, W.H., Peters, B.A.M., 1997. How soil-borne pathogens may affect plant competition. *Ecology* 78, 1785–1795.
- Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., Villalba, R., 1994. Disturbance regime and disturbance interactions in a Rocky-Mountain sub-alpine forest. *J. Ecol.* 82, 125–135.

- Wallin, K.F., Raffa, K.F., 2000. Influences of host chemicals and internal physiology on the multiple steps of postlanding host acceptance behavior of *Ips pini* (Coleoptera: Scolytidae). *Environ. Ent.* 29, 442–453.
- Wallin, K.F., Raffa, K.F., 2001. Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? *Ecology* 82, 1387–1400.
- Wallin, K.F., Raffa, K.F., 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecol. Monogr.* 74, 101–116.
- Wardle, D.A., Walker, L.R., Bardgett, R.D., 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305, 509–513.
- Witcosky, J.J., Schowalter, T.D., Hansen, E.M., 1986. *Hylastes-nigrinus* (Coleoptera, Scolytidae), *Pissodes-fasciatus*, and *Steremnius-carinatus* (Coleoptera, Curculionidae) as vectors of black-stain root disease of Douglas-Fir. *Environ. Ent.* 15, 1090–1095.
- Wood, D., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Ann. Rev. Ent.* 27, 411–446.
- Zhu, J., Rasmussen, J.G., Møller, J., Aukema, B.H., Raffa, K.F., 2008. Spatial-temporal modeling of forest gaps generated by colonization from below- and above-ground bark beetle species. *J. Am. Stat. Assoc.* 103, 162–177.