Landscape Ecology **14:** 105–120, 1999.

Plant-pest interactions in time and space: A Douglas-fir bark beetle outbreak as a case study

Jennifer Sarah Powers[1,*], Phillip Sollins[1], Mark E. Harmon[1] and Julia A. Jones[2]
[1]*Department of Forest Science, Oregon State University, 020 Forestry Sciences Laboratory, Corvallis, Oregon 97331–7501, USA;* [2]*Department of Geosciences, Oregon State University, Corvallis, Oregon 97331–5506, USA; (Corresponding author. Present address: Nicholas School of the Environment, Duke University, PO Box 90328, Durham, NC 27708-0328, E-mail: powers@pinus.env.duke.edu.)*

Received 20 June 1997; Revised 20 January 1998; Accepted 24 January 1998

Key words: bark beetle epidemic, Douglas-fir, hierarchy theory, multiple spatial and temporal scales

Abstract

A conceptual model of Douglas-fir bark beetle (*Dendroctonus pseudotsugae)* dynamics and associated host tree mortality across multiple spatial and temporal scales was developed, then used to guide a study of the association between the occurrence of beetle-killed trees and factors that might render trees more susceptible to attack. Long-term records of beetle kill showed that beetle epidemics were associated with windstorms and drought at statewide and local spatial scales. At the landscape scale, beetle kill was associated with (i) portions of the landscape that were potentially drier (southern aspects, lower elevations) and (ii) portions of the landscape that had more mature and old-growth conifer vegetation. The patches of beetle-killed trees were aggregated with respect to other patches at scales of approximately 1 and 4 km. At the scale of the individual tree, there was not a strong relationship between beetle kill and resistance to attack measured by tree growth rate prior to attack. Our results show that landscape-scale phenomena and temporal patterns were more strongly correlated with beetle-kill events than was recent growth history at the scale of individual trees. We suggest that the multi-scale approach we employed is useful for elucidating the relative roles of fine- versus coarse-scale constraints on ecological processes.

Introduction

From 1992–1993 the forests of the Western Cascades in Oregon experienced the largest Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) epidemic in over 35 years. Efforts to mitigate economic losses due to the beetle have often overlooked potential coarse-scale constraints on beetle population dynamics and failed to consider patterns of bark-beetle induced tree mortality within the larger context of landscape and ecosystem processes and tree decline concepts (Castello et al. 1995). The magnitude and frequency of bark-beetle outbreaks reflect the population dynamics of the insects as well as the susceptibility of the host plants to attack. Specifically, beetle population density and associated tree mortality at a given point in time reflect the previous beetle generation's numbers and the availability of suitable breeding habitat (i.e., weakened trees). We propose that tree resistance to attack is influenced by a spectrum of environmental variables operating across a range of spatial and temporal scales. Thus we expect that both fine-scale and coarse-scale environmental phenomena influence beetle dynamics via differential effects on host resistance. The hypothesized role of environmental variables in predisposing trees to attack is similar to Manion's concept of the decline disease spiral, where a temporal sequence of abiotic and biotic stresses precede the death of individual trees (1981). Mueller-Dombois (1986) extends this concept to forest stands by hypothesizing that a sequence of climatic events such as droughts followed by rain storms cause the dieback of *Metrosideros polymorpha* stands in Hawaii and that the spatial patterns of mortality are influenced differentially by soil substrate and forest life stage. Our work draws upon both of these models by relating spatial and temporal

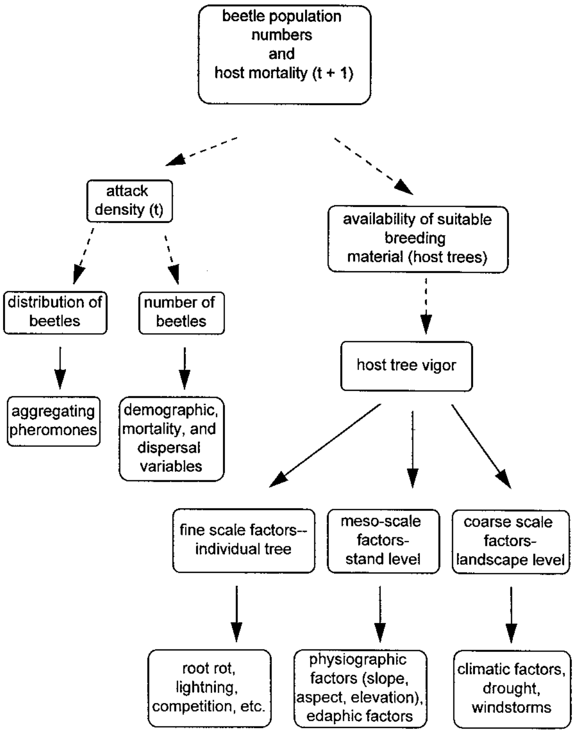


Figure 1. Conceptual model of the hierarchy of host-resistance factors that interact with Douglas-fir bark-beetle life history traits. Factors acting on beetles are presented on the left side of the figure while factors acting on host tree resistance are presented on the right side. Dashed arrows point from boxes which are functions of the factors in the boxes they point to (e.g., attack density is a function of the distribution of beetles), and solid arrows point from boxes which are influenced by the boxes they point to (e.g., the distribution of beetles is influenced by aggregating pheromones).

patterns of tree mortality at the scale of individuals and groups of trees to environmental variables which predispose trees to attack.

A conceptual framework for understanding how beetle life-history traits interact with the hierarchy of factors that influence host-tree vigor is illustrated in a 'concept map' (Figure 1). By using a multi-scale approach, we were able to quantify fine- versus coarse-scale constraints on beetle dynamics and the associated host mortality. Placing bark-beetle population dynamics within the larger context of the spatial patterns of environmental variables has important implications for both theoretical landscape ecology (e.g., the effects of spatial pattern on ecological processes, sensu Turner 1989) and forest management.

General background

Bark beetles and their associated host trees are an interesting system in which to study spatial pattern/process relations because successful reproduction of the beetle usually results in death of the host tree, producing a strong spatial signal. Species of facultatively parasitic bark beetles such as the Douglas-fir bark beetle can usually only attack weakened host tree Douglas-fir trees (*Pseudotsuga menziesii*). The beetles serve as the vector for a blue-stain fungus that acts in concert with the beetles to kill the host tree. Host resistance is deemed the most important factor regulating population densities of the Douglas-fir beetle (Furniss et al., 1979; Rudinsky 1966; Wright 1984). The beetles usually persist at low levels, breeding in weakened trees damaged by inciting factors such as lightning, root rot, or crown snap. However, events such as large windstorms provide abundant habitat and beetle numbers can quickly increase. At increased densities, the beetles can overcome the defenses of healthier hosts (i.e., act like parasites). Similarly, sustained stresses such as prolonged drought can lower the resistance of large tracts of trees and render them susceptible to attack, even at low beetle densities. Thus the potential habitat available for the beetles to exploit varies with beetle population numbers and stresses imposed on host trees. Population explosions can be damped by density-dependent processes such as increased abundance of specialized predators or pathogens or decreased brood survival due to intra-specific competition.

Each tree has a certain resistance to attack by beetles, which presumably varies with genotype and time as a function of the amount of photosynthate allocated to defensive systems. Factors that alter tree physiological status and carbon allocation to defensive systems will directly or indirectly influence susceptibility to attack by bark beetles (Waring and Schlesinger 1985). Environmental sources of variation in tree resistance include factors that affect trees at the scale of (i) individual trees (e.g., certain diseases, lightning strikes, tree age/size etc.), (ii) groups of trees (e.g., diseases such as root rot, intraspecific competition, edaphic factors, physiographic variables, etc.), and (iii) entire forests (e.g. air pollution, drought, fire suppression, etc).

Conceptual model and objectives

Using the conceptual model presented in Figure 1 as a hypothesis expressing the interactions between beetle populations dynamics and host resistance, we asked what controls the presence or absence of bark-beetle kill at different spatial and temporal scales. The underlying operational hypothesis was that at a fine spatial scale weaker trees succumb to beetle attack more frequently than vigorous trees, and that landscape-scale combinations of environmental factors render certain areas more susceptible to beetle kill by constraining tree growth. Similarly, certain climatic events (i.e., droughts and large windstorms) influence the probability of beetle epidemics through time. The objective of our work was to use a multi-scale approach to determine what influenced the magnitude and frequency of beetle epidemics, whether there was any pattern to the distribution of beetle kill across the landscape, and what influenced which individual trees succumb to beetle attack. As such, specific questions were (i) was there a temporal sequence of other disturbances that precede Douglas-fir bark beetle epidemics and was beetle kill correlated with climatic phenomena, (ii) was there a non-random pattern to the distribution of patches of bark-beetle kill across the landscape with respect to one another and with respect to landscape-scale variables, and (iii) was there a difference in the vigor of trees killed by the beetle and adjacent, living Douglas-fir. In the absence of prior information, our *a priori* assumption was that the strength of the relationships between the presence of bark-beetle kill and the explanatory variables across all spatial and temporal scales was similar. By utilizing this multi-scale approach, we were able to detect whether fine- or coarse-scale environmental variables were more correlated with bark-beetle kill. We then used this information to refine the original conceptual model.

Methods

In keeping with a multi-scale approach, three linked studies were designed. Field studies were nested within landscape-scale analyses of beetle kill in space and time: spatial patterns of beetle kill in 1992 were studied across a 12 000 ha landscape, time-series analyses of beetle kill spanned a range of nested spatial scales, and relationships between growth rates and susceptibility to bark beetles were studied at the scale of individual trees.

Study area

Observations were carried out at three nested spatial scales: the state of Oregon (2.51×10^7 ha), the Willamette National Forest in the Western Cascades (6.78×10^5 ha), and the Detroit Ranger District (1.22×10^5 ha; latitude 44° 45′ N, longitude 121° 52′30″ W) (Figure 2). This Ranger District was selected for detailed analyses because of the large amount of Douglas-fir bark-beetle activity during the summer of 1992 and the availability of air photos. The Detroit Ranger District is in the Western Hemlock zone (*Tsuga heterophylla*) but most forest stands are dominated by the early seral species Douglas-fir (Franklin 1979). The topography is mountainous and mean annual precipitation is 220 cm. District silviculturalists speculate that the 1992 beetle kill was the largest outbreak since the 1950's (Lyle Ang pers. comm). The extreme conditions in the Detroit Ranger District during 1992–1993 provided an excellent opportunity to study the spatial patterns of controls on an outbreak.

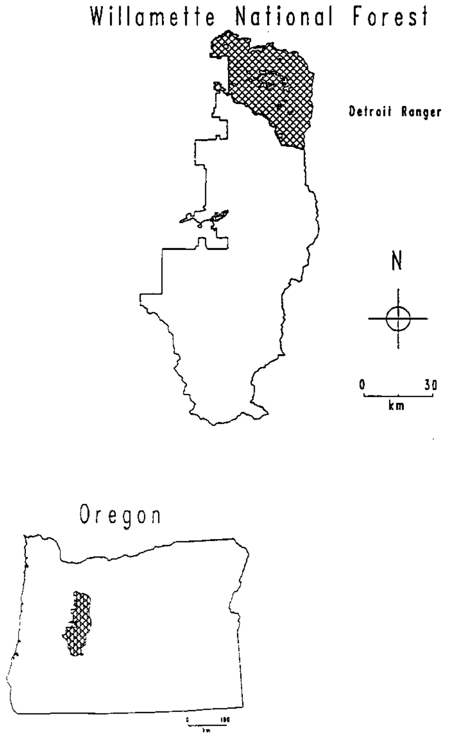


Figure 2. Location of the Willamette National Forest and the Detroit Ranger District within the state of Oregon, USA.

Spatial Patterns of Beetle Kill at a Landscape Scale

Objectives were (i) to characterize the spatial pattern of patches of beetle kill in the landscape (i.e., randomness of locations with respect to other patches of beetle kill) and, (ii) to examine the distribution of beetle-kill patches with respect to landscape structure (the composition and configuration of patches of beetle habitat as defined below) and topography. An area of approximately 12 000 ha within the Detroit Ranger District and the adjacent Mt. Hood National Forest was analyzed. The data were collected from a variety of sources described below. The distribution of patches of beetle kill was mapped from air photos. The resulting map was overlaid on various other maps which were derived from satellite imagery or generated from digital elevation models.

A beetle-kill GIS layer was generated by digitizing locations of dead tree crowns from a set of color-infrared air photos taken in late summer 1992. Single dead trees were left out of the beetle-kill layer to avoid misidentification as snags or individual dead trees of other species. Thus, all beetle-kill patches in the map contain two or more trees. Digitizing and ground- truthing procedures are described in full elsewhere (Powers 1995). Briefly, ground reconnaissance revealed that there were no errors of commission (i.e., patches of dead trees other than Douglas-fir), but eleven out of twenty-seven of the sampled patches were not detected in the photointerpretation process. More small patches were omitted than large patches. The largest observed patch contained 53 dead trees, but most patches contained considerably fewer. Accuracy and precision of the beetle-kill layer were limited by the scale and quality of the photography and errors in the photointerpretation process. The relatively large number of patches omitted in the photointerpretation process should be borne in mind as a caveat when interpreting the spatial analyses. Nevertheless, we believe that the strongest relationships between tree mortality and environmental variables would be manifested in the larger beetle-kill patches, most of which appear in the coverage. For map overlay purposes, the beetle-kill coverage was transformed into a point coverage (381 points) based on the centroid of the patch polygon.

A classified 1988 Thematic Mapper Satellite image (25 m pixels, developed by Cohen et al. 1995) was used as a vegetation base map. Seven of the twelve categories that Cohen et al. distinguished occurred in the study landscape: water, hardwood/conifer forest (open, semi-open, and closed), and coniferous forest (young, mature, and old growth). The point map of beetle-kill patches was overlaid on the vegetation map. Potentially suitable beetle habitat was then defined as vegetation classes that had at least one beetle-kill patch in the center of at least one polygon of that class. Based on these observations young, mature, and old-growth coniferous forest were considered to be potentially suitable beetle habitat in subsequent analyses.

Point pattern analysis

The distribution of patches of beetle kill was characterized utilizing second-order point pattern analysis, a method for quantifying the scale(s) at which a collection of mapped points exhibits clustering or dispersal (i.e., a regular spacing) (Boots and Getis 1988). This method compares the number of observed pairs with the number expected at all distances, taking into consideration the density of points, the borders, and the sample size (Boots and Getis 1988). An 8.9 km^2 area was clipped out of the beetle-kill point coverage and exported as X and Y coordinates for analysis. Values of the Ripley's K statistic, K(d), were calculated at 50 meter lag distances from 0 to 4500 m (half of the dimension of the study area). In practice, values of K(d) are transformed by the square root function to make them linear and stabilize the variance (Moeur, 1993). The observed pattern, referred to as L(d), was then compared to an approximate 95% simulation envelope (i.e., confidence intervals) generated from 19 Monte Carlo simulations (Moeur 1993).

Landscape pattern analysis and fragmentation indices

We examined the possibility that landscape structure (i.e., the arrangement and distribution of potentially suitable beetle habitat) might influence the location or abundance of beetle-kill patches. Landscape pattern was described and quantified using a moving window technique by creating 14 landscape structure layers at 2 spatial scales: window sizes of 20 ha (0.45 km^2) and 123 ha (1.11 km^2). These sizes were chosen to bridge 1 km, a distance at which point pattern analysis showed significant clustering of patches of beetle kill (see Results). An off-shoot of the program Fragstats (McGarigal and Marks 1994), Window, computed the following indices of landscape pattern for patches of suitable habitat: percent of the window in the chosen class (cover) type, number of patches, mean patch size, patch-size coefficient of variation, edge density, mean nearest-neighbor distance, and nearest-neighbor coefficient of variation (refer to Table 1 for descriptions). Window moves a user-defined square window across a gridded landscape and calculates the value of one of seven class metrics for a chosen cover type. The value of the cell at the center of the window is replaced with the value of the class metric for the window. Thus the output of Window is a new landscape containing the values of the chosen metric for every window examined (referred to as class index maps). The vegetation map (derived from the TM image) was smoothed and the old growth and mature conifer classes (i.e., suitable beetle habitat excluding young planted stands) were combined before the analyses in order to reduce the computer time necessary to run Window (Powers 1995). A set of 330 random points was generated for comparison to the beetle-kill coverage. Both point coverages (random and beetle kill) were overlaid on the 14 class index maps and the distributions of the 14 landscape structure layers were compared using the Wilcoxon rank sum test.

Relationship between beetle-kill patches and topography

We examined whether certain areas in the landscape are more prone to beetle infestation by determining if beetle-kill patches were differentially distributed with respect to topography. A digital elevation model (30 m resolution) was used to generate maps of aspect, slope, and elevation (referred to as feature maps). Each topographic feature was divided into seven or eight classes. The observed beetle-kill point coverage was overlaid on the feature map and the number of patches (points) in each feature class was calculated. The expected number of beetle-kill patches in each feature class was calculated by multiplying the proportion of potentially suitable beetle habitat occurring in that class by the total number of beetle-kill patches observed in the study area (381), correcting for the amount of the landscape in that class. Observed and expected distributions were compared using Chi-square tests.

Beetle activity over time

To identify the factors that influence the frequency and magnitude of beetle epidemics, we characterized the nature of beetle dynamics using the area affected by beetles as a proxy for beetle population numbers and then we related beetle kill to the climatic phenomena/disturbances (drought and windstorms) implicated in epidemics. The U.S. Forest Service has aerially surveyed all Region 6 (Pacific Northwest) forest lands annually since approximately 1951 in order to map and quantify the damage caused to trees by insect pests, diseases, wind storms and other physical agents. We accessed data on beetle kill since 1951 at the U.S. Forest Service Region 6 Forest Pest Management office in Portland (David Bridgewater pers. comm.) and analyzed the data at three nested spatial scales. The records include Douglas-fir beetle kill in Oregon from 1951–1993 (acres), in the Willamette National Forest from 1956–1992 (acres, and in numbers of trees killed from 1969–1992), and in the Detroit Ranger District from 1969 to 1992 (numbers of trees killed). As some of the data were reported in acres, we express them in acres. The time series for the state of Oregon was missing a datum for the total number of beetle-kill acres in 1983, which we estimated as the mean of the values for 1982 and 1984.

A list of severe windstorms that caused unusual amounts of blow-down throughout Oregon was compiled from Forest Pest Conditions in the Pacific Northwest Reports and the monthly Storm Data and Unusual Weather Phenomenon reports (National Climatic Data Center, 1962–1990). Large windstorms occurred in 1951, 1952, 1958, 1962, 1964, 1970, 1971, 1981 and 1990.

A precipitation index (annual deviation from the long term mean) spanning 1951 to 1993 was constructed for the state of Oregon from yearly records at four to six meteorological stations, representing most of the state’s climatic provinces. A different drought index that reflected the hydrologic year was used for the Willamette National Forest and Detroit Ranger District data because of the availability of long-term records of monthly precipitation for Detroit Dam in the Detroit Ranger District. Annual precipitation was calculated on a water year basis (i.e., September to August) and the index was calculated as the annual deviation from the long term mean (Graumlich 1987).

Characterizing beetle dynamics: time-series analysis

The time series of beetle kill in terms of the number of dead trees or the acres affected by the beetle were analyzed using the autocorrelation function and the partial autocorrelation function (Turchin et al. 1991; Box and Jenkins 1976; Statgraphics 1993). Any value of zero in the data was changed to one before the analyses because a population of zero cannot produce a new generation; records were then log transformed. The abundance data was not divided by the total area in Douglas-fir forest to obtain estimates of relative beetle population density as in Turchin et al. (1991), because the exact area in forest through time for each of the 3 spatial scales was unknown.

Table 1. Descriptions of class metrics calculated by 'Window' for the old conifer cover type (definitions are from McGarigal and Marks 1994)

Class metric	Description
Percent of landscape	percentage of the landscape in mature/old-growth conifer
Number of patches	number of mature/old-growth polygons
Mean patch size	mean mature/old-growth patch size (in ha)
Patch-size coefficient of variation	variability in patch size relative to mean patch size
Mean nearest-neighbor distance	average distance between patches of mature/old-growth
Nearest-neighbor coefficient of variation	variability in nearest-neighbor distances relative to the mean nearest-neighbor distance
Edge density	sum of all mature/old-growth edge lengths divided be total landscape area (m/ha)

Relationships between beetle populations dynamics, windthrow and drought: regression analyses

The association between beetle kill (within the entire state of Oregon, the Willamette National Forest, and the Detroit Ranger District) and climatic phenomena was investigated with a mixed model approach. In these analyses, we are assuming that the number of dead trees is a proxy for beetle population size. Two different measures of beetle population dynamics were used as response variables with the Oregon data: the difference in acres between one year and the preceding year measured the change in the absolute amount of beetle kill for each year (referred to as the difference), and r, the intrinsic rate of increase (the natural log of the fundamental net reproductive rate, i.e., $r = \ln[N_0/N_1]$ where N_0 is the population at the one time period and N_1 is the population one generation later) indexed the change in the growth rate of the population from year to year. For the state-wide scale, it was necessary to use the difference in acres instead of the actual acre values because the acre series was too autocorrelated. The untransformed acre values and number of dead trees were used as response variables for the Willamette National Forest and Detroit Ranger District series, respectively, in addition to the intrinsic rate of increase. Five explanatory variables were considered. The possibility that windstorms influence beetle populations (via windthrow) in a delayed or lagged manner was examined by constructing four indicator variables to represent the occurrence of a major state-wide windstorm in the current year (t), the previous year (t-1), two years prior (t-2), and three years prior (t-3). The precipitation index was also included as an explanatory variable (the Oregon analysis used the precipitation index computed from state-wide records whereas the Willamette N.F. and Detroit R.D. analyses used the precipitation index from the Detroit Dam records).

The SAS procedure MIXED was used to regress the response variables on the explanatory variables. The advantage of using a mixed model in this situation is that it allows analysis of data with multiple sources of variation (SAS 1992). The two sources of variation in this analysis were the variation due to the main effects of the explanatory variables and the autocorrelation of the response. The autocorrelation of the response variables was taken into account when the main effects and their standard errors were calculated. Several different covariance structures for the autocorrelation of the response variable were specified and Akaike's Information Criterion (AIC) was used to compare model adequacy. After the appropriate structure for the covariance matrix was found, AIC was used to compare models with different combinations of explanatory variables. The four windthrow variables were not independent of one another; to avoid multicollinearity, models were built starting with the simplest model, then other explanatory variables were added.

Susceptibility of individual trees to attack

In this part of the study we addressed whether there were differences in growth rates between Douglas-fir trees killed by the beetle and adjacent Douglas-fir that were not killed, i.e., does tree health influence which individual trees in a stand are killed by bark beetles? We used an index of tree vigor based upon tree ring widths assuming that stressed trees allocate less carbon to both defense and stemwood production (Waring and Schlesinger 1985). Thus, we assumed that recent growth history serves as an integrator of whole-tree carbon balance and physiological processes.

Individual dead Douglas-fir trees or groups of dead trees separated from other similar groups by at least two live tree crowns were defined as ‘beetle-kill patches’. Fourteen beetle-kill patches distributed throughout the Ranger District were sampled. Site selection was based primarily upon accessibility; however, an effort was made to obtain sites which comprised a balanced distribution of patch size (i.e., the number of dead trees), aspect, and elevation. Statistical inferences must be restricted to the 14 sites because they do not constitute a random sample of beetle-kill patches.

Douglas-fir trees in each patch were categorized as beetle-killed, the nearest living neighbor to a beetle-killed tree, or ‘control’ trees (defined as the living tree closest to a ‘nearest neighbor’, moving outward from the center of the patch). In total 56 beetle-killed trees, 58 nearest neighbors, and 48 control trees were sampled. For each sampled tree, diameter at breast height was measured to the nearest 2 mm and two ∼10 cm increment cores were extracted. Tree ring widths were measured for the years 1950–1992 on every core; we then averaged the two ring-width values per year for each tree.

Tree vigor, as manifested in annual stemwood growth, was assessed with an index of relative basal area increment. Relative basal area increment (RBAI) was calculated for 8 five year periods from 1951–1990 as follows:

$$\mathrm{RBAI} = [\pi \mathrm{r}^2 - \pi(\mathrm{r} - \mathrm{i})^2]/\mathrm{CSA},$$

r = radius of tree excluding outside bark; i = width of current 5 tree rings; CSA = cross-sectional area at breast height.

Due to large variations in tree diameter between sites, basal-area increment was divided by cross-sectional area (at breast height) to give a dimensionless relative index of stemwood growth (referred to as relative basal-area increment or RBAI). Values were expressed in terms of the total growth for each five year period, as opposed to the mean growth over five years. Analysis of variance was used to test for differences in RBAI between trees categorized as beetle-killed, nearest neighbor, or control.

Results

Spatial patterns of beetle kill at a landscape scale

Analyses of the spatial distribution of beetle-kill patches across the landscape revealed significant non-random patterns and correlations with landscape structure/topographic variables. Three hundred and eighty-one patches of beetle kill were identified via photointerpretation in the approximately 12 000 ha area. Although beetle-kill patches occurred in every vegetation category, the majority (sixty- seven percent) fell within one of the coniferous vegetation categories (Table 2). Twenty-four percent of the patches occurred within the semi-open vegetation class, which could contain some conifers. However, closer examination of the map revealed that extremely few of the patches (approximately 1.4% of the total number of beetle-kill patches) occurred in the interior of semi-open polygons. Furthermore, the majority of the beetle-kill patches located in semi-open polygons were adjacent to coniferous forest polygons, suggesting that these beetle kill patches were at edges of coniferous forest that was adjacent to the semi-open areas, but the patches had been misregistered in the process of photointerpretation or because the vegetation base map was prepared from 25 m resolution TM scene. The same is probably true for the small fraction of patches that fell in open and closed hardwood areas.

Point pattern analysis revealed a non-random arrangement of patches of beetle kill with respect to one another (Figure 3). The observed values of Ripley’s K, L(d), indicated that there was statistically significant aggregation of patches of beetle kill at all spatial scales tested (0–4500 m). Moreover, the values of L(d) peaked at an approximate lag of 1000 m and again at a lag of 4200 m. In sum, the analysis indicated clustering at three nested spatial scales: at the finest scale there was clustering among individual trees into patches of beetle kill of 2 to 53 trees (represented by points in this analysis), these patches were clustered at a scale of 1 km, and at a larger scale of approximately 4 km there was further clustering of the aggregations of patches of beetle kill.

Table 2. Distribution of beetle kill (all size patches) with respect to vegetation cover types defined by a classified TM image.

Vegetation class/cover type	Number of beetle-kill patches	Percent of total beetle-kill patches	Percent of total area occupied by this cover type
Open	16	4.5	9.3
Semi-open	86	24.4	27.9
Closed hardwood	16	4.5	3.1
Young conifer	49	13.9	9.6
Mature conifer	53	15.0	12.3
Old conifer	133	37.7	37.8

At the 20-ha window the median values for three landscape-structure metrics quantifying suitable beetle habitat (percent mature forest area, mean patch size, and edge density) were significantly higher ($p < 0.01$) for the beetle-kill than the random distributions (Table 3). Two of the landscape metrics differed significantly between beetle-kill and random points at the 123-ha window size, percent mature forest area and mean patch size. Hence, groups of beetle-killed trees are surrounded by more old growth/mature forest in larger patches than are random points, especially at scales of approximately 20 ha, but the shapes of the patches of forest might be more complex around beetle kill, as suggested by the higher edge density at the smaller window size. None of the measures of variability (patch-size coefficient of variation or nearest-neighbor coefficient of variation) differed significantly at either window size, indicating that the ranges of the values around the mean were similar. The distributions of beetle-kill patches in different aspect and elevation categories differed statistically from the expected distributions ($\chi^2 = 60.94$, d.f. = 7, $p < 0.0001$; $\chi^2 = 44.8$, d.f. = 7, $p < 0.0001$, respectively), but there was no observed association between beetle kill and slope classes ($\chi^2 = 9.93$, d.f. = 5, $p = 0.135$) (Figure 4). From visual inspection of the frequency histograms, bark-beetle killed patches were relatively more prevalent on eastern, southern, and southwestern slopes, and at below median elevation (1000 m).

Beetle activity over time

At the three spatial scales examined (Detroit Ranger District, Willamette National Forest, and the state of Oregon), beetle-kill damage in terms of numbers of trees and affected acres varied over the time periods by at least two orders of magnitude (Figure 5). By far the largest beetle outbreak occurred in the early 1950's with subsequent smaller episodes in the early 1960's, the mid 1960's, the mid 1970's, and the 1990's.

The amount of beetle kill in one year is a strong predictor of beetle kill in the subsequent year. The autocorrelation functions (ACF) and the partial autocorrelation functions (PACF) for Oregon, the Willamette (in terms of acres), and the Detroit Ranger District were similar, but the results were clearest for Oregon (Figure 6). A positive peak is evident at the first lag of the ACF, but there is no evidence of delayed density-dependent regulation (which would be indicated by positive or negative spikes at the second lag). This is further corroborated by the PACF plot which indicates that the autoregressive process is first order (i.e. there is a peak above the 95% confidence interval at the first lag). ACF and PACF plots for the Willamette in terms of the number of dead trees showed that the numbers for each year were independent of one another. The lack of agreement between the two estimates of beetle activity, acres affected and number of dead trees, for the Willamette National Forest illustrates the drawbacks of using aerial survey data as a proxy for beetle population counts.

The precipitation and windthrow indices were correlated with the beetle population growth rates and the area affected in different ways at the three nested spatial scales (Table 4). Statewide, the rate of increase in beetle populations and the acreage affected depended on the occurrence of a windstorm in that year and the total precipitation. This means that at a state-wide level the rate of population growth (using beetle-killed trees as a proxy for beetle population numbers) changes fastest during the year in which large amounts of suitable habitat are present. The best

Table 3. P-values for Wilcoxon rank-sum tests of differences in landscape metrics between the beetle-kill point distribution and random points.

Landscape metric	Small window (20.25 ha)	Large window (123 ha)
Number of patches	0.3626	0.4143
Percent area in mature forest	0.0001	0.0001
Mean patch size	0.0001	0.0001
Patch-size coefficient of variation	0.5911	0.4858
Mean nearest-neighbor distance	0.3626	0.8891
Nearest-neighbor coefficient of Variation	0.1261	0.9942
Edge density	0.0001	0.3571

regression models for the area affected statewide (the area difference) and r (the intrinsic rate of increase) were identical, although the structure of the covariance matrix differed. Precipitation alone did not influence the difference in acres affected by the beetle from year to year, but if there was a windthrow event, lack of precipitation influenced the magnitude of the epidemic. None of the windthrow variables nor the precipitation index was significant in explaining variation in the two response variables for the Willamette National Forest beetle-kill records in acres. The results for the Willamette National Forest time series (in terms of the number of dead trees) and the Detroit Ranger District (number of dead trees) are similar to one another but differ from both the Oregon results and the Willamette National Forest (acres) results. Models for the number of dead trees and the intrinsic rate of increase differed with respect to explanatory variables. In summary, some climatic variables helped to explain more variation at certain spatial scales than at others.

Susceptibility of individual trees to attack

Tree growth rates, as expressed by relative basal-area increment, varied considerably over time and among the 14 sites. Based on ANOVA's, growth rates did not differ significantly ($p > 0.05$) for beetle-killed, nearest neighbor, and control trees in any 5-year period over the 40 years from 1951 to 1990 [p-values for the significance of class effects at each time period were: (1951–1955) 0.72, (1956–1960) 0.25, (1961–1965) 0.25, (1966–1970) 0.10, (1971–1975) 0.09, (1976–1980) 0.08, (1981–1985) 0.13, and (1986–1990) 0.17]. If a more lenient α-level is used ($p = 0.10$), there are differences among the three tree categories for periods 1971–1975 and 1976–1980. Furthermore, the differences between beetle- killed trees, and the nearest neighbor and control trees appeared to increase through time.

Discussion

There is increasing recognition of the role of spatial processes in governing the population dynamics insects (Godfray and Hassell 1997). The objective of these studies was to develop a hierarchical model of Douglas-fir beetle dynamics by measuring the association between the presence of beetle kill and potential explanatory variables across a range of spatial and temporal scales. Taken as a whole, the results indicate that coarse-resolution factors such as the precipitation regime, windthrow disturbance, and physiographic constraints of the mountainous topography are as important if not more important than tree-level physiological processes in controlling the dynamics of the beetle-host interaction. That is to say, one could develop a rough hazard rating model to predict the some of the location and timing of beetle kill epidemics based upon weather phenomena, topography, and a vegetation map, but it would be difficult to predict which specific trees within a stand would succumb to the beetle (see for example the windthrow hazard rating model of Sinton 1996). For non-epidemic years (in contrast to our study) it is possible that recent growth history is sufficient to identify individual trees within a stand that are most susceptible to attack. Results of the three component studies are discussed separately below and then synthesized by refining the original conceptual model of beetle dynamics.

Table 4. Results from mixed-model regression analyses of measures of beetle kill dynamics across various spatial scales on climatic variables. Blank cells indicate climatic variables not included in the best-fit model, as determined by Akaike's Information Criterion.

Location spatial scale	Measure of population dynamics	Precipitation index	Significance of model terms			
			Windthrow current year	Windthrow-1 year	Windthrow-2 year	Windthrow-3 years
Oregon	difference in acres	0.0033	0.0124			
	intrinsic rate of increase	0.3819	0.0098			
Willamette National Forest	number of beetle-killed trees				0.0563	
	intrinsic rate of increase	0.5365	0.6656			
Detroit ranger district	number of beetle-killed trees	0.7809	0.9943	0.5121	0.0379	
	intrinsic rate of increase	0.6620	0.5499			

Spatial patterns of beetle kill at a landscape scale

Point pattern analysis indicated clustering of patches of beetle kill at a scale of 1 km and further aggregation of these clusters at a scale of 4 km. At the finest scale, the spatial distribution of dead trees in groups of 2 to 53 can most likely be explained by the pheromonally induced aggregating behavior of the beetles. The statistically significant aggregation of patches of beetle-kill at approximately 1 km and 4 km suggests the existence of some underlying factors that create pattern at this scale. These underlying factors could be biological (e.g. beetle pheromones might only be effective over a distance $<$ 1 km), physical (e.g. warmer, southern aspects might occur in $\sim$1 km^2 patches), or the consequence of forest management practices (e.g., the distribution of suitable habitat across the landscape might be a function of previous cutting history). A definitive explanation of the mechanisms responsible for the observed pattern of clustering of beetle kill at two spatial scales requires further study.

The distribution of beetle-kill patches across the landscape is necessarily superimposed upon the distribution of Douglas-fir. The legacy of the silvicultural practice of clearcutting has fragmented the matrix of conifer forests (Franklin and Forman 1987). The largest clearcut in our study area was 44 ha. The dispersion of clearcuts with respect to other patches of suitable habitat was not examined. However, the dispersed spatial arrangement of clear cuts may contribute to the clustering of beetle-kill patches by partitioning the matrix of old conifer into patches of 1 and/or 4 km.

Beetle kill occurred in larger than random patches that tended to be mature conifer forest, at both the 0.45 and 1.11 km^2 scales of the smoothed landscape, but also was more frequent in patches with higher than

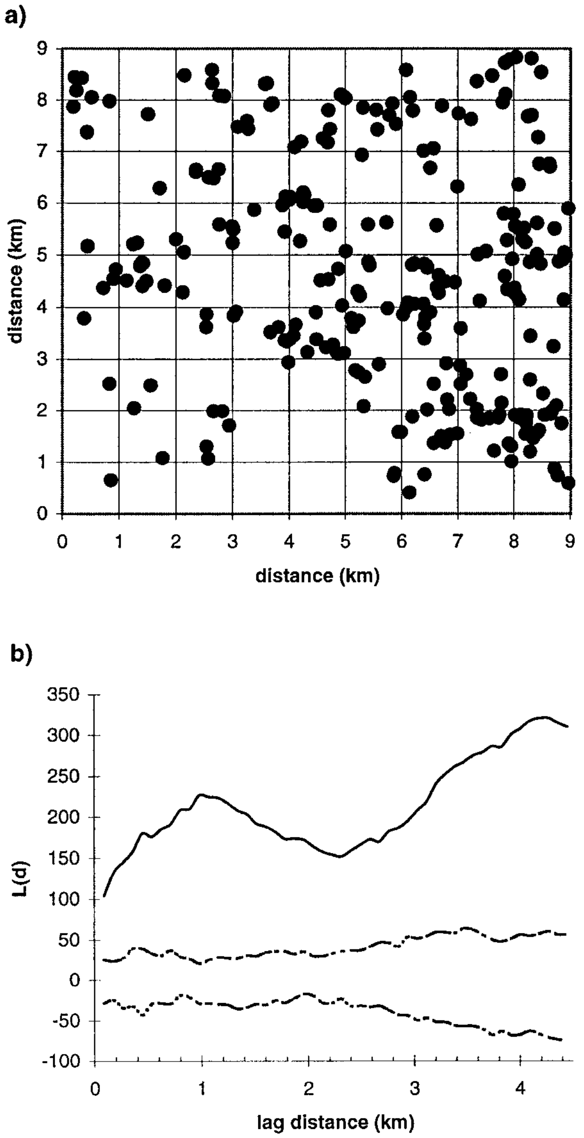


Figure 3. (a) Actual point pattern of beetle-kill locations within a 9 km^2 study area, and (b) Ripley's K over distance lag (solid line) and the 95% confidence envelope (broken line)

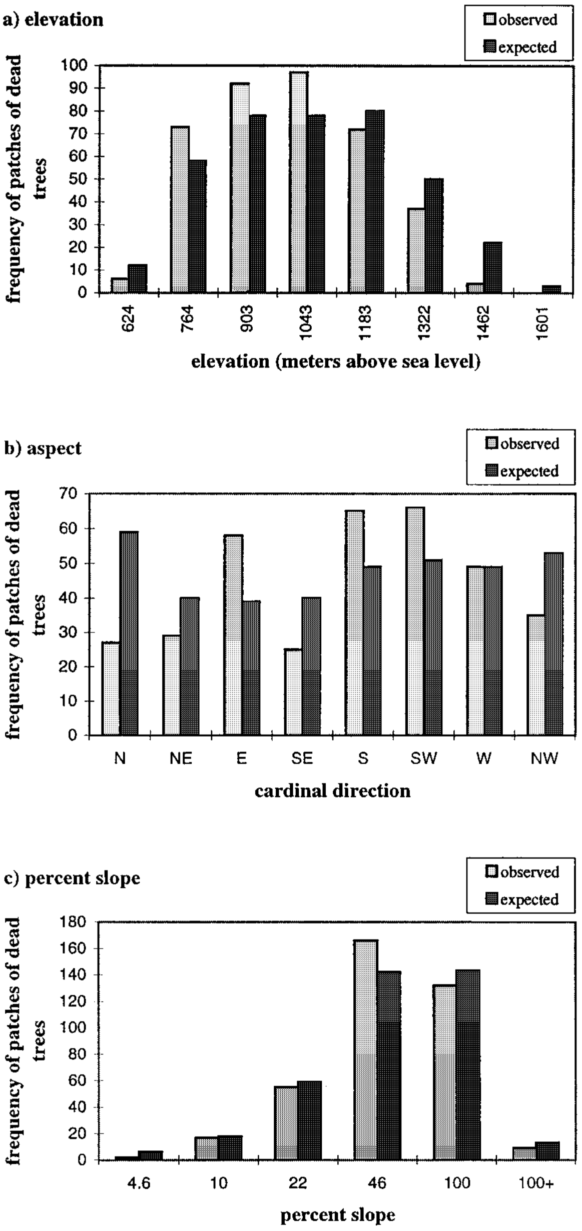
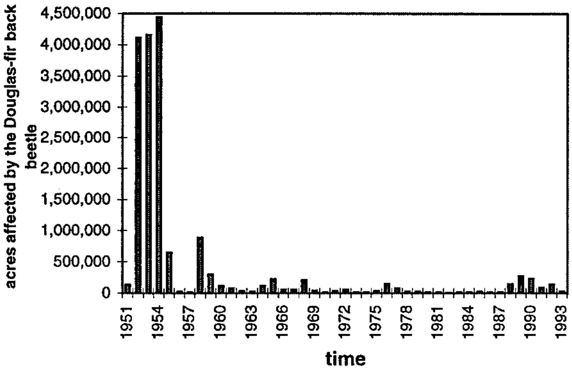


Figure 4. Frequency distributions of beetle-kill patches in 1992 within the Detroit Ranger District with respect to (a) elevation, (b) aspect, and (c) percent slope

average edge density at the 0.45 km^2 scale. It should be noted that the beetle kill point distribution (most of which fell in the mature conifer cover type) was compared to a set of random points, distributed irrespective of cover type. Together these observations suggest that the proportion of suitable habitat (mature/old-growth) in a large area determines whether the land will be susceptible to beetle kill but the actual configuration of that habitat (e.g., patch size and shape or edge characteristics) determines the location of beetle activity at a finer scale. A further step in this analysis would be to test whether the number of beetle kill patches is proportional the area of the mature conifer in a patch of forest, or increases with decreasing mature conifer patch size as a result of edge effects.

In this study area in the Detroit Ranger District, beetle kill was more frequent at lower elevations and on southern, southwestern, and eastern aspects, which

a) acres of forest affected by the Douglas-fir bark beetle



b) statewide precipitation as deviation from the 43 year mean

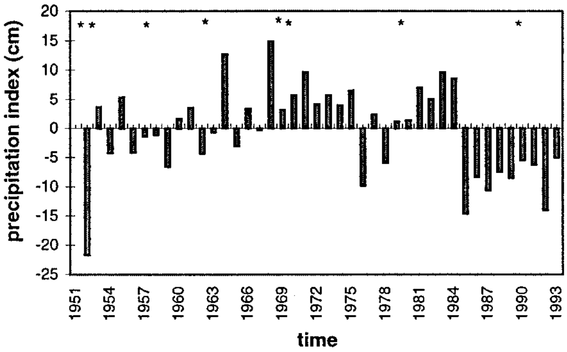


Figure 5. Area affected by beetle kill (acres) from Forest Service records, the precipitation index, and the occurrence of windstorms in the state of Oregon (1951, 1952, 1958, 1962, 1964, 1970, 1971, 1981 and 1990)

also tend to get more solar radiation and have higher potential evapotranspiration. Others have documented a higher proportion of patches of Douglas-fir beetle-killed trees in Idaho on 'warmer' aspects (Furniss et al. 1979). There are two plausible explanations for these observations, which are not mutually exclusive. Trees growing on southern aspects might grow less vigorously due to increased moisture stress (Kaufmann and Ryan 1986), which could render these trees less resistant to the beetle. Tree growth rates averaged over all sample plots from this study show similar trends of decreased growth rates during drier years (Powers 1995). In addition, at cooler temperatures the initial dispersal flight of the beetle is thought to be oriented towards warmer places in the stand, in the absence of monoterpene attractants from dead or weakened trees (Rudinsky 1966). This behavior could possibly account for the nonrandom distribution of beetle kill, especially during an epidemic year when fewer host trees are weak and beetles are numerous.

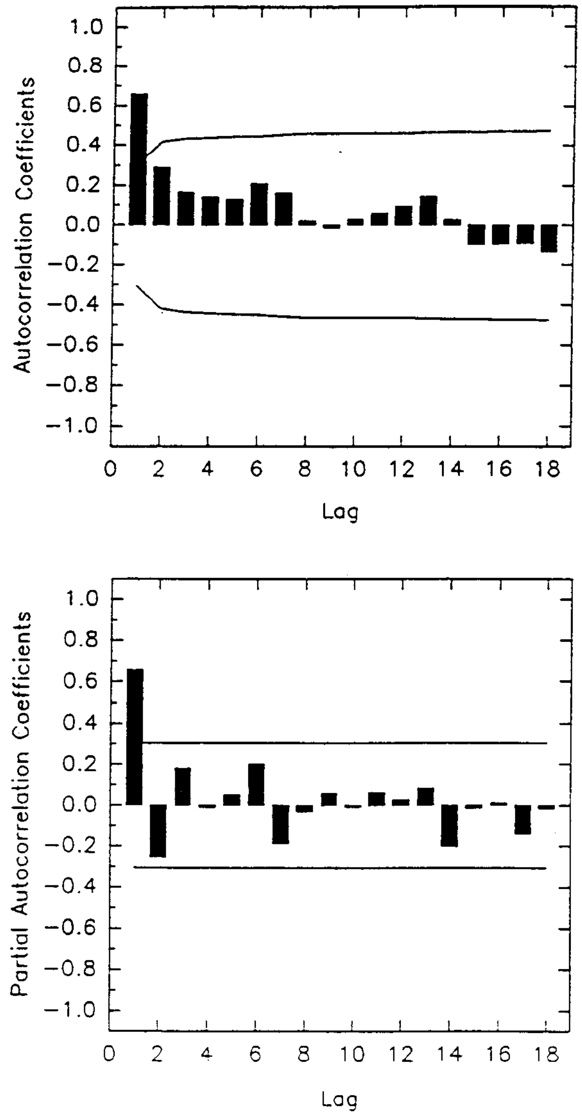


Figure 6. Autocorrelation and partial autocorrelation functions for the annual amount of beetle kill in the state of Oregon from 1951–1993.

The greater occurrence of beetle-kill patches at lower (warmer) elevations than expected most likely reflects changes in species composition across the elevational gradient, but could also reflect temperature-dependent activity of the beetle. At elevations anywhere above 610 to 1500 m, the dominant species shifts from Douglas-fir to true fir (Franklin, and Dyrness 1973). While we do not have detailed information about the distribution of Douglas-fir with elevation in the Detroit Ranger District, we observed more Douglas-fir-dominated stands at elevations around 700–1000 m than at higher elevations. Not surprisingly, the frequency of Douglas-fir beetle- killed trees in a stand depends upon the proportion of Douglas-fir in that stand.

In summary, there was evidence that beetle kill is differentially distributed with respect to certain landscape-scale factors. Patches of beetle kill were clustered at scales of 1 and 4 km, and were more frequent in portions of the landscape that received more solar radiation and had potentially greater moisture stress, and in large patches of mature and old growth conifer, often with a higher edge density. This suggests that the fine scale population dynamics of bark beetles respond to landscape-scale patterns of temperature and vegetation type.

Beetle activity over time

Most major beetle-kill episodes were evident at all three spatial scales examined, thus the timing and frequency of beetle-kill events appear to be similar across spatial scales. However, different locations experienced the most severe beetle-kill in each episode (i.e., the magnitude of the activity was not consistent over spatial scale). For example in the Willamette National Forest, the 1965 beetle outbreak was much more extensive than the 1959 episode, whereas the 1959 outbreak for Oregon was much more extensive than the 1965 event. This suggests that local conditions may be important in determining the extent of beetle kill.

There was evidence for both density-dependent and density-independent population regulation of the bark beetle. For the temporal records of beetle kill at nested spatial scales (i.e., Oregon, Willamette in acres, and Detroit) time-series analysis supports the existence of first-order density-dependent regulatory mechanisms, such as intraspecific competition and generalized predation. These results should be taken with caution because the ACF and the PACF assume a linear relationship between the log-transformed population densities. For definitive results one would have to employ nonlinear models (see Turchin 1990).

However, density-independent phenomena such as climate and especially the availability of recently windthrown trees also regulate beetle population densities. Others have noted that the beetle populations can increase 10 fold in one generation (Atkins and McMullen 1960). Presumably, then, these large numbers of beetles emerge from the windthrow and attack surrounding green trees. However, the intrinsic rate of increase was not related to climatic variables at the scale of the Willamette National Forest or the Detroit Ranger District, indicating that other variables influence the rate of beetle population growth at these scales.

Interestingly, beetle kill dynamics were related to different climatic variables for the Willamette National Forest and the Detroit Ranger District than at the state-wide scale. At these scales the magnitude of beetle kill depended upon the presence of windthrow two years prior to the current year. The relationship between the magnitude of beetle kill and windthrow two years prior is exactly what is predicted by our current understanding of beetle population dynamics. Why this is not reflected in the population growth rate is unclear. It is possible that the variation in numbers of beetle-killed trees from year to year is not large enough to cause large variations in the growth rate. A second alternative is that the number of beetle-killed trees is not an adequate index of beetle populations.

Taken together, the results from the time-series and regression analyses indicate that both density-dependent and density-independent processes operate to regulate Douglas-fir bark beetle dynamics, corroborating theoretical epidemiological models (Berryman 1982). We infer that density-independent processes are more important in regulating beetle populations at low densities whereas density-dependent processes are more important when beetles are abundant, i.e., there exists a certain level above which density-independent processes give way to density-dependent processes. According to this scenario, beetles remain at low densities at endemic levels due to generalized predators and the lack of available habitat. Catastrophic disturbances such as large windstorms can precipitate epidemics by weakening large numbers of trees. At a statewide level, populations seem to grow faster in the year of the windstorm. Low annual precipitation coincident with a windstorm can heighten the effects of the windthrow by increasing the magnitude of the tree mortality. Beetles never remain at high population densities for many years in a row, as indicated by the time-series analyses. Beetle outbreaks are most likely damped by density-dependent processes such as increased intraspecific competition among larvae which decreases brood survivorship. The picture that emerges from these results is consistent with the understanding of beetle population dynamics in the literature (e.g., Furniss et al. 1981; McMullen and Atkins

1961). The implications of this for forest management are that Douglas-fir beetle outbreaks attenuate themselves quickly over time and that efforts to stop outbreaks after they have started would be redundant.

The fact that different climatic variables seem to influence the magnitude of beetle kill and the growth of beetle populations at different spatial scales can most likely be attributed to the importance of local phenomena in mediating the characteristics of outbreaks. For example, whether windthrow occurs in large patches or affects widely spaced, single trees has large implications for possible ensuing beetle outbreaks (Furniss 1962; Orr 1963). The beetles avoid attacking the sides of windthrown trees that are exposed to the sun (Furniss 1962). Thus, large patches of windthrown trees will have less concentrated attacks and produce far fewer beetles than individual windthrown trees or small patches that are partially shaded by standing trees (Orr 1963). It is interesting to note that within the 42-year period of beetle-kill records for Oregon, six episodes were classified as beetle epidemics, whereas 9 storms were classified as large and state-wide. Thus beetle epidemics can be the results of windstorms but not all windstorms produce epidemics. Similarly, local conditions may mediate the spatial and temporal distribution of bark-beetle mortality. If it is cool and cloudy when the beetles emerge in the spring, dispersal is curtailed and new attacks are restricted to the vicinity of the original host trees (Atkins 1959). Conversely, if the weather is warm and/or clear the beetles might fly many miles before establishing new infestation centers (Atkins 1959).

Stand level studies

There is much debate about the influence of physiological status of host trees on the performance of phytophagous insects and the mechanisms responsible. According to Larsson (1989), bark beetles (cambium feeders) show more selectivity for stressed host trees than do insects that suck, mine, chew, or form galls. Others have documented such a relationship for other conifer/bark beetle associations including lodgepole-pine and mountain-pine beetle (host resistance was measured by basal area growth/sapwood area growth) and for mixed pine species (measuring tree vigor by radial growth) and resistance to the southern-pine beetle (Kushmaul et al. 1979: Waring and Pitman 1980).

We found little evidence for a strong relationship between Douglas-fir vigor (measured by relative basal area increment) and whether a tree was beetle-killed, nearest neighbor, or control. This could be due to several factors. First, relative basal area increment might be an inadequate measure of a tree's resistance to attack by bark beetles. The variables used to measure tree vigor should reflect some characteristic that beetles can sense and respond to (Barbosa and Wagner 1989). It is possible that there exist other more sensitive indicators of Douglas-fir beetles' response to host stress, such as oleoresin exudation pressure (Rudinsky 1966). However, indices of tree growth derived from tree ring widths are the only ones available for a retrospective study such as this. On the other hand, there may be no association between tree vigor and bark-beetle kill, especially during epidemic conditions. In beetle-killed Douglas-fir trees in Northern Colorado, Lessard and Schmid (1990) found that relative growth rate increased for several years preceding an epidemic. It could be that in the summer of 1991 beetles in the Detroit Ranger District were so numerous that they could overwhelm healthy trees with their massive numbers. That the number of beetle-killed trees in a patch was not correlated with mean site vigor suggests that small patches of one or two beetle-killed trees did not occur in stands that were growing more vigorously, and similarly, that stands with many beetle-killed trees were not growing slower than other stands.

A third possibility is that the sample size was inadequate to detect differences between beetle-killed trees and adjacent living trees at a 0.05 level of significance given the variability among trees. The data seem to support this possibility. Of the fourteen maximum and minimum values of relative basal area increment (RBAI) for the most recent time period (1986–1990), only two of the maximum values and eight of the minimum values were for beetle-killed trees. Furthermore, for three of the sites the minimum value of RBAI was considerably lower than for the rest of the values for the site. A fourth possibility is that the mean growth rate for the stand is not relevant to predict beetle attack. Instead, a single weak, slowly growing tree might act as a focal point for attack, attracting beetles that then attacked other neighboring trees at these sites. Lastly, we only sampled sites which contained at least one beetle-killed tree and not the full range of stand conditions. It is possible that if we had randomly sampled other Douglas-fir stands that contained no beetle-killed trees in addition, we might have observed a relationship between tree growth rates and beetle-kill, such as that implied by the concentration of beetle kill in presumably stressed south and west facing slopes.

Conclusions

Hierarchy theory posits that ecological systems are constrained by processes that are best studied at nested levels of spatial and temporal scales. This idea can provide a useful heuristic tool for designing field studies. In this study we considered a single ecological phenomenon, trees that succumbed to the Douglas-fir bark beetle, across a hierarchy of spatio-temporal scales. We hypothesized that tree vigor was the mechanism that linked phenomena at different scales in space (i.e., the weakest or most stressed stands within the landscape would experience beetle kill and within those areas the weakest trees would die) and in time (i.e., drought and wind storms would weaken or kill trees and precipitate epidemics). We compared the apparent strength of controls on beetle-kill patterns shown by our analyses across the range of scales (Figure 7).

Beetle kill was not well correlated with fine-scale tree-level variables but was well correlated with certain coarse-scale landscape-level variables. At the landscape scale areas susceptible to beetle kill could be predicted based on aspect, elevation, and the amount and distribution of old conifers. However, our results could not predict exactly where these patches would be located for any given epidemic, or which individual trees might die. This implies that patterns at the landscape scale act as a coarse-scale context for bark beetle activity. Yet within these constraints which individual trees succumb to the beetle during epidemic years is stochastic or is related to other factors that we did not examine. A very similar conclusion was reached by Sinton (1996) about the prediction of windthrow in Western Oregon, which our study shows to be a critical precursor of bark beetle outbreaks.

At the scale of multiple decades, beetle populations appear to be regulated by density-dependent factors at epidemic levels and density-independent factors at endemic levels in Western Oregon. Prior windthrow and relatively dry conditions, both regional phenomena, appear to increase beetle epidemics.

In summary, by utilizing a multi-scale approach we detected strong correlations between bark-beetle kill and factors contributing to tree stress at the landscape level spatial scale, and the multi-decade time scale, but only weak correlations between beetle kill and factors measured at the stand or individual tree scale. This illustrates the utility of conducting ecological investigations simultaneously at a variety of complementary scales, particularly in the study of disturbance processes such as disease outbreaks or windthrow.

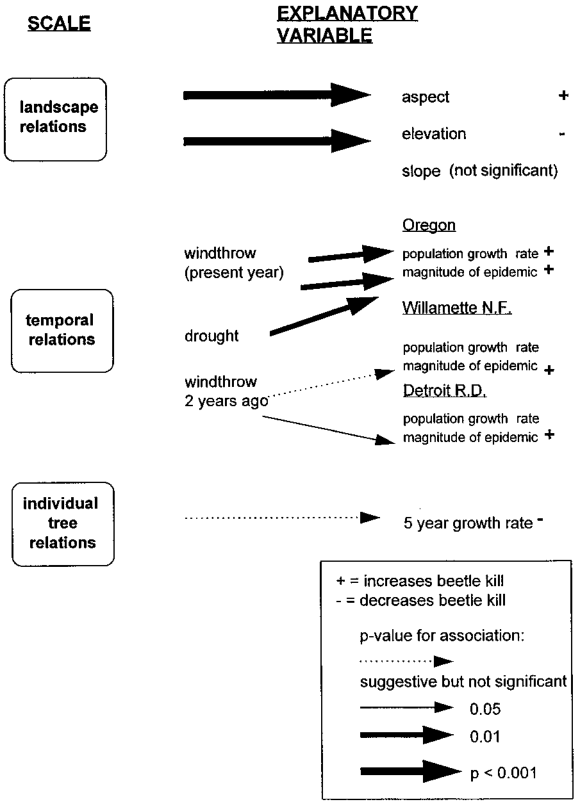


Figure 7. Refined hierarchical model of Douglas-fir beetle dynamics incorporating significant and non-significant results. The strength of the association between beetle kill and each factor was measured by p-values and is depicted as the width of the arrow linking the two phenomena.

Acknowledgments

We wish to thank an anonymous reviewer for comments which improved the manuscript and David Wallin and Don Sachs for their moral support during Jennifer Powers' M.S. degree. We also thank the National Science Fondation (BSR-90-11663) for providing support and infrastructure to the H.J. Andrews LTER.

References

Atkins, M.D. 1959. A study of the flight of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) I. Flight preparation and response. Can Entomol 91: 283–291.

Atkins, M.D. and McMullen, L.H. 1960. On certain factors influencing Douglas-fir beetle populations. Fifth World Forestry Congress Proceedings (Seattle, WA) 2: 857–859.

Barbosa, P. and Wagner, M.R. 1989. Introduction to Forest and Shade Tree Insects. Academic Press, San Diego.

Berryman, A.A. 1982. Biological control, thresholds, and pest outbreaks. Env Entomol 11: 544–549.

Boots, B.N. and Getis, A. 1988. Point Pattern Analysis. Sage Publications, Newbury Park, CA.

Box, G.E. and Jenkins, G.M. 1976. Time Series Analysis: Forecasting and Control. Holden-Day, San Francisco.

Castello, J.D., Leopold D.J. and Smallidge, P.J. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience 45: 16–24.

Cohen, W.B., Spies, T.A. and Fiorella, M. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, USA. Int J Remote Sensing 16: 721–746.

Franklin, J.F. 1979. Vegetation of the Douglas-fir region. pp. 93–112. *In* Forest Soils of the Douglass-fir Region. Edited by Heilman, P.E., Anderson, H.W. and Baumgartner, D.M. Washington State University Cooperative Extension, Pullman, WA.

Franklin, J.F. and Dyrness, C.T. 1973. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Franklin, JF and Forman, T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landsc Ecol 1: 5–18.

Furniss, M.M. 1962. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in southern Idaho. J Econ Entomol 55: 486–491.

Furniss, M.M, McGregor, M.D., Foiles, M.W. and Partridge, A.D. 1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. USDA Forest Service General Technical Report INT-59, Odgen, UT.

Furniss, M.M., Livingston, R.L. and McGregor, M.D. 1981. Development of a stand susceptibility classification for Douglas-fir beetle. *In* Hazard-rating systems in forest insect pest management: symposium proceedings. USDA Forest Service General Technical Report WO-27.

Godfray, H.C.J. and Hassell, M.P. 1997. Hosts and parasitoids in space. Nature 386: 660–661.

Graumlich, L.J. 1987. Precipitation variation in the Pacific Northwest (1675–1975) as reconstructed from tree rings. Ann Assoc Am Geograph 77: 19–29.

Kaufmann, M.R. and Ryan, M.G. 1986. Physiographic, stand, and environmental effects on individual tree growth and growth efficiency in subalpine forests. Tree Physiol 2: 47–59.

Kushmaul, R.J., Cain, M.D., Rowell, C.E. and Porterfield, R.L. 1979. Stand and site conditions related to southern pine beetle susceptibility. For Sci 25: 656–664.

Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. Oikos 56: 277–283.

Lessard, E.D. and Schmid, J.M. 1990. Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in Northern Colorado. Great Basin Naturalist 50: 333–338.

Manion, P.D. 1981. Decline diseases of complex biotic and abiotic origin. *In* Tree Disease Concepts. pp. 324–339. Prentice-Hall, Inc., Englewood Cliffs, NJ.

McGarigal, K. and Marks, B.J. 1994. Fragstats: spatial pattern analysis program for quantifying landscape structure. Forest Science Department, Oregon State University.

McMullen, L.H. and Atkins, M.D. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. For Sci 7: 197–203.

Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. For Sci 39: 756–775.

Mueller-Dombois, D. 1986. Perspectives for an etiology of stand-level dieback. Ann Rev Ecol Syst 17: 224-43.

National Climatic Data Center. 1962–1990. Storm Data and Unusual Weather Phenomenon Reports, volumes 4–32. Ashville, NC.

Orr, P.W. 1963. Windthrown timber survey. USDA Forest Service Insect and Disease Control Branch. U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Powers, J.S. 1995. Spatial and temporal dynamics of the Douglas-fir bark beetle (*Dendroctonus pseudotsugae*, Hopk.) in the Detroit Ranger District: a landscape ecology perspective. MS thesis, Oregon State University.

Rudinsky, J.A. 1966. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. Can Entomol 98: 98–111.

SAS Institute. 1992. SAS technical report P-229. SAS/STAT Software: Changes and Enhancements, Release 6.07. Cary, North Carolina.

Sinton, D.S. 1996. Spatial and temporal patterns of windthrow in the Bull Run Watershed, Oregon. P.h.D. Dissertation, Dept. of Geosciences, Oregon State University.

StatgraphicsPlus. 1993. Reference Manual Version 7. Manguistics, Inc., Cambridge, MA.

Turchin, P. 1990. Rarity of density dependence or population regulation with lags? Nature 344: 660–663.

Turchin, P., Lorio, P.L. Jr., Taylor, A.D. and Billings, R.F. 1991. Why do populations of southern pine beetles (Coleptera: Scolytidae) fluctuate? Env Entomol 20: 401–409.

Turner, M.G. 1989. Landscape ecology: the effect of pattern upon process. Ann Rev Ecol Syst 20: 171–197.

Waring, R.H. and Schlesinger, W.H. 1985. Forest Ecosystems: Concepts and Management. Academic Press, San Diego.

Waring, R.H. and Pitman, G.B. 1980. A simple model of host resistance to bark beetles. Oregon State University Forest Research Laboratory Research Note 65.

Wright, L.C., Berryman, A.A. and Wickman, B.E. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. Can Entomol 116: 293–305.