Pathogens and insects in a pristine forest ecosystem: the Sierra San Pedro Martir, Baja, Mexico

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Abstract: We determined the incidence of pathogens and insects across mixed-conifer stands in the Sierra San Pedro Martir (SSPM) of northern Baja, Mexico, to assess the role of pests in a pristine forest ecosystem. We also determined the spatial distribution of the two most common pests, mistletoe, *Phoradendron pauciflorum* Torrey, and the fir engraver, *Scolytus ventralis* LeConte, of white fir (*Abies concolor* (Gord. & Glend.) Lind.) across a 25-ha grid to assess spread and what host and pest variables were related. In these open parklike stands the mean tree density was 160 trees/ha, of which 58% were trees >20 cm diameter at breast height (DBH). In these low-density, mixed-aged stands we found that mixed-conifer species were well represented with no one species being completely dominant. Percent cumulative mortality for the SSPM was 12.7%, ranging from 2 to 24%, with the greatest amount of mortality occurring in the larger size classes, trees ≥50 cm DBH. Multiple linear regression analysis showed that 78% of the mortality we observed was explained by pathogens and bark beetles ($r^2 = 0.78$, $P = 0.0001$, $F = 84$). Mean pest incidence for Jeffrey pine (*Pinus jeffreyi* Grev. & Balf. in A. Murray), white fir, and sugar pine (*Pinus lambertiana* Doug.) was 21, 88, and 2%, respectively. We found a number of relationships among host and pest variables, as well as a pathogen–insect interaction, and across the SSPM we found that nonhost species may be interfering in certain host–pest interactions. Spatial patterns from the 25-ha grid survey revealed that both *P. pauciflorum* and *S. ventralis* incidence were widespread. *Phoradendron pauciflorum* showed no spatial structure across the 25 ha but *S. ventralis* showed some degree of spatial structuring across the survey area. We also found that mistletoe severity was negatively correlated with regeneration of white fir. In pristine forests, pathogens and insects influence mortality and regeneration success, affecting stand structure and composition.

Résumé : Nous avons déterminé l’incidence des organismes pathogènes et des insectes dans des peuplements mixtes de conifères de la Sierra San Pedro Martir située dans le nord de la région de Baja, au Mexique, pour évaluer le rôle des ravageurs dans un écosystème forestier vierge. Nous avons aussi déterminé la distribution spatiale des deux ravageurs les plus communs, le gui (Phoradendron pauciflorum Torrey) et le scolyte du sapin (Scolytus ventralis LeConte), chez le sapin concolore (Abies concolor (Gord. & Glend.) Lind.) dans une zone quadrillée de 25 ha pour évaluer leur dispersion ainsi que les relations entre les variables qui caractérisent les hôtes et les ravageurs. Dans ces peuplements ouverts semblables à des clairières, la densité moyenne atteignait 160 arbres/ha, dont 58% étaient des arbres de plus de 20 cm au diamètre à hauteur de poitrine (dhp). Dans ces peuplements inéquitables de faible densité, nous avons constaté que les diverses espèces de conifères étaient bien représentées sans qu’aucune ne soit complètement dominante. Le pourcentage cumulatif de mortalité dans la Sierra San Pedro Martir était de 12,7%, variant de 2 à 24%, et la plus forte mortalité survenait dans les classes de plus forts diamètres, les arbres avec un dhp ≥50 cm. L’analyse de régression linéaire multiple montre que 78% de la mortalité observée est expliquée par les organismes pathogènes et les scolytes ($r^2 = 0.78$, $P = 0.0001$, $F = 84$). L’incidence moyenne des ravageurs était respectivement de 21, 88 et 2% pour le pin de Jeffrey (Pinus jeffreyi Grev. & Balf. in A. Murray), le sapin concolore et le pin à sucre (Pinus lambertiana Doug.). Nous avons trouvé plusieurs relations entre les variables qui caractérisent les hôtes et les ravageurs de même qu’une interaction entre organismes pathogènes et insectes. De plus, nous avons trouvé que, dans l’ensemble de la Sierra San Pedro Martir, les espèces non-hôtes peuvent interférer avec certaines interactions hôtes-ravageurs. Les patrons spatiaux obtenus à partir de la zone quadrillée de 25 ha révèlent que l’incidence de *P. pauciflorum* et de *S. ventralis* est généralisée. *Phoradendron pauciflorum* n’a démontré aucune structure spatiale dans la zone quadrillée de 25 ha, mais *S. ventralis* a un certain degré de structuration spatiale dans la zone inventoriée. Nous avons également trouvé que la sévérité des dommages causés par le gui est négativement corrélée avec la régénération du sapin.
Dans les forêts vieilles, les organismes pathogènes et les insectes influencent la mortalité et le succès de la régénération, ce qui se répercute sur la structure et la composition du peuplement.

[Intué par la Rédaction]

Introduction

Most forests in North America have been affected by modern human practices such as logging and (or) fire suppression. The mixed-conifer forests of the Sierra San Pedro Martir (SSPM) of northern Baja, Mexico, provide a unique opportunity to study an ecosystem in which forest structure and the natural disturbance regimes that contribute to ecosystem function have been relatively unaltered by humans (Minnich and Franco-Vizcaino 1997; Minnich et al. 2000). Floristically, the SSPM shares many of the same conifer and shrub species as the Sierra Nevada; however, there are differences in herb and grass species. The SSPM is ecologically very similar to the mixed-conifer forests of the Sierra Nevada of California, but human influences have been minimal because of their remote location. SSPM forests have never been logged and still experience historical unmanaged fire regimes (Minnich et al. 2000). Limited grazing in the montane meadows of the SSPM has occurred since the 18th century, but its impact on forest ecosystems appears to be slight (Minnich et al. 2000). Minnich et al. (2000) provide evidence that these forests may provide baseline information to which modern California forests can be compared.

Historically, in North American forests, pathogens and insects have often been treated as pests by foresters. However, the fact that many of these organisms are endemic to their respective forests indicates they can play a key role in ecosystem dynamics (Burdon and Chilvers 1974; Worrall and Harrington 1988; Dickman and Cook 1989; Harrington et al. 1989; Schowalter 1991; Haack and Byler 1993; Holah et al. 1993). Fire suppression in the western United States has led to changes in forest species composition and structure (Kilgore 1981; Swetnam 1993; SNEP Science Team 1996; Ansley and Battles 1998) and in turn has altered the response of forest pathogens and insects (Wickman 1992; Campbell and Leigle 1996; Ferrell 1996). A number of endemic bark beetle and pathogen outbreaks have been tied to increased host tree densities resulting from fire suppression policies and drought (Ferrell 1996; P.E. Maloney and D.M. Rizzo, unpublished data). Our knowledge of pest species in mixed-conifer forests in the western United States is based largely from research done in forests with a history of human intervention. In the Sierra Nevada and most western forests, ideal reference sites are nonexistent (Millar and Woofenden 1999), but by gathering information from a nearly comparable, contemporary forest, we may be able to assess the effects of human actions and the current roles of pest species in mixed-conifer forests. The SSPM provides an excellent site in which to examine pest species in an historical forest structure of widely spaced trees.

In this study, our main objective was to identify the major pathogens and insects of the mixed-conifer forest in the SSPM and correlate their occurrence with forest structure, composition, and mortality. We also examined the spatial patterns of two of the most ubiquitous pest species. The information provided by this study, as possible reference conditions of pest species, may be useful in guiding forest management policies in the SSPM and for evaluating restoration strategies in mixed-conifer forests of the Sierra Nevada.

Materials and methods

Study area

Our research was conducted in the SSPM in northern Baja, Mexico. The SSPM is centered at 115°W, 31°N. The forested area covers approximately 100,000 ha of which 39,000 ha are the southern extension of Sierran mixed-conifer forest (Minnich and Franco-Vizcaino 1997; Minnich et al. 2000). Substrate in the SSPM is largely granitic with some areas of metamorphic rock (Gastil et al. 1975). The mixed-conifer forests of the SSPM are found between 1900 and 2500 m, and contain many of the same species as the Sierra Nevada: white fir (Abies concolor (Gord. & Glend.) Lindl.), incense cedar (Calocedrus decurrens (Torrey) Florin), lodgepole pine (Pinus contorta Dougl. ex Loud.), Jeffrey pine (Pinus jeffreyi Grev. & Balf. in A. Murray), and sugar pine (Pinus lambertiana Dougl.). Northern Baja lies at the southern margin of the North American Mediterranean climatic zone. Like the Sierra Nevada, winter frontal storms in the SSPM bring rain or snow between November and April, and summers are dry with the exception of afternoon mountain thunderstorms. In the SSPM, snowfall provides >50% of the annual precipitation above 2188 m (Minnich and Franco-Vizcaino 1997). Mean annual winter temperature and summer temperatures are 1.4°C and 16.3°C, respectively, and mean annual precipitation is 65 cm (Minnich et al. 2000).

Minnich et al. (2000) suggest that the fire regime in the SSPM is largely dominated by high-intensity surface fires, <16 ha in area, forming open forests of mature trees. A combination of spot burns and infrequent landscape-scale burns account for most disturbance and consumption of fuels in the SSPM, with a mean fire-return interval of 52 years (Minnich et al. 2000).

Field sampling

In the SSPM, forest stands were located and selected based on species composition that most closely resembled mixed-conifer forests of the Sierra Nevada (Rundel and Parsons 1988), as well as SSPM vegetation studies described by Minnich (1987) and Minnich and Franco-Vizcaino (1997). Mixed-conifer forests will vary in species composition across stands. Those species include white fir, red fir (Abies magnifica A. Murray) incense cedar, lodgepole pine, Jeffrey pine, and sugar pine (Rundel and Parsons 1988). Sample stands cover the range of variability associated with the composition of mixed-conifer forests. We located approximately 20 stands from which 13 stands were randomly selected and sampled. Within a stand, we chose a random starting point and a random compass bearing for a 240 m long transect. Sampling
occurred in 15 m diameter plots (~706 m²) located every 30 m along the 240 m long transects. Based on our stand locations in relation to fire map data of Minnich et al. (2000), our study sites have not experienced fire in the last 20–50 years.

In each plot, tree species (live and dead) were identified and placed in one of four diameter classes (DBH, diameter at breast height). As a measure of recruitment, seedlings, saplings, and small trees >30 cm tall and <20 cm DBH were classified and recorded within a 100-m² circular plot centered at each plot center. The four diameter classes were as follows: (1) ≤20 cm, (2) 20.1–50 cm, (3) 50.1–100 cm, and (4) ≥100.1 cm. Diameter at breast height was taken on those trees at least 1.5 m tall, trees smaller than 1.5 m were recorded as seedlings. The above four size classes reflect position in the canopy: understory, midstory, and overstory. Year of death was estimated for snags, downed logs, and stumps based on bark, twig, and needle retention. Shrub and herb cover and litter depth were also estimated at each plot. The slope and aspect of each plot per transect were also recorded. Tree and recruitment data were used at each plot to quantify stand structure, composition, and density.

Signs and symptoms of pathogen or insect colonization, such as browning, dieback, or foliage chlorosis were recorded. Pathogen and insect presence were noted for live and dead trees (Scharpf 1993; Furniss and Carolin 1977). Dead trees were closely examined to determine apparent mortality agent(s). Bark was removed from trees to identify characteristic bark beetle galleries. Stumps of trees were examined for the presence of root pathogens by identifying fruiting bodies and characteristic decay patterns. Stems and branches were examined for bark beetles (e.g., boring dust, pitch tubes, galleries, resin streaming), stem pathogens (presence of fruiting bodies), and branch pathogens (e.g., sporulation of rust species, presence of mistletoe, and symptomatic browning). Visible signs of past fire (i.e., basal fire scars or lightning strike scars) were also recorded.

Phoradendron pauciflorum Torrey (mistletoe) and Scolytus ventralis LeConte (fir engraver beetle) on white fir were the most ubiquitous and visible pest problems in the SSPM. Boschniakia incana (fruiting bodies), and branch pathogens (e.g., Sclerotinia), and Penicillium were also recorded. The slope, aspect, and other topographical features (e.g., creek, rock outcroppings) of each cell were noted.

Statistical and spatial analyses

Correlation analyses (Pearson’s or Spearman’s rank) were used to determine relationships between stand and host characteristics and pest incidence as well as between bark beetle and pathogen incidence. Multiple linear regression was used to determine the relationship between mortality and pest variables. Data were transformed if normality assumptions were violated; where transformations did not improve normality, nonparametric tests were used. For all tests $P = 0.05$ was defined as significant. We also used a correlation analysis to determine the relationship between mortality and tree density. To investigate this relationship we reconstructed stand density to a date (1985) prior to the most recent drought event (1987–1990). This reconstruction was possible, because we accounted for all dead and downed trees on the plots. All statistical procedures were performed using SAS (version 6).

To analyze spatial patterns of *P. pauciflorum* and *S. ventralis* we used variograms (semivariance) (see Isaaks and Srivastava 1989; Legendre and Fortin 1989; Rossi et al. 1992). Variograms determine the degree of spatial autocorrelation or spatial dependence. Values that remain constant mean that the variance does not change with distance, indicating that there is some continuity in the variability across space (Rossi et al. 1992). Small variogram values at short lags or distances correspond to data that are more similar or spatially dependent, whereas large variogram values indicate data that are more dissimilar or spatially independent (Rossi et al. 1992). For spatial analyses of *P. pauciflorum* and *S. ventralis* occurrence we used the residuals from the regression of disease and insect incidence on host density. Real and McElhany (1996) recommend using the residuals to uncouple the spatial structure of a pest from the spatial structure of the host so that one is left with the sole effect of space. A best fit model was calculated for all analyses using GS+ software (Robertson 2000). The *P. pauciflorum* and *S. ventralis* data were both fit to a spherical model. All variograms were run with GS+ software (Robertson 2000).

Results

Site and stand characteristics

The mean slope for mixed-conifer stands was 9% (range 2–15%), and the mean aspect for stands was 200° (range 0–320°). Elevation of the 13 transects ranged between 2200 and 2900 m. Mean litter depth for stands was 0.92 cm (range 0.3–1.8 cm) and the mean herb and shrub cover was 17% (range 7.5–36%). Evidence of fire, presence of basal fire scars and lightning strikes, was observed in 7 of the 13 stands.

Mean density was 160 trees/ha, of which 42% were trees less than 20 cm DBH (Fig. 1). Our density data for these mixed-conifer forests are similar to other studies from this area, which reported 162, 140, and 156 trees/ha (Savage 1997; Minnich et al. 1995, 2000, respectively). Minnich et al. (2000) reported ~248 saplings/ha, which is, on average, much higher than what we found. One explanation might be...
that we calculated density from counts of all trees in a plot, whereas the other studies used the point-center-quarter method, which may slightly inflate density estimations. The diameter distributions for four of the six mixed-conifer species show relatively uneven-aged size structures (Fig. 2). White fir generally had the highest densities, followed by Jeffrey pine, sugar pine, and lodgepole pine, respectively (Fig. 2). Overall, no one species was completely dominant in any one of the diameter classes in these mixed-conifer stands (Fig. 2). There were differences in the diameter distributions of live and dead trees, with the majority of live trees less than 100 cm DBH, and the majority of dead trees greater than 50 cm DBH (Fig. 3).

Diseases, insects, and fire

Diseases and insects were primary causes of mortality in these forests (Table 1). Aside from fire, other abiotic disturbances (e.g., wind, rockslides) were not observed as causes of mortality. Fire was an agent of mortality for 6% of the dead trees in the SSPM. Trees either died and remained standing (snags) or died and fell because of rotted roots. Overall, mean pest incidence on Jeffrey pine, white fir, and sugar pine was 21, 88, and 2%, respectively (Table 2). There was wide variation in specific disease and insect incidences from stand to stand (Table 2).

Three common pathogens in these stands were (i) *Phoradendron pauciflorum*, a true mistletoe, on white fir, (ii) *Elytroderma deformans* (Weir) Darker, a needle cast on Jeffrey pine, and (iii) *Heterobasidion annosum* (Fr.:Fr.) Bref, a root pathogen on white fir (Table 2). *Phoradendron pauciflorum* accounted for 60% of the mean pest incidence on white fir with ranges between 0 and 100%; only 2 of 12 stands with white fir had 0% incidence (Table 2). *Elytroderma deformans* has its greatest effects on small trees, but moderate to severe infections on large trees can predispose these trees to bark beetle attack (Scharpf 1993). *Elytroderma deformans* was found in 4 of the 13 stands in which Jeffrey pine was present. We generally found a low incidence of root diseases in the SSPM. *Heterobasidion annosum*, which is believed to predispose trees to bark beetle attack (Cobb et al. 1974; Goheen and Hansen 1993), was found in 5 of the 12 stands in which white fir was present. It is probable that we have underestimated the actual amount.

Fig. 1. Mean density (stems/ha) with standard deviations of trees in four diameter classes in the SSPM from 13 transects.

Fig. 2. Density and diameter distribution of four conifer species in sampled stands: (a) Jeffrey pine, \( N = 13 \); (b) sugar pine, \( N = 9 \); (c) white fir, \( N = 12 \); and (d) lodgepole pine, \( N = 2 \). \( N \), number of transects where species was present.
of root disease on these sites because of the difficulty of diagnosing disease on the root system of trees (the disease was mostly diagnosed in uprooted trees and stumps).

Bark beetles were found on the four conifer hosts we sampled in these stands, and the combined incidence of all bark beetle species was 39%. _Scolytus ventralis_ was associated with 87% of dead white fir. Evidence of attack on living trees (e.g., dead tops, resin streaming) was much less in 1997–1998, with a mean incidence of 10%. While _Dendroctonus jeffreyi_ Hopkins was associated with 71% of all dead Jeffrey pine in the SSPM stands, incidence of beetles on living Jeffrey pines was very low, <2% of the trees showing signs of recent _D. jeffreyi_ attack. Low levels of mortality resulting from _Dendroctonus ponderosae_ Hopkins were noted on sugar pine (Table 2).

Relationships were found between host and pest variables and between one pathogen and one insect. The number of Jeffrey pine trees with _D. jeffreyi_ was weakly correlated with the density of Jeffrey pine (r = 0.31, P = 0.003, N = 90), but a stronger correlation was found between the number of white fir trees with _S. ventralis_ and the density of white fir (r = 0.56, P = 0.001, N = 86). _Phoradendron pauciflorum_ was also positively correlated with white fir density (r = 0.66, P = 0.001, N = 78), but the severity of mistletoe was negatively correlated with host density (r = -0.28, P = 0.03, N = 57). However, mistletoe severity across these stands was significantly and positively correlated with host size (r = 0.32, P = 0.01, N = 57); that is the larger the tree, the more severe the infection. Across these mixed-conifer stands, incidence of _S. ventralis_ was positively correlated with incidence of mistletoe (r = 0.28, P = 0.001, N = 78).

We found that there was a degree of interference by nonhost trees in certain host–pest interactions. There were significant and negative correlations between the number of trees attacked by _S. ventralis_ or infected with mistletoe and frequency of Jeffrey pine, a nonhost (r = -0.36, P = 0.01, N = 85; r = -0.51, P = 0.01, N = 77, respectively). However, the severity of mistletoe was not negatively correlated but positively correlated with frequency of Jeffrey pine (r = 0.35, P = 0.008, N = 57), suggesting that Jeffrey pine interferes in the spread of mistletoe but not intensity of infection. The number of trees attacked by _D. jeffreyi_ and the frequency of white fir were significantly and negatively correlated (r = -0.27, P = 0.01, N = 84).

### Tree mortality

Percent cumulative mortality for the SSPM was 12.7%, ranging from 2% to 24%, with the greatest amount of mortality occurring in the larger size classes (Fig. 3). An earlier study in the SSPM reported only 4% cumulative mortality (Savage 1997). This mortality figure is lower than ours, because Savage (1997) only counted standing dead trees and used the point-center quarter method, whereas we counted all standing and downed dead trees within a plot. The mean annual mortality rates in these stands are less than 1%/year, and tree density was weakly correlated with mortality (r = 0.22, P = 0.02, N = 105). Multiple linear regression analysis showed that 78% of mortality in the SSPM was explained by pathogens (mistletoe, mistletoe severity, and _E. deformans_) and bark beetles (_S. ventralis_ and _D. jeffreyi_) (r^2 = 0.78, df = 5, P = 0.0001, F = 84). Fire was not included in the multiple linear regression analysis, but we know that approximately 6% of trees died because of the effects of fire. The cause of death of the remaining trees was listed as unknown. In these instances, potential pathogens and insects were not visible or may have been obscured by other saprobic organisms. Another cause of mortality aside from pests and fire could be drought. The species composition of dead stems is largely dominated by white fir, for trees ≤50 cm DBH (Table 1). In the larger size classes, trees ≥50 cm DBH, there was a more even distribution of dead trees between white fir and Jeffrey pine (Table 1). Sugar pine trees make up a very small percentage of dead trees in the SSPM (Table 1).

### Grid survey and spatial patterns

The intensive survey of _P. pauciflorum_ and _S. ventralis_ on white fir was conducted in a stand. A 25-ha grid was established across a mixed-conifer stand with rocky outcrops throughout, and a seasonal creek that ran south to north (Table 4). To the west of the creek the forested area was on a relatively steep east-facing slope. Mean slope across the grid was 9% with a range of 0–30%, and mean aspect was 180° with a range of 4–356°. We found that mistletoe is widely distributed throughout this location and incidence is high, with a mean of 51% (Table 4, Figs. 4a and 4b). The highest fir densities were found in the western portion of the grid (Fig. 4c).

_Phoradendron pauciflorum_ on white fir in the SSPM did not show any clear spatial structuring (Fig. 5a). Spatially structured variance accounted for only 35% of the total model sample variance. The variogram for _S. ventralis_ shows a slight degree of spatial structure, with 87% of model sample variance spatially dependent within a 300 m range of separation (Fig. 5b).

From the intensive survey, mistletoe incidence and severity were significantly and negatively correlated with host density (r = -0.45, P = 0.001, N = 100; r = -0.41, P = 0.0001, N = 100, respectively). However, mistletoe incidence and especially severity were positively correlated with host DBH (r = 0.29, P = 0.004, N = 100; r = 0.44, P = 0.0001, N = 100, respectively). We also found a negative relationship between mistletoe incidence and white fir recruitment (r = -0.36, P = 0.003, N = 100). Both mistletoe incidence and severity were positively correlated with _S. ventralis_ incidence.
**Table 1. Pathogens and insects of conifers observed in the Sierra San Pedro Martir, Baja.**

<table>
<thead>
<tr>
<th>Host</th>
<th>Pest</th>
</tr>
</thead>
<tbody>
<tr>
<td>White fir</td>
<td><em>Phoradendron pauciflorum</em> (mistletoe), <em>Heterobasidion annosum</em> (root disease), <em>Phaeolus schweinitzii</em> (root disease), <em>Echinodontium tincturam</em> (trunk rot), <em>Scolytus ventralis</em> (bark beetle)</td>
</tr>
<tr>
<td>Jeffrey pine</td>
<td><em>Elytroderma deformans</em> (needle cast), <em>Dendroctonus jeffreyi</em> (bark beetle), <em>Dendroctonus valens</em> (bark beetle), <em>Ips</em> spp. (bark beetles), <em>Neodiprion</em> spp. (sawfly)</td>
</tr>
<tr>
<td>Sugar pine</td>
<td><em>Phellinus pini</em> (stem rot), <em>Dendroctonus ponderosae</em> (bark beetle), <em>Ips</em> spp. (bark beetles)</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td><em>Dendroctonus ponderosae</em> (bark beetle)</td>
</tr>
</tbody>
</table>

**Table 2. Overall mean incidence (%) of most common diseases and insects on Jeffrey pine, white fir, and sugar pine in the SSPM.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Overall pest incidence (%)</th>
<th>Most common pests and percent incidence*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jeffrey pine</td>
<td>21</td>
<td>Ely, 8 (0–47)</td>
</tr>
<tr>
<td>Sugar pine</td>
<td>2</td>
<td>Php, 1 (0–10)</td>
</tr>
<tr>
<td>White fir</td>
<td>88</td>
<td>Mt, 60 (0–100); Ha, 3 (0–7); Sv, 26 (9–42)</td>
</tr>
</tbody>
</table>

*Values in parentheses are incidence ranges. Pathogen abbreviations are as follows: Ely, *Elytroderma deformans*; Ha, *Heterobasidion annosum*; Php, *Phellinus pini*; Mt, *Phoradendron pauciflorum*. Bark beetle abbreviations are as follows: Dj, *Dendroctonus jeffreyi*; Dp, *Dendroctonus ponderosae*; Sv, *Scolytus ventralis*. 

**Table 3. Species composition of dead stems from the four diameter size classes (diameter class 1, 20 cm DBH; diameter class 2, 20.1–50 cm DBH; diameter class 3, 50.1–100 cm DBH; diameter class 4, 100.1 cm DBH) as a percentage of all stems in each class.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Class 1</th>
<th>Class 2</th>
<th>Class 3</th>
<th>Class 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jeffrey pine</td>
<td>10</td>
<td>35</td>
<td>47</td>
<td>44</td>
</tr>
<tr>
<td>Sugar pine</td>
<td>0</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>White fir</td>
<td>90</td>
<td>60</td>
<td>49</td>
<td>55</td>
</tr>
</tbody>
</table>

(r = 0.50, P = 0.0001, N = 100; r = 0.25, P = 0.01, N = 100, respectively). *Scolytus ventralis* was also positively correlated with host density and DBH (r = 0.25, P = 0.01, N = 100; r = 0.25, P = 0.01, N = 100, respectively). Although our overall survey data showed interference, the intensive survey showed no interference relationships for *P. pauciflorum* and *S. ventralis* with nonhost frequency.

**Discussion**

Fires in the SSPM are relatively frequent events and the primary mode of stand thinning and mortality of subcanopy trees (trees 4–20 cm DBH), which results in an open, parklike forest structure (Minnich et al. 2000). Aside from these episodes of fire-mediated mortality, most mortality in the SSPM is occurring to larger overstory trees (trees 4–20 cm DBH), with about 6% of trees dying because of fire-related causes. Seventy-eight percent of the mortality in the SSPM was explained by the presence of pathogens and bark beetles. While other papers (Hawksworth and Weins 1996; Savage 1997) have reported the presence of various insects and diseases in the SSPM, our study is the first to make a comprehensive examination of the distribution of these organisms as mortality agents in the SSPM. Overall, the identity of pathogens and insects is the same as is found in the Sierra Nevada; no new pathogens or insects were detected in the SSPM. In addition, no major differences in life histories of these pest organisms were noted. The only major difference in the pest composition between the Sierra Nevada and the SSPM was that the introduced pathogen, *Cronartium ribicola* J.C. Fisch. (causal agent of white pine blister rust), was not found at all in this location.

Environmental stresses, such as fire and drought, are also likely to be involved indirectly as predisposing factors in tree mortality in the SSPM. Both fire and drought can increase the activity of a number of bark beetle species (Paine and Baker 1993; McCullough et al. 1998). *Dendroctonus jeffreyi* is a bark beetle that can mass attack and kill healthy trees, but when *D. jeffreyi* population densities are low they usually colonize and kill only trees of low vigor (e.g., trees that are fire scorched, drought stressed, or diseased) (Paine et al. 1997).

Tree mortality in the SSPM was weakly density dependent, unlike what has been found in present-day mixed-conifer forests in the Sierra Nevada (P.E. Maloney and D.M. Rizzo, unpublished data). The three most prevalent pests...
(P. pauciflorum, S. ventralis, and D. jeffreyi) from our transect survey in the SSPM were correlated with their respective host densities. However, in the intensive 25-ha grid survey, P. pauciflorum was negatively correlated with host density and S. ventralis was positively correlated with host density. Tree density in the SSPM is low when compared with other mixed-conifer forests (Savage 1997; Minnich et al. 2000), and this may explain why pest-caused mortality was not strongly density dependent in our survey. All three of the major pest species are dispersed by flight: bark beetles fly in search of hosts and Phoradendron is bird dispersed. So the relative proximity of hosts rather than the absolute number of hosts may be more important in these three host–pest interactions. Bark beetles often kill trees in clusters or groups, and the absolute density of hosts is not always positively correlated with bark beetle activity (Berryman 1982). That is, at small spatial scales (<0.1 ha) density may not be important. In our study, most pest-specific tree mortality did not appear to depend on tree diameter. However, we did find that P. pauciflorum severity was positively correlated with host size. Two possible explanations for this relationship might be (i) bigger trees are a larger target (or preferable perch for birds dispersing mistletoe seeds), or (ii) bigger trees provide more available area per tree for established infections to spread and intensify. Incidence of S. ventralis was also correlated with DBH in our intensive survey.

Scolytus ventralis and Phoradendron spp. have long been implicated in predisposing one another to attack. While this species of true mistletoe generally does not directly kill white fir, it may predispose trees to other pests, as well as negatively affect tree growth and reproduction (Bega 1978). In our research, we found that there was a positive relationship between P. pauciflorum and S. ventralis. Scolytus ventralis is considered a secondary bark beetle, which is only capable of colonizing weakened, stressed, or recently killed trees (Paine et al. 1997). Thus, increased bark beetle activity on white fir has often been associated with the presence of mistletoe and other pathogens (Raffa and Berryman 1982; Ferrell 1996).

Across the SSPM, we found that nonhost tree species may be interfering in certain host–pest interactions. In this mixed-conifer forest, Jeffrey pine may influence the white fir – Scolytus and white fir – Phoradendron interactions, and white fir may influence the Jeffrey pine – Dendroctonus interaction. Many insects, including bark beetles, fly randomly to both hosts and nonhosts (Raffa and Berryman 1980). Mixtures of species are known to limit the dispersal capabilities of both pathogens and insects by decreasing the probability of finding a suitable host (Kareiva 1983; Burdon 1987). In these mixtures, with a degree of species evenness, nonhost species may provide host plant protection from their respective pests (Wills 1996). However, we did not observe this effect in the 25-ha mixed-conifer grid, suggesting that this relationship may be scale and species dependent.

Spatial patterns from our grid survey revealed that both P. pauciflorum and Scolytus incidences across a 25-ha area were fairly widespread. However, P. pauciflorum showed no...
spatial structuring in our intensive survey. Two reasons may explain this lack of spatial pattern, one being the length of time this area has been infected with this parasitic plant and the second being the widespread nature of bird movement. Avian dispersers have been shown to be responsible for certain patterns of spread if bird movement is biased towards certain sizes of trees (Lamont 1985); however, that is not the case in our study. We did find a degree of spatial structuring in \textit{S. ventralis} incidence. Perhaps, once beetle populations are established, their pattern of spread may be influenced in a direction because of mistletoe-infected trees and environmental factors predisposing individuals to bark beetle attack.

Mistletoe severity in the 25-ha grid was negatively correlated with regeneration of white fir. White fir can be fairly prolific, producing smaller and more abundant seeds than both Jeffrey pine and sugar pine and generally reproducing at an earlier age (Burns and Honkala 1990). Mistletoe can have a negative effect on cone production, especially if a tree has parasitized branches near the upper portion of the crown where most cone production occurs (Laacke 1990). In these mixed-conifer stands, mistletoe may be acting as a natural biological control agent, maintaining tree species diversity and evenness. Savage (1997) also found that regeneration was balanced in the SSPM, suggesting some factor existed that maintained forest tree diversity and evenness.

The relative importance of fire and pest organisms appears to be different between the SSPM and the mixed-conifer forests of the Sierra Nevada. While fire is mainly responsible for subcanopy mortality in the SSPM, pests are important to overstory mortality. Mortality rates are generally constant and deviate because of spatially restricted episodes of bark beetle mediated mortality. In contrast, in Sierra Nevada mixed-conifer forests, stand thinning is taking place at a much later time in stand development (i.e., when trees are larger than 20 cm DBH) (P.E. Maloney and D.M. Rizzo, unpublished data). It appears in these fire-suppressed forests, insects and diseases in association with periodic drought events have now largely replaced fire as the main stand thinning agents in the Sierra Nevada, while insects, diseases, and fire maintain tree diversity and evenness in the SSPM.

Conservation of the SSPM is critical, as it is the last landscape-scale remnant of old-growth, mixed-conifer forest that still experiences a natural wildfire regime (Minnich and Franco-Vizcaino 1997; E. Franco-Vizcaino, personal communication). Preserving this ecosystem can provide possible reference conditions to assist in restoration and management objectives in dry mixed-conifer forests elsewhere. Throughout the western United States, forest managers and researchers are attempting to return fire to various forest types (e.g., Covington et al. 1997; Fule et al. 1997; Moore et al. 1999; Stephenson 1999). In many of these forest types, it has generally been considered that prior to fire suppression and extensive grazing, the forests were much more open with fairly low stand densities that are similar to that currently found in the SSPM. Rarely have the role of pathogens and insects been considered in these restoration efforts (Hansen and Goheen 2000). While the influences of many diseases and insects may be considered a "natural" part of these ecosystems, we must not assume they are acting in the same manner as in historic times (Hansen and Goheen 2000). Pathogen and insect population levels may be considerably higher because of past Euro-American management. This situation is common in many second growth forests throughout western U.S. conifer forests where past cutting practices have increased pathogen populations dramatically (Hansen and Goheen 2000). While the SSPM may differ in details from other forested areas in western North America, the SSPM provides a unique glimpse into the role of pathogens and insects in a forested landscape that has not been extensively influenced by human management.

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Maloney and Rizzo


