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Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona

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Abstract

We studied the bark beetle guild (Coleoptera: Scolytidae) in the ponderosa pine forests of northern Arizona to explore if the species assemblages and relative abundance differ between managed and unmanaged stands. Four stand conditions were assessed: (1) unmanaged stands with high tree density, (2) thinned stands, (3) thinned and burned (with prescribed fire) stands and (4) stands that had been burned by stand replacing wildfires. The study was conducted in the ponderosa pine forests of the Coconino Plateau, northern Arizona. For several decades this area has been relatively free of bark beetle outbreaks despite the current overstocked condition of many stands. We found that a similar species assemblage composed of *Dendroctonus frontalis*, *D. brevicomis*, *D. valens*, *D. approximatus*, *D. ponderosae*, and *Ips pini* occurred across all four stand conditions over 3 years of study. The population levels of all these species were endemic across all stand conditions. The non-aggressive *D. approximatus* and *D. valens* were indicator species for thinned and unmanaged stands, respectively, but this was not consistent among years. The ambrosia beetle *Gnathotrichus* sp. and the bark beetle predator *Enoclerus* sp. consistently indicated stands burned by wildfire. In addition to our field experiment, we analyzed the historical pattern of attacks of bark beetles in our area of study. Our findings suggest that the pattern of attack of *D. brevicomis* (the only *Dendroctonus* species for which attacks have been reported) and *Ips* spp. has been through scattered small infestations in groups of 1–10 trees. Whereas small infestations by *Ips* spp. are increasing, those for *D. brevicomis* are decreasing. Although we agree that the high density stands in northern Arizona are in an "unhealthy" condition, our results do not show that they were supporting large bark beetle outbreaks. Our results challenge the theoretical assumptions about the relationship between stand structure, tree resistance and bark beetle performance.

Keywords: Ponderosa pine; Bark beetles; *Dendroctonus* spp.; Stand structure; Forest health; Indicator species

1. Introduction

Forest health specialists agree that the current highly dense condition of ponderosa pine forests of northern Arizona are unhealthy and at risk to stand replacing wildfires and bark beetle outbreaks (Covington and Moore, 1994; Covington et al., 1997; Kolb et al., 1998; Feeney et al., 1998). Before Euro-American settlement, mature ponderosa pine stands apparently had an open-growth, park-like structure, with an average tree density of 54–57 trees ha^{-1} and basal area of approximately 15 $m^2\,ha^{-1}$ (Covington and Moore, 1994; Covington et al., 1997). At present, many stands contain more than 1800 postsettlement trees per hectare and high basal areas (Covington and Moore, 1994; Covington et al., 1997; Kolb et al.,

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1998). Although some debate still exists regarding an average historical tree density, most specialists agree that the density of ponderosa pine forests in northern Arizona is much higher to date than in the past. Current forest structure resulted from the removal of most large overstory, the introduction of cattle and the exclusion of fire during the later part of the 19th and early 20th century (Covington and Moore, 1994; Covington et al., 1997).

Concerns and predictions of potential bark beetle outbreaks in the ponderosa pine forest of northern Arizona are valid since they are built upon existing knowledge of the interactions among stand structure, tree resistance and bark beetle population dynamics. In general terms, overstocked stands are considered more susceptible to bark beetle attacks than open grown stands (Sarwell and Stevens, 1975; Mitchel et al., 1983). For example, Sarwell and Stevens (1975) and Mitchel et al. (1983) found significantly higher tree mortality due to *Dendroctonus ponderosae* Hopkins in stands with 27–35 $m^2 ha^{-1}$ of basal area in comparison to stands with basal area of 20 $m^2 ha^{-1}$ or less. Mitchel et al. (1983) observed that although attacks by *D. ponderosae* on lodgepole pine are related to stand density, this species avoids high density stands (ca. 68 $m^2 ha^{-1}$) composed of small diameter trees which are unsuitable for insect reproduction. However, other bark beetle species infest trees with either smaller or larger diameters (Wood, 1982).

The most robust theoretical models on the population dynamics of bark beetles (Berryman, 1982, 1997) indicate that at endemic population levels, bark beetles infest stressed or non-vigorous trees whereas at epidemic levels bark beetles suppress the resistance mechanisms of vigorous trees through mass attack. Sarwell and Stevens (1975) Mitchel et al. (1983), Christiansen et al. (1987) and others hypothesize that tree competition in dense stands diminishes vigor and limits the allocation of carbon for defense against insects.

Studies in the Coconino National Forest in northern Arizona have demonstrated that ponderosa pine trees growing at high densities in unmanaged stands indeed have the lowest resin flow in comparison with trees growing at lower densities in managed stands (Feeney et al., 1998; Kolb et al., 1998). Resin flow is considered as one of the most important tree resistance mechanisms to bark beetle attack (Christiansen et al., 1987; Raffa and Berryman, 1987; Berryman et al., 1989). Covington et al. (1997), Feeney et al. (1998) and Kolb et al. (1998) hypothesize that silvicultural treatments such as thinning and prescribed burning enhance the tree resistance mechanisms against bark beetle attack. Nevertheless, Kolb et al. (1998) suggest that trees growing in very dense stands (BA 78 $m^2 ha^{-1}$) may also be at low risk of attack by species such as *D. ponderosae* because small diameter trees with thin phloem are unsuitable for the insect. Kolb et al. (1998) suggest that stands with moderate basal area (between 18.4 and 27.6 $m^2 ha^{-1}$) may be more at risk to bark beetle attack since trees growing under these conditions produce low resin flow and have thicker phloem. These studies indicate that, from a physiological standpoint, the mechanism of tree resistance against bark beetle attacks can be improved through silvicultural treatments; however, the bark beetle component itself was not studied.

Bark beetle populations in the ponderosa pine forest of the Coconino National Forest have remained endemic for almost 1 century (unpublished Insect Control Annual Reports, USDA, Forest Service Region 3, 1924–1952; Annual Insect and Disease Aerial Detection Survey maps of the USDA Forest Service, Region 3, Flagstaff, 1976–2000, USDA, 1999). Perhaps this is why research on the bark beetle guild of this region is lacking. Indeed, the unpublished Insect Control Annual Reports of the USDA, Forest Service Region 3, 1924–1952, indicated normal or below normal tree mortality by bark beetles within the Coconino National Forest in the first half of the 20th century. More recent insect aerial detection survey maps from 1976 to 2000 (Steve M. Dudley, USDA Forest Service, personal communication) show that *Dendroctonus brevicomis* LeConte is widely scattered across the landscape, but at endemic conditions (scattered groups from 1 to 5 killed trees). Although a few small *Ips* pockets have occurred in some years, a major outbreak of the primary *Dendroctonus* species within the ponderosa pine forest of the Coconino National Forest has not been reported in the past 100 years.

From a utilitarian perspective, the risk of bark beetle outbreaks indicates possible economic losses, unattractive landscapes, and increased risk of wildfires. From an ecological perspective we believe that both the occurrence and absence of bark beetle outbreaks within unhealthy forests are of concern, as bark beetles perform ecologically relevant functions. As ecosystem engineers (Gurney and Lawton, 1996; Jones et al., 1997), bark beetles are organisms that modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. Bark beetles add diversity and dynamics to the forest ecosystems by creating habitats and food sources for other organisms (Amman, 1984; Jones et al., 1997; Lundquist, 1995; Coulson et al., 1999a). Therefore, extreme bark beetle population levels including either epidemics or local extinction are of ecological relevance to forest health.

In the present study, we assessed the bark beetle guild of the ponderosa pine forests of northern Arizona in terms of species assemblage and relative abundance, under a broad range of stand conditions. The objectives of this study were to: (1) test if the bark beetle species assemblage differed between managed and unmanaged stands; (2) test if any bark beetle species would serve as an indicator of specific stand conditions; (3) analyze the historical pattern of attacks of bark beetles in the ponderosa pine forest of the Coconino Plateau.

Unmanaged stands are unhealthy because they have high tree density and high fuel loads that in theory make them susceptible to stand replacing wildfires and/or bark beetle outbreaks. Managed stands are healthier (in theory) because they have an appropriate tree density, lower fuel loads and more growing space for the understory vegetation. We believe that if the stand structure–bark beetle resistance hypothesis applies to the ponderosa pine forest of northern Arizona then the relative population levels of aggressive and secondary species (i.e. *D. brevicomis* and *Ips* spp.) should be higher in the most dense (unmanaged) stands relative to managed stands. We also hypothesize that if the different bark beetles species vary in their responsiveness to changes in stand conditions (i.e. thinning treatment, prescribed fire, wildfire), then the relative abundance of the different species among the stands can serve as indicators of forest health.

2. Materials and methods

The study was conducted in the ponderosa pine forests of the Coconino Plateau, northern Arizona (35°08′N, 111°40′W) as part of a long-term project started in 1997, examining forest health (Bailey et al., 1999). The following criteria to classify four stand conditions were established:

1. *Unmanaged stands*. Dense stands having not received any silvicultural treatment within the last 20–30 years. The stand structure is characterized as second growth ponderosa pine even-aged stands, with dense patches of small diameter trees (pole size), few clumps of old-growth ponderosa pine trees, high basal area, high fuel loads and simplified understory.
2. *Commercially thinned stands*. Mature even-aged ponderosa pine stands with >30% of the basal area removed between 1987 and 1994, at least 50% of which came from diameter classes <30.5 cm. No more than 10 over-mature trees (>64 cm dbh) per hectare.
3. *Thinned and broadcast burned stands*. Commercially thinned, even-aged stands like the above which had received a broadcast burn within 3–4 years of thinning with overstory survival >90%.
4. *Wildfire areas*. Formerly dense stands with no management during the past 20–30 years, which had been burned by stand replacing wildfires within the last few years. Current structure consists of wide-open burned areas with great numbers of dead trees, broken snags and early successional plants in the understory.

Stands ranged from 20 to 40 ha and were dispersed within a radius of ca. 30 km from Flagstaff, AZ. Initially, we identified 10 stands representing each condition; however, sampling all 40 stands would consume time and resources beyond our capacity. Therefore, for the purpose of this study we randomly selected four stands of each treatment to produce a complete randomized experimental design of 4 (stand conditions) $\times$ 4(replicates). Each stand condition was considered as a treatment. Wildfire areas resulted from stand replacing wildfires occurred in 1996. Response variables were the number and abundance of flying bark beetle species (Coleoptera: Scolytidae) that were collected (pooled sampling dates) in each stand.

Tree and stand structure measurements in our 16 randomly selected stands were made through the establishment of 10 permanent plots per stand $(20.1\,\text{m} \times 20.1\,\text{m})$ installed systematically along a

Table 1
Tree and stand characteristics of a field experiment to assess the bark beetle diversity in the ponderosa pine forests of the Coconino Plateau, northern Arizona[a]

Treatment	Average tree dbh in cm	Stand density index[b]	Relative density index[c]	Average BA/ha (m^2)	Average number of trees/ha
Unmanaged	22.15 (0.68)	306.5 (22.51)	0.68 (0.049)	33.4 (2.46)	778.75 (87.82)
Thinned	26.95 (1.20)	207.5 (23.71)	0.46 (0.052)	24.05 (2.86)	415 (66.81)
Thinned and burned	29.70 (2.27)	116.75 (10.68)	0.26 (0.0239)	14.17 (1.08)	215 (12.07)
Wildfire	0	0	0	0	0

[a] Values enclosed in parenthesis correspond to 1 S.E.

[b] Stand density index is the number of trees, for a stand, that have an equivalent average diameter at breast hight of 25 cm (Smith et al., 1997).

[c] Relative density index is the ratio between the actual number of trees in a stand and the maximum number of trees, of that average tree size, that the stand could sustain (Smith et al., 1997).

200 or 150 m grid according to the stand size. Tree and stand characteristics of each treatment are summarized in Table 1.

2.1. Bark beetle rating and insect sampling

In addition to standard forestry measurements, all trees within the permanent plots were rated for the presence of bark beetle attacks based on DeMars and Roettgering (1982) and Parker (1991). Tree rating was defined as follows: 0, no bark beetle attack; 1, old attack; 2, fresh attack.

Bark beetles were sampled every summer from 1998 to 2000. In 1998, we installed one-eight-unit Lindgren funnel trap (Phero Tech., Delta, BC, Canada) baited with turpentine, near the center of each stand. These traps served as a source of attraction for *Dendroctonus valens* and as passive traps for any other bark beetle species.

Because other bark beetle species besides *D. valens* were rarely captured with passive traps and no evidence of current outbreaks was observed in 1998, we decided to use commercially available bark beetle lures in 1999 and 2000 to attract other species that could be present within the stands. In these years (summers of 1999 and 2000), we used two funnel traps per stand: one-eight-unit trap baited with turpentine to attract *D. valens* and one-twelve-unit trap baited with a commercially available bark beetle lure (Phero Tech., Delta, BC, Canada) appropriate for our target insects (Table 2). Traps were hung from a branch of a ponderosa pine tree (near the center of the stand) about 1 m away from the tree bole and the trap bottom was 1.6 m above the ground. Insect lures were deployed according to the flight period of the target species (see sampling period in Table 2). The flight period for *I. pini* (Say) in northern Arizona occurs from May to July (Villa-Castillo, 1994). We used the USDA forest

Table 2
Trap system used to characterize the diversity and abundance of bark beetles in ponderosa pine forests of the Coconino Plateau, northern Arizona

Target insect	Insect lure[a]	Trap size (funnels)	Sampling period		
			1998	1999	2000
D. valens and bark beetles in general	Turpentine	8-Unit	June 16–August 20	May 26–August 24	July 14–August 1
I. pini	Ipsdienol +50/−50 and lanierone	12-Unit		May 26–July 6	May 31–July 15
D. brevicomis	Frontalin, exo-brevicomin, myrcene	12-Unit		August 9–September 22	July 14–September 1
D. ponderosae	*trans*-Verbenol, myrcene, exo-brevicomin	12-Unit		July 6–August 10	July 31–September 1

[a] Commercial formulas (Pherotech) for *I. pini* (product code L1-2300/000), *D. brevicomis* (product code L1-2060/000) and *D. ponderosa* (product code L1-2011/000) were used.

insect guidelines (DeMars and Roettgering, 1982; Schmid, 1972; Mata, 1998) as general references for the flight periods of western pine beetle (WPB) and mountain pine beetle.

Bark beetles were collected from the funnel traps every 2 weeks during the sampling period and preserved in vials with 75% ethanol. Voucher specimens were mounted for identification and all specimens were sorted and counted. We used the taxonomic monograph for bark and ambrosia beetles (Wood, 1982) as the reference for the identification to the species level. Scott Kelley (University of Colorado, personal communication) confirmed the identification of different *Dendroctonus* species. A voucher collection was prepared and left at the Northern Arizona University, Forest Entomology Lab. Bark beetle predators (from the families Cleridae and Ostomidae) present in our traps were collected and identified based on Furniss and Carolin (1980).

2.2. Statistical analysis

2.2.1. Bark beetle infestation rating

Data were summarized in a descriptive table and a one-way ANOVA was conducted to detect any difference in the number of infested trees among treatments.

2.2.2. Species assemblages and indicator species

For the 1998 insect collection, we used one-way ANOVA (SAS Institute, 1996), to test the null hypothesis of no treatment effects on the abundance of Scolytidae in general ($p < 0.05$). Although very few specimens of *Dendroctonus* spp. and *Ips* spp. were captured we noted their presence to improve our sampling system in the next 2 years.

For 1999 and 2000 data, we used multiple response permutation procedure (MRPP) (Zimmerman et al., 1985; McCune and Mefford, 1995), a non-parametric technique designed to detect differences in species assemblages among different treatments. MRPP is an alternative to multivariate analysis of variance (MANOVA) that does not require normal distribution and homogeneous variance of the data, because the hypothesis testing depends only on the internal variability of the sample. The p value is obtained through a permutation procedure that involves all possible arrangements of the N observations to the different treatments, under the null hypothesis that all permutations have the same probability of occurrence (Zimmerman et al., 1985; McCune and Mefford, 1995). In this analysis, we used the Euclidean distance ($v = 1$) to detect concentrations within groups.

The MRPP involves the computation of non-parametric statistics that deserve some description. The observed δ represents the weighted average of within-group pairwise distance measures for the g groups. This statistics indicates the concentration of the object measurements within the treatments (Zimmerman et al., 1985). The smallest the value of observed δ the more concentrated are the measurements within the groups. According to Zimmerman et al. (1985) and McCune and Mefford (1995), the observed δ is defined as

$$\delta = \sum_{i=1}^{g} C_i \xi_i$$

where $C_i = n_i/N$ for $i = 1, 2, \ldots, g$, n_i is the number of objects (replicates) in treatment i; N the total number of objects in all treatments; ξ_i the average distance of pared objects within treatment i.

The standardized test statistic T of MRPP indicates the separation between treatments. This statistic is computed as $T = (\text{observed}\,\delta - \text{expected}\,\delta)/\text{standard}$ deviation of observed δ.

The statistic R describes the within-group homogeneity relative to random expectation. Since $R = 1 - (\text{observed}\,\delta/\text{expected}\,\delta)$, then the maximum possible value for R is 1, assuming that all the object measures within groups are the same. R close to 0 suggests that the heterogeneity within groups is similar to that expected by chance alone. A negative R means that the heterogeneity within groups exceeds that expected by chance (McCune and Mefford, 1995). More mathematical details on MRPP can be found in Zimmerman et al. (1985) and McCune and Mefford (1995).

Our second analysis for the 1999 and 2000 data sets was the indicator species analysis (Dufrêne and Legendre, 1997; McCune and Mefford, 1997). According to Dufrêne and Legendre (1997) indicator species analysis is appropriate to evaluate the impact of management practices on species abundance. Under this procedure, an indicator species is defined as the most characteristic species of a particular group (treatment) based on the representation and abundance of that species within the experimental units comprising the group. We used this method to detect if any bark beetle species or their predators were indicative of a particular stand condition (e.g. unmanaged stands). We included predators and other Scolytidae in this analysis because the method evaluates the abundance of every species in a group independent of the presence and abundance of other species. Thus, the indicator value index for any given species is independent of other species within the treatment (Dufrêne and Legendre, 1997). Comparisons of the abundance of one species relative to the abundance of other species are not valid under the Dufrêne and Legendre method. For both MRPP and indicator species analysis, we used PC-ORD (McCune and Mefford, 1995; McCune and Mefford, 1997).

2.2.3. Bark beetle infestation pattern and trend

We used ArcInfo V.8 (ESRI, 1999) to analyze the most recent bark beetle infestation records for our general area of study (north half of the Coconino National Forest). Geographic extents of damage-causing agents were obtained at the Arizona Zone Office of Entomology and Pathology, USDA, Forest Service, in Flagstaff Arizona (Steve M. Dudley, personal communication). The geographic extent of bark beetle damage and beetle outbreaks was built based on the Annual Insect And Disease Aerial Detection Survey maps of the USDA Forest Service, Region 3, in Flagstaff (Steve M. Dudley, personal communication). Extent of damage by causal agents was available for every year from 1976 to 2000 (except 1980). Two bark beetle species for ponderosa pine forests are recorded in those damage estimates (*D. brevicomis* and *Ips* spp.). Infestations of several sizes are recorded. We used ArcInfo to analyze the frequency of small (1–5 trees), mid-size (6–20 fading trees) and larger (>20 fading trees) infestations by *D. brevicomis* and *Ips* spp. occurring every year. *D. brevicomis* is considered a primary species that is capable of large outbreaks (Miller and Keen, 1960). *Ips* spp. in North America are considered as secondary species. We were interested in determining the prevailing pattern of infestation (small infestations vs. large infestations) and to see if that pattern changed with time (i.e. increase or decrease of the number of large infestations per year). We arranged infestation size frequency data in a univariate fashion and performed individual ANOVA (SAS Institute, 1996) for each infestation size. We selected time period as treatment factor (1976–1979, 1981–1985, 1986–1990, 1991–1995, 1996–2000) and infestation size as the response variables. We tested for differences in the occurrence of a particular infestation size during these periods. Separate ANOVAs are appropriate because the infestation size data sets are independent (we assumed that the occurrence of an infestation is independent of any other infestation).

Complementary to the statistical analyses, we reviewed historical descriptive reports on bark beetle infestations for the Coconino National Forests (USDA, 1924–1952) to see if large outbreaks had occurred in the past. We also analyzed the climatic records for Flagstaff, AZ, for the last 100 years (NOAA, 1977, 1985, 1992, 1999) to see if dry years were followed by large bark beetle infestations.

3. Results

3.1. Bark beetle infestation rating

We found very little evidence of bark beetle attacks within the permanent plots located in our experimental stands. From 2136 sampled trees only 16 (0.75% of sample) had evidence of unsuccessful old attacks and five trees had fresh attacks (Table 3). Based on the average number of old infested trees per 400 m^2 plot, the ANOVA detected no difference in infestation rates among treatments ($F_{2,9} = 0.47$, $p = 0.6363$). The mean number of infested trees (S.E.) for every 400 m^2 plot was 1.75 (0.85), 0.75 (0.25) and 1.5 (0.9574) for unmanaged, thinned, and thinned and broadcast burning treatments, respectively.

3.2. Bark beetle species assemblages and indicator species

3.2.1. 1998

For the 1998 insect collection we found differences in Scolytidae species richness ($p < 0.001$) and abundance ($p < 0.001$) associated with the treatments. We observed that *D. valens* was equally represented in all stand conditions, but the specificity and abundance of the ambrosia beetle *Gnathotrichus* sp. and the

Table 3
Bark beetle infestation rates on ponderosa pine trees growing under three different stand management treatments in the Coconino Plateau, northern Arizona[a]

Stand treatment	Stand no.	Sampled plots	Sampled trees	Bark beetle rating[b]		
				Class 0	Class 1	Class 2
Unmanaged	1	10	289	285	4	0
	2	10	418	415	0	3
	3	10	257	256	1	0
	4	10	229	226	2	1
Thinned	1	10	103	102	1	0
	2	9	181	180	1	0
	3	10	223	223	0	0
	4	10	94	93	1	0
Thinned and burned	1	10	95	95	0	0
	2	10	91	88	2	1
	3	10	89	85	4	0
	4	10	67	67	0	0

[a] We excluded the wildfire treatment in this analysis because all trees within the plots were killed directly by the stand replacing wildfires.
[b] Bark beetle rating: 0, non-infested tree; 1, old bark beetle attack; 2, fresh bark beetle attack.

presence of *D. brevicomis* and *Dendroctonus frontalis* (only one specimen) in wildfire burned stands contributed to the statistical differences (Fig. 1). Very few specimens of *Hylastes* sp. and *Hylurgops* sp. (not shown in Fig. 1) were caught and included in the analysis. Because we used only turpentine as the insect attractant and few specimens of other *Dendroctonus* and *Ips* species were collected, we used these preliminary results only as a guide to refine or sampling method in the following 2 years.

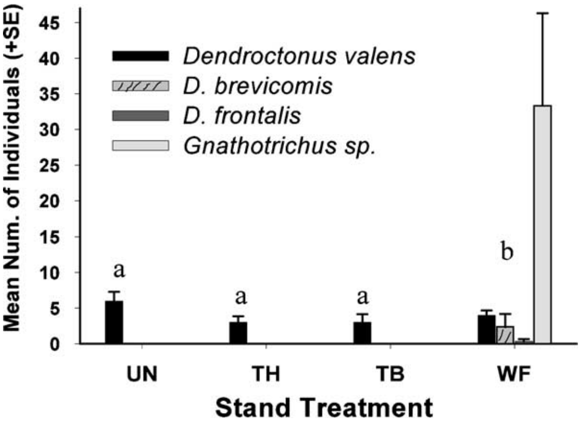

Fig. 1. Number of insects collected in 1998 under four ponderosa pine stand conditions in northern Arizona. The insects were collected with Lindgren funnel traps (one per stand) baited with turpentine. Stand treatment codes are: (UN) unmanaged, (TH) thinning, (TB) thinning and prescribed burn and (WF) stand replacing wildfire. Lines above the mean indicate +1S.E. Letters above bars indicate differences in species richness among treatments (Tukey's HSD test $p = 0.05$).

3.2.2. 1999

By adding bark beetle pheromones to our trapping system in 1999, we detected five *Dendroctonus* species, *I. pini* and *Ips* sp. With the exception of *D. ponderosae* (only two specimens captured in two thinned stands), most species occurred across all the stand conditions represented in our experiment (Fig. 2).

We found that the WPB lure attracted both *D. brevicomis* and *D. frontalis* Zimmerman. These two species were the most abundant in all stand types. A random sub sample of 762 beetles, from the complete insect sample of seven stands, gave an overall *D. frontalis* to *D. brevicomis* ratio of 4:1 despite the fact that *D. brevicomis* was the targeted species. Each tree supporting the funnel trap was attacked by these two species when the WPB lure was installed; however, by the next year only the trees in the thinning and broadcast burning treatment were killed (three trees that contained the trap and one neighbor tree). The WPB lure also attracted *D. approximatus*.

MRPP suggested different bark beetle species assemblages among treatments (observed $\delta = 340.8$,

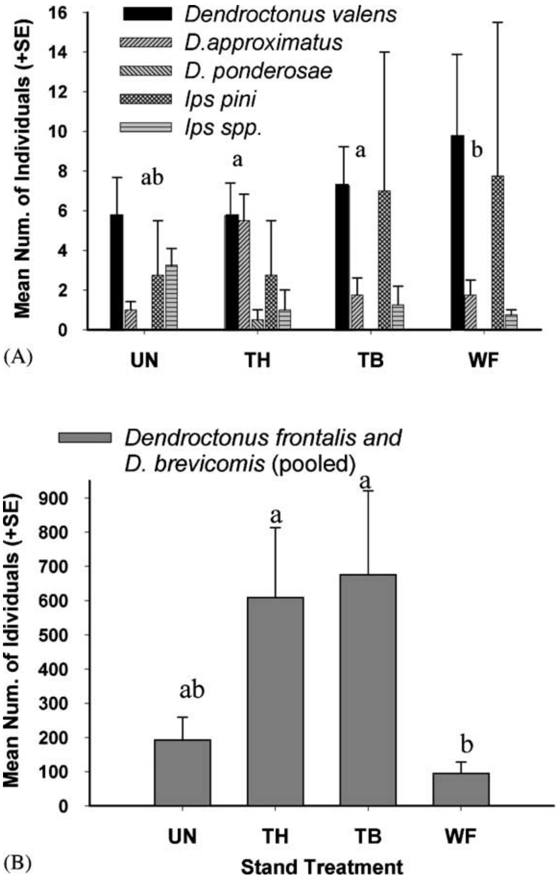

Fig. 2. Number of insects collected during the summer of 1999 under four ponderosa pine stand conditions in northern Arizona. The insects were captured with two Lindgren funnel traps per stand, one baited with turpentine and the other with species-specific pheromones (*I. pini* lure, WPB lure and mountain pine beetle lure). Stand treatment codes are: (UN) unmanaged, (TH) thinning, (TB) thinning and prescribed burn and (WF) stand replacing wildfire. The figure is partitioned (A and B) to represent the appropriate scale of the less abundant species. Lines above the mean indicate +1S.E. Treatments with different species assemblages were separated through paired comparisons in MRPP and are represented with different letters above the mean bars.

expected $\delta = 416.0$, $T = -1.8498$, $p = 0.0522$, $R = 0.1824$). Paired comparisons with the group exclusion option in MRPP (PC-ORD) indicated that managed stands (thinned, and thinned and broadcast burned stands) have a common bark beetle assemblage, whereas unmanaged stands and wildfire areas form another group. The mean number of individuals per species showed that the only difference between managed and unmanaged stands was the abundance of the complex *D. frontalis/brevicomis* (Fig. 2B) and that the abundance had an effect in the analysis. However, the indicator species analysis suggested that the relatively higher abundance of *D. frontalis/brevicomis* in thinned, and thinned and broadcast burned stands was not sufficient to allow these species to be classified as indicator species (Table 4). The only bark beetle species with significant attachment to a stand condition in 1999 was *D. approximatus*, which was an indicator species for thinned stands (Table 4). *D. ponderosae* was present in thinned stands only, but in insufficient numbers to be classified as an indicator species. The ambrosia beetle *Gnathotrichus* sp. and the predator *Enoclerus* sp. were indicator species for wildfire burned stands.

3.2.3. 2000

Our bark beetle sampling in the year 2000 confirmed the presence of five *Dendroctonus* species and *I. pini* in our study area. With the exception of *D. ponderosae* (only one specimen captured), most species occurred across all the stand conditions represented in the experiment (Fig. 3).

Although *D. frontalis* and *D. brevicomis* were again the most abundant species in all stands during 2000, both species were similarly distributed across the four stand conditions ($p = 0.3074$). The thinning stand treatment had the largest mean for *D. frontalis* but the largest variation as well (Fig. 3B). On the other hand, the abundance of *D. frontalis* in wildfire burned stands, which have only dead trees, was similar to the abundance of this species in other stand conditions. The MRPP detected no statistical differences in bark beetle species assemblages among stand treatments in 2000 (observed $\delta = 230.9$, expected $\delta = 235.3$, $T = -0.3654$, $p = 0.3074$, $R = 0.0185$) indicating that all species are similarly represented among stand conditions. These results were consistent with the indicator species analysis (Table 5). The only species that served as an indicator in 2000 was *D. valens*, which had maximum presence in unmanaged stands (Table 5). *D. ponderosae* was present only in the unmanaged stand condition; however, because only one specimen was captured, this species did not qualify as an indicator species.

Our results from 2000 confirmed that the WPB lure attracted higher numbers of *D. frontalis* than

Table 4
Bark beetle diversity in four ponderosa pine stand conditions in northern Arizona during 1999 according to the indicator species method of Dufrêne and Legendre (1997)

Species	Relative abundance (%)[a]				Relative frequency (%)[b]				Indicator value index[c]				p for maximum indicator value[d]
	UN[e]	TH[f]	TB[g]	WF[h]	UN	TH	TB	WF	UN	TH	TB	WF	
D. valens	20	20	25	34	100	100	100	100	20	20	25	**34**	0.655
D. frontalis and *D. brevicomis*	12	39	43	6	100	100	100	100	12	39	**43**	6	0.259
D. approximatus	10	55	18	18	75	100	75	75	8	**55**	13	13	0.013*
D. ponderosae	0	100	0	0	0	50	0	0	0	**50**	0	0	0.176
I. pini	14	14	35	38	75	75	100	100	10	10	35	**38**	0.587
Ips sp.	52	16	20	12	100	25	50	75	**52**	4	10	9	0.087
Gnathotrichus sp.	0	1	0	99	0	25	0	100	0	0	0	**99**	0.005*
E. lecontei	54	23	13	10	100	75	100	100	**54**	17	13	10	0.087
Enoclerus sphegus	26	38	24	12	100	100	100	75	26	**38**	24	9	0.310
Enoclerus sp.	0	0	0	100	0	0	0	100	0	0	0	**100**	0.005*
Temnochila sp.	28	35	19	17	100	100	100	100	28	**35**	19	17	0.681

[a] This column indicates the abundance of a species in one stand condition relative to the overall abundance of that species.

[b] Values in this column represent the percentage of stands with a given treatment that contained the species (i.e. four stands = 100%).

[c] The indicator value results from the product of the two previous columns. Bolded values are maximum indicator values for each species.

[d] Significant indicator values are denoted by an asterisk.

[e] Unmanaged.

[f] Thinned.

[g] Thinned and broadcast burned.

[h] Wildfire burned stands.

Table 5
Bark beetle diversity in four ponderosa pine stand conditions in northern Arizona during 2000 according to the indicator species method of Dufrêne and Legendre (1997)

Species	Relative abundance (%)[a]				Relative frequency (%)[b]				Indicator value index[c]				p for maximum indicator value[d]
	UN[e]	TH[f]	TB[g]	WF[h]	UN	TH	TB	WF	UN	TH	TB	WF	
D. valens	50	31	17	2	100	75	100	25	**50**	23	17	1	0.045*
D. frontalis	11	44	22	24	100	100	100	100	11	**44**	22	24	0.747
D. brevicomis	21	38	32	10	100	100	100	100	21	**38**	32	10	0.134
D. approximatus	44	8	30	18	100	50	100	25	**44**	4	30	5	0.178
D. ponderosae	100	0	0	0	25	0	0	0	**25**	0	0	0	1.00
I. pini	17	28	31	24	100	75	75	100	17	21	**24**	**24**	0.993
Ips sp.	0	100	0	0	0	25	0	0	0	**25**	0	0	1.00
Gnathotrichus sp.	0	0	5	95	0	0	25	100	0	0	1	**95**	0.002*
E. lecontei	18	41	28	14	100	75	75	75	18	**30**	21	10	0.782
Enoclerus sphegus	17	38	38	8	100	75	75	75	17	**28**	**28**	6	0.844
Enoclerus sp.	0	0	0	100	0	0	0	75	0	0	0	**75**	0.031*
Temnochila sp.	23	18	39	20	100	100	100	100	23	18	**39**	20	0.715

[a] This column indicates the abundance of a species in one stand condition relative to the overall abundance of that species.

[b] Values in this column represent the percentage of stands with a given treatment that contained the species (i.e. four stands = 100%).

[c] The indicator value results from the product of the two previous columns. Bolded values are maximum indicator values for each species.

[d] Significant indicator values are denoted by an asterisk.

[e] Unmanaged.

[f] Thinned.

[g] Thinned and broadcast burned.

[h] Wildfire burned stands.

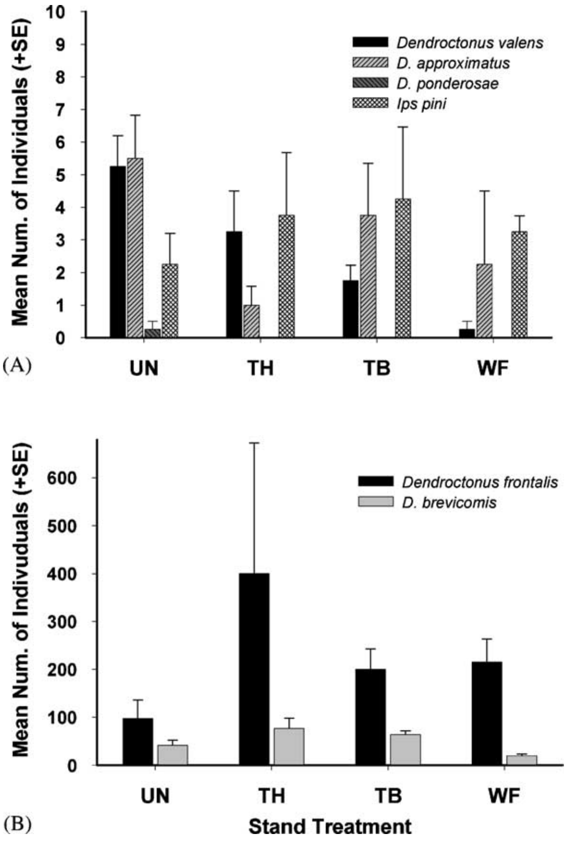

Fig. 3. Number of insects collected during the summer of 2000 in four ponderosa pine stand conditions in northern Arizona. The insects were captured with two Lindgren funnel traps per stand, one baited with turpentine and the other with species-specific pheromones (*I. pini* lure, WPB lure and mountain pine beetle lure). Stand treatment codes are: (UN) unmanaged, (TH) thinning, (TB) thinning and prescribed burn and (WF) stand replacing wildfire. The figure is partitioned (A and B) to represent the appropriate scale of the less abundant species. Lines above the mean indicate +1S.E.

D. brevicomis. Similarly, most trees containing the funnel traps with this lure were lightly attacked by these species. In addition, the WPB lure attracted most specimens of *D. approximatus* reported in this study. Finally, this analysis confirmed the fidelity of *Gnathotrichus* sp. and the predator *Enoclerus* sp. to wildfire burned stands and the general distribution of other bark beetle predators (*Enoclerus lecontei*, *E. sphegus* and *Temnochila* sp.) across all stand conditions.

3.3. Bark beetle infestation pattern and trend

Data from the Annual Insect and Disease Aerial Detection Survey maps for 1976–1999 suggest that, at the landscape level, the small size infestation pattern (groups of 1–5 fading trees) predominated over the moderate or large infestation size, for both *D. brevicomis* and *Ips* spp. However, whereas for *Ips* spp. the number of small infestations is slightly increasing (Fig. 4A), small infestations by *D. brevicomis* are decreasing (Fig. 4B). ANOVA indicated significant differences in the number of small infestations by *D. brevicomis* (1–5 fading trees) among the five predefined periods ($F_{4,19} = 2.88$, $p = 0.0506$). Because of the marginal p value obtained

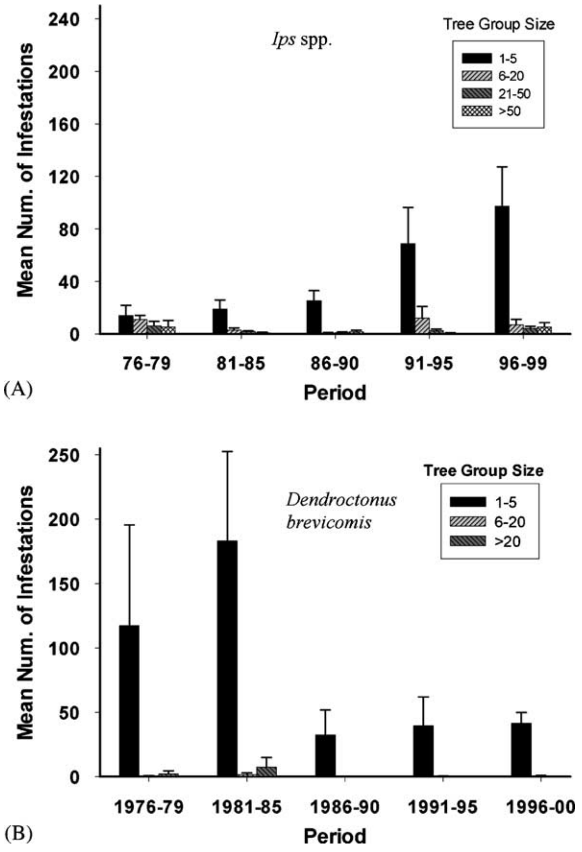

Fig. 4. Average number of infestations by *Ips* spp. (A) and *D. brevicomis* (B) on ponderosa pine forests within the north half of the Coconino National Forest, northern Arizona. Data from the USDA Aerial Detection Surveys, Region 3, 1976–2000. Lines above the mean indicate +1S.E.

with Tukey's HSD procedure, it was difficult to separate groups of means without much overlapping; however, results indicate that during 1976–1985 small infestations occurred in larger numbers than during the previous 15 years (Fig. 4B). No significant differences occurred for infestations of 6–20 trees ($F_{4,19} = 0.46$, $p = 0.7624$) and >20 trees ($F_{4,19} = 0.7980$, $p = 0.5412$) among the different periods and were almost non-existent for the last 15 years. Similarly, ANOVA indicated significant differences in the number of small infestations by *Ips* spp. (1–5 fading trees) among the five predefined periods ($F_{4,18} = 3.58$, $p = 0.0257$), but not for infestations of size 6–20 ($F_{4,18} = 1.178$, $p = 0.3535$), 21–50 ($F_{4,18} = 1.690$, $p = 0.1947$) of >50 trees ($F_{4,18} = 6.977, p = 0.4442$). Tukey's HSD test again failed to clearly separate different groups of means for small infestations, but results suggest that infestations of size 1–5 trees have been increasing for the last 9 years (Fig. 4A).

Climatic records for Flagstaff, AZ, from 1900 to 1999, indicate that some years have had an annual precipitation way below the long-term mean annual precipitation of 53.31 cm (NOAA, 1977, 1985, 1992, 1999). The driest year of the 20th century was 1942

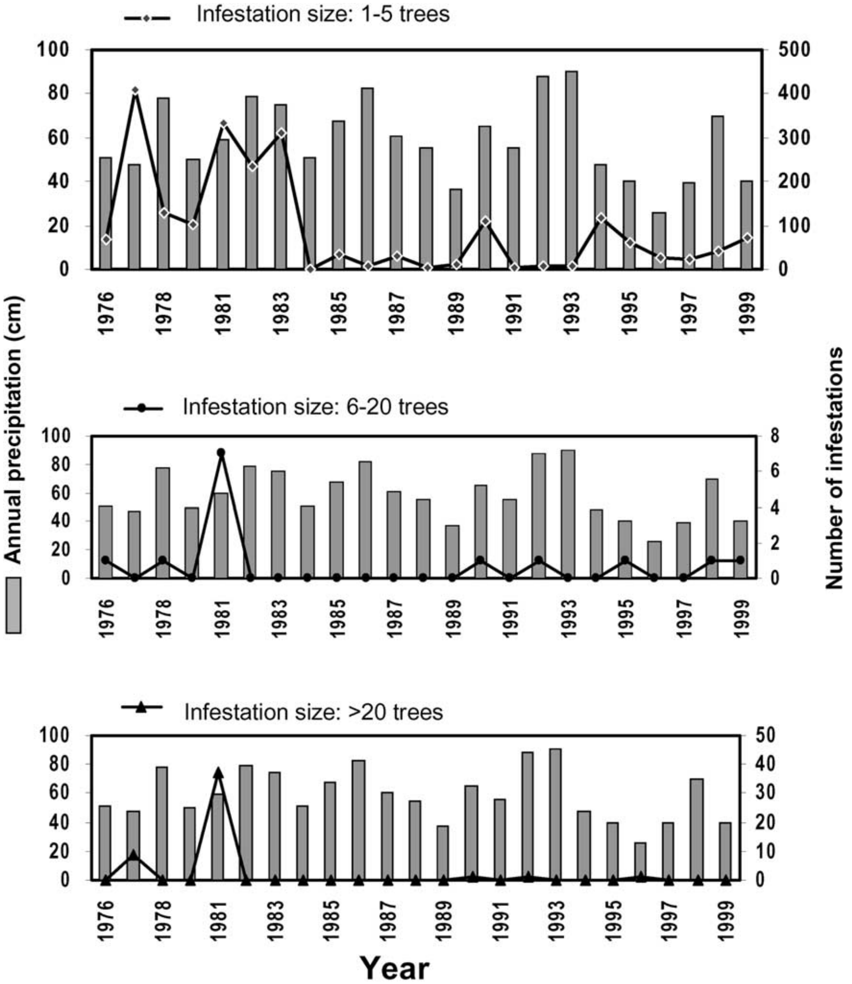

Fig. 5. Infestations by *D. brevicomis* on ponderosa pine forests within the north half of the Coconino National Forest, northern Arizona, relative to the annual precipitation in Flagstaff during 1976–1999. Infestation data from the USDA Aerial Detection Surveys, Region 3, 1976–2000. Precipitation data from NOAA (1977, 1985, 1992, 1999).

with 47% of the mean annual precipitation. However, historical records indicate that "normal or below normal" bark beetle infestations occurred for the Coconino National Forest in 1942 and during the following years after this dry year (unpublished Insect Control Annual Reports, USDA, Forest Service Region 3, 1924–1952). Other years with low annual precipitation were 1950 and 1956 with 51 and 49% of the mean annual precipitation but no infestation records were found for this period. The latest driest years in Flagstaff occurred in 1995, 1996 and 1997 with 74, 48, and 74%, respectively, of the long-term mean annual precipitation; however, our analyses on the infestation trend suggest that rather than observing an increase of large size infestations by *D. brevicomis* through time, there is a decrease in the number of small infestations (1–5 fading trees) and no change in low number of moderate (6–20 fading trees) and large infestations (>20 fading trees) in our area of study (Fig. 5).

4. Discussion

Our results indicate that the bark beetle guild of the ponderosa pine forests of the Coconino Plateau was composed of *D. frontalis*, *D. brevicomis*, *D. valens*, *D. approximatus*, *D. ponderosae*, *I. pini* and *Ips* sp. (possibly *I. latidens*). All species occurred at similar endemic levels across all stand conditions independent of thinning and independent of the occurrence or absence of fire. Fresh infestations were almost absent under any stand condition. Other researchers have found that thinning and prescribed burning improve the tree physiological conditions associated with resistance to insects (Covington et al., 1997; Feeney et al., 1998; Kolb et al., 1998). However, in our study area, we found no evidence to support the hypothesis that trees growing in dense stands are more colonized by bark beetles. Our findings, however, are not inconsistent with the hypothesis that these forests are in an unhealthy condition, they simply indicate that the relative population levels of bark beetles show no significant sensitivity to changes is stand structure and fire occurrence or that changes are not apparent at the stand level. We agree that high density conditions in unmanaged stands make them susceptible to other disturbances such as stand replacing wildfires, but their susceptibility to large bark beetle outbreaks could not be demonstrated on our study sites during this time period.

Results from the analysis of aerial detection surveys maps indicate that, at the landscape level, and in a temporal scale of 24 years, the number of small infestations by *Ips* spp. is increasing, but the number of small infestations by the primary species *D. brevicomis* is decreasing. These opposite trends neutralize the absolute number of small bark beetle infestations, which has been relatively steady during the last 3 decades. No change was observed in the attack pattern of the primary species *D. brevicomis* and the secondary *Ips* spp. that can be described as scattered attacks in group of 1–5 trees. For these reasons, we found no evidence to support the hypothesis that the second growth ponderosa pine forests of the Coconino Plateau in northern Arizona are experiencing more bark beetle outbreaks than in the past. We found only a trend suggesting that *Ips* spp. is becoming more prevalent than *D. brevicomis*.

From an ecological perspective, the lack of bark beetle attacks in unhealthy forests is as relevant as the occurrence of epidemics, because the low or below normal levels of natural disturbance agents may indicate stagnation of stand dynamics, interruption of important ecological processes (e.g. tree decomposition), and poor habitat diversity (e.g. for wildlife). Local climatic records indicate that drought has occurred at least in 5 years during the 20th century. If bark beetles were to respond as the theory suggests, then we would have observed an increasing number of large infestations to date. This pattern did not occur. Therefore, our results suggest that *Dendroctonus* species that are commonly known as aggressive in other ecosystems (*D. frontalis*, *D. brevicomis* and *D. ponderosae*) have so far behaved non-aggressively in the ponderosa pine forests of the Coconino Plateau.

Whether the low population levels of *D. ponderosae* in our area of study is indicative of a species in the process of local extinction or colonization of a new habitat is unknown since no infestations have been reported for the Coconino National Forest. In contrast, the nearby old-growth ponderosa pine forests of north Kaibab Plateau have historically sustained frequent outbreaks by this species (Blackman, 1931; Douglas and Stevens, 1979). Comparisons between the forest structure and the bark beetle assemblages of these two ecosystems may provide valuable information to understand the different bark beetle regimes in northern Arizona.

In the early part of the 20th century, Hopkins (1909) identified a species known as *Dendroctonus arizonicus* Hopkins. Later, based on morphological characteristics, Wood (1982) placed this species in *syinonymy* with *D. frontalis*. Hopkins (1909) pointed out that *D. arizonicus* (collected from Flagstaff and Williams, AZ) was observed nearly always associated with *D. barberi* Hopkins (now *D. brevicomis*). His observations are in agreement with our findings of *D. frontalis* and *D. brevicomis* in the same traps and lead us to suggest that a genetic study is necessary to determine if the *D. frontalis* and *D. brevicomis* existing in our area are indeed different species as originally classified by Hopkins (1909). Although *D. frontalis* was the most abundant in our traps, an outbreak by *D. frontalis* has never been reported for northern Arizona. Genetic differences may explain the non-aggressive behavior of bark beetles of the Coconino Plateau. For instance, in a previous case, *Dendroctonus rhizophagus* Thomas and Bright was treated as *D. valens* (Wood, 1982) but the distinct behavior and genetic analysis have proved its actual taxonomic classification (Thomas and Bright, 1970; Wood, 1982; Kelley and Farrell, 1998). A recent study on the genetics of *D. brevicomis* (Kelley et al., 1999) suggests that this species may also be composed of two cryptic species that match with the distribution of the two varieties of ponderosa pine (var. *scopolorum* and var. *ponderosa*).

Another explanation of the relative low population levels of the aggressive bark beetle species in ponderosa pine forests of the Coconino Plateau is the lack of abundant suitable hosts. According to Olsen et al. (1996), *D. ponderosae* in other ponderosa pine ecosystems prefers trees with dbh between 23 and 33 cm, whereas *D. brevicomis* prefers more mature ponderosa pine trees (150–300 years) with dbh between 60 and 81 cm (Miller and Keen, 1960). The average tree dbh in our four stand conditions were $\leq$29.7 cm well below the preferred host size for *D. brevicomis*. Indeed, unmanaged stands had an average tree dbh of only 22.2 cm which is below the lowest threshold level of preference for *D. ponderosae*. We believe that the low abundance of large diameter trees in the unmanaged ponderosa pine stands limits the population levels of these two species. Historical records indicate that large outbreaks were uncommon in the 20th century. Large outbreaks by *D. brevicomis* may occur as the stands reach larger diameters.

Forest health specialists in other ecosystems had demonstrated the association between lightning struck trees and bark beetle attacks. This factor is indispensable for the maintenance of endemic levels of the southern pine beetle guild (*D. frontalis*, *D. terebrans* (Oliver), *Ips calligraphus* (Germar), *Ips grandicollis* Eichhoff and *Ips avulsus* Eichhoff) and for the initiation of infestations by *D. frontalis* in Texas (Coulson et al., 1986; Lovelady et al., 1991; Coulson et al., 1999a,b). In another ecosystem, Palik and Pederson (1996) found that lightning strikes kill 22% of *Pinus palustris* Miller, with the largest trees (25–50 cm dbh) being the most struck. These trees are later colonized by a bark beetle guild composed of the non-aggressive *D. terebrans* and *Ips* spp. We hypothesize a similar scenario of lightning struck trees regulating the endemic conditions of the bark beetle guild of the ponderosa pine forests of the Coconino Plateau, in the absence of abundant suitable hosts. With an average of 50 thunderstorms per year in Flagstaff (WRCC, 2000), and knowing that cloud to ground lightning strikes tend to hit the largest trees (Palik and Pederson, 1996), we think that lightning provides sufficient numbers of vigorous (but suddenly weakened) hosts to maintain a steady endemic population.

Bentz et al. (1993) point out that the reasons why several hazard rating systems fail to predict bark beetle outbreaks with accuracy are: (1) the lack of consideration of bark beetle population levels at the time of system development; (2) the minimal information on bark beetle population dynamics; and (3) the minimal information on spatial dynamics of insects and stands. We believe that the pattern of attack by bark beetles in ponderosa pine forests of the Coconino Plateau differs from other ecosystems; therefore, the theoretical principles regarding the relationship between stand density–stress–insect attacks does not apply to this ecosystem despite the highly dense conditions of many stands.

In a similar study in Finnish and Russian Karelia, carried out under endemic bark beetle population levels, Martikainen et al. (1996) found little difference in the bark beetle species richness and abundance between unmanaged stands with high densities and intensively managed forests (frequently thinned). Similarly, Weslien and Schroeder (1999) found that pheromone traps attracted an equal number of the primary bark beetle *Ips typographus* and three other bark feeding species in both managed and unmanaged spruce stands. They also found higher numbers of bark beetle predators in unmanaged stands than in managed stands suggesting that predators are more sensitive to management activities. In our study, only *Enoclerus* sp. was specific to wildfire burned stands and all other known predators were equally represented in managed and unmanaged ponderosa pine stands.

Although the use of pheromone traps and a single funnel trap per stand (per bait) could place some constraints on our sampling method, we believe these limitations are overcome because we used a consistent method during 3 years. Turchin and Odendaal (1996) point out that pheromone-baited traps can attract bark beetles from a wide area being a reasonable method to sample relative populations of sparse insects. They suggest that baited pheromone traps will capture flying beetles from hundreds of meters away. Turchin and Odendaal (1996) caution that during active infestations with clumped distribution, the effective area of a trap could be affected by the distance of the trap relative to the infestation point; however, this effect is reduced if the trap is placed randomly with respect to any infested clump. Since our stands did not have any evident infestation in progress then the clumping effect is non-existent. In addition, Cronin et al. (2000) point out that as few as three funnel traps per county are effective to monitor the population trends of *D. frontalis* in south-eastern United States, when the traps are installed away from infestations. Our wildfire burned stands had literally only dead trees (killed by stand replacing wildfires in 1996) within a radius of at least 300 m and still caught targeted bark beetles. Therefore, it was clear that the traps were catching the bark beetles from a radius of hundreds of meters.

As far as we know, this is the first empirical study that evaluates the bark beetle guild of ponderosa pine forests in northern Arizona. The study was carried out under the endemic bark beetle conditions that prevail in our study area and we believe that the results are of ecological and economic relevance. Traditionally, bark beetle specialists have focussed on the aggressive species and areas with frequent epidemics and justify their research on the economic damage caused by a few species. We believe that forest entomologists today require new approaches to understand the role of these organisms from a more holistic perspective.

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