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# Thinning of mature lodgepole pine stands increases scolytid bark beetle abundance and diversity

**Trevor D. Hindmarch and Mary L. Reid**

**Abstract**: Thinning of forests has been used as a management tool for bark beetles; however, its effects have only been studied in a limited number of bark beetle species, and the causes of its effectiveness remain unclear. We sampled the abundance and diversity of secondary bark beetles in mature thinned and unthinned lodgepole pine, *Pinus contorta* Dougl. ex Loud., stands (ca. 840 and 2500 trees/ha, respectively) near Whitecourt, Alberta. We examined the factors that might influence any differences in abundance and diversity between thinned and unthinned stands. Breeding habitat for secondary bark beetles (fresh coarse woody debris) was much more abundant in thinned stands than in unthinned stands in the first year after thinning but then returned to background levels. Temperature and wind speeds were higher in thinned stands in all 3 years after thinning. The abundance of striped ambrosia beetles, *Trypodendron lineatum* Olivier, and pine engravers, *Ips pini* (Say), captured in baited funnel traps and window traps remained significantly higher in thinned stands than in unthinned stands in all 3 years after thinning, while the diversity of bark beetles remained constant or increased over this period. Our data suggest that the persistent changes in microclimate following thinning, especially increased wind, were partly responsible for thinned stands having more secondary bark beetles than unthinned stands.

**Résumé** : L'éclaircie des forêts a servi d'outil d'aménagement dans le cas des rongeurs de l'écorce. Cependant, ses effets n'ont fait l'objet d'étude que chez un nombre limité d'espèces de perceurs de l'écorce, et les raisons de son efficacité demeurent obscures. Nous avons analysé l'abondance et la diversité des rongeurs secondaires de l'écorce dans des peuplements matures, éclaircis et non éclaircis (ca. 840 et 2500 tiges/ha, respectivement), de pin tordu latifolié, *Pinus contorta* Dougl. ex Loud., près de Whitecourt, en Alberta. Nous avons examiné les facteurs susceptibles d'influencer toute différence d'abondance et de diversité entre les peuplements éclaircis et non éclaircis. L'année suivant l'éclaircie, les sites de reproduction des perceurs secondaires de l'écorce (débris ligneux grossiers) étaient plus nombreux dans les peuplements traités que dans les peuplements témoins; cependant, leurs densités revenaient par la suite aux niveaux d'avant le traitement. Au cours des 3 années suivant le traitement, la température et la vitesse du vent étaient plus élevées dans les peuplements éclaircis. Pendant cette même période, l'abondance des scolytes birayés *Trypodendron lineatum* Olivier, et des scolytes du pin, *Ips pini* (Say) capturés dans des pièges appâtés, à entonnoir ou à fenêtre, était significativement plus élevée dans les peuplements éclaircis que dans les peuplements témoins, alors que la diversité des perceurs de l'écorce demeurait constante ou augmentait. Nos données montrent que les changements microclimatiques persistants, subséquents à l'éclaircie, en particulier la vitesse plus élevée du vent, étaient en partie responsables des plus fortes densités de perceurs secondaires du bois retrouvées dans les peuplements traités, comparativement aux peuplements témoins.

[Traduit par la Rédaction]

## Introduction

Thinning of forest stands has been proposed as a management tool to reduce the success of bark beetles (Coleoptera: Scolytidae) (Mason 1969; Nebeker and Hodges 1985; Schmitz et al. 1989). However, the mechanisms responsible for the reduced success of these beetles in thinned stands

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have not been directly tested. One possibility is that increased tree vigour resulting from reduced competition between the remaining trees makes them more resistant to bark beetle attack (Mitchell et al. 1983). This change may take one or more years to take effect (Amman et al. 1988). A more immediate effect of reduced tree density and canopy closure is an altered microclimate, especially higher temperatures and wind speeds, that may deter bark beetles (Bartos and Amman 1989; Schmitz et al. 1989; Schmid et al. 1991, 1992*a*, 1992*b*; Bartos and Booth 1994). Here, it is presumed that decreased abundance of dispersing beetles reduces the risk of beetle colonization of trees.

Although the short-term effects of a reduction in tree density are presumed to negatively affect bark beetles, this may not always be the case. High temperatures may mean that temperature thresholds for flight are reached more often than in unthinned stands (Byers and Lofqvist 1989; Hindmarch

1999). Increased wind following thinning may deter flight (Seybert and Gara 1970; Salom and McLean 1991*a*, 1991*b*), although not necessarily (Safranyik et al. 1989; Hindmarch 1999). Moreover, the tendency for most bark beetles to fly in the mid-bole region of the forest (Forsse and Solbreck 1985; Schmitz et al. 1989; Safranyik et al. 1992) suggests that bark beetles seek uncluttered flight paths, perhaps making thinned stands more attractive than unthinned stands (Hindmarch 1999). Thus, it is important to establish the relationships between specific changes in stand characteristics resulting from reduced tree density and the abundance and diversity of bark beetles.

Thinning has the additional consequence of immediately increasing the amount of fresh coarse woody debris in the stand, especially when the tops and limbs of harvested trees are left in the stand. This debris would release large plumes of host volatiles (kairomones), potentially attracting bark beetles from a large area into thinned stands. For those species of bark beetles that breed almost exclusively in freshly dead material (often termed secondary bark beetles; Raffa et al. 1993), host finding would be enhanced because of the large amount of fresh coarse woody debris available in thinned stands. However, the long-term dynamics of coarse woody debris abundance in thinned stands are unknown. Input of coarse woody debris may remain high following thinning, because the remaining trees are more exposed to wind and are less supported by surrounding trees than in unthinned stands (Quine et al. 1995), thereby perpetuating high levels of bark beetle activity in thinned stands. Alternatively, input of coarse woody debris may quickly return to preharvest levels, forcing beetles to go elsewhere to find hosts.

In this study, we quantify the effects of thinning mature lodgepole pine, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., stands on secondary bark beetle abundance and diversity in the first 3 years after thinning. We further identify which aspects of thinning (tree density, temperature, wind speed, and host availability) best explain patterns of abundance and diversity. By focussing on secondary bark beetle species, we remove the proposed influence of live tree vigour on bark beetles. Two of the most common secondary bark beetles in this habitat, striped ambrosia beetles, *Trypodendron lineatum* Olivier, and pine engravers, *Ips pini* (Say), have negative economic impacts through degrading harvested logs (Safranyik 1995). Furthermore, pine engravers occasionally kill living trees (Schenk and Benjamin 1969). However, these species have rarely been studied in the context of thinning (Safranyik et al. 1999).

## Methods

### Study sites

This study was conducted in thinned mature lodgepole pine stands and matched unthinned stands near Whitecourt, Alberta, Canada (54°N, 115°W). Thinned stands were approximately 50 ha and had a 1-ha unthinned control plot (internal control plot) on one side (Fig. 1). A 1-ha unthinned control plot (external control plot) was established in the continuous forest surrounding each thinned stand to control for possible edge effects in the internal control stand (Fig. 1). A 1-ha plot was also established in each thinned stand to ensure equal sampling effort in thinned, internal, and external control plots (Fig. 1).

**Fig. 1.** Schematic of a single study site, not drawn to scale. Each site consisted of a 50-ha thinned stand (stippled area), with a 1-ha unthinned control stand (internal control stand) on one side (shaded area). There was a 1-ha unthinned control stand (external control stand) in the continuous forest (shaded) surrounding each thinned stand. A 1-ha plot was established in the thinned stand to ensure equal sampling in thinned and unthinned stands. Four such sites were sampled.
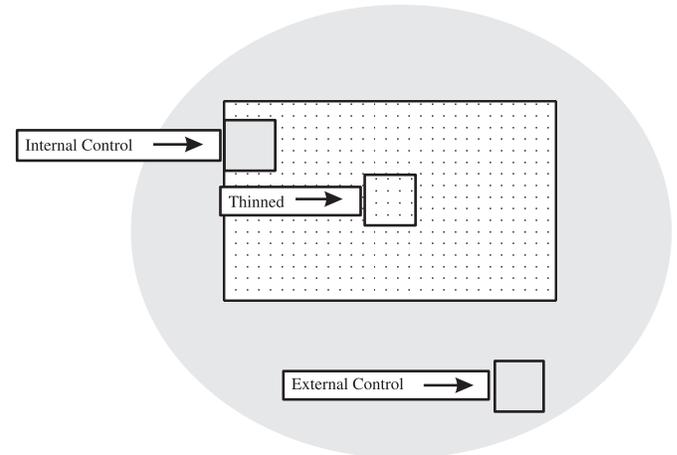


We sampled at three sites (stands aged 60, 70, and 100 years) during 15 June – 31 August 1996, 3 May – 12 August 1997, and 1 May – 30 June 1998, while a fourth site (100 years old) was sampled on these dates in 1997 and 1998 only. The internal control plot at the fourth site was harvested between the first and second year of sampling, and therefore, comparisons in the second year of sampling for this site were between the thinned and external control plots only. At all sites, thinning occurred the winter before sampling began.

During thinning, approximately two-thirds of the trees were removed from each stand. Tree densities were 841 ± 171 trees/ha (means ± SE) in thinned plots, 2703 ± 289 trees/ha in internal controls, and 2346 ± 371 trees/ha in external controls. The crowns and limbs of harvested trees were left in the stand.

### Microclimate

We measured maximum temperature and wind speed at the centre of each plot once a week. We focussed on maximum rather than minimum temperature, because insect activity is affected more by high temperatures than low ones (Ruel and Ayres 1999). Maximum temperature was measured using a digital thermometer (Micronta, model No. 63-867) attached to the north side of a tree at breast height. Wind speed was measured using a hand-held anemometer (SIMS model DIC) at 2 m above ground level. All plots at a site were sampled in random order within a 4 h midday period on the day we collected beetles from traps (see below). To detect consistent differences among stand types despite daily and seasonal variation in weather, we calculated the residuals of the average maximum temperature and wind speed of all three stands at a site for each week.

### Host availability

We used the line intersect method (Van Wagner 1968) to measure fresh coarse woody debris each year after the spring flight of bark beetles. Fresh coarse woody debris was defined as any tree or piece of a tree >3 cm that had been cut or fallen in the winter before sampling. Five random transects were done in each plot. Each transect was an equilateral triangle with 30 m sides.

**Beetle abundance and diversity**

We sampled secondary bark beetles using three methods: commercially baited funnel traps (Lindgren 1983), acrylic window traps hanging over logs, and by excavating coarse woody debris. These methods sample different aspects of beetle activity, and in combination provide the greatest insight into patterns of abundance and diversity.

We sampled the beetles flying through each stand by placing three 12-unit funnel traps (Lindgren 1983) at least 20 m apart in each plot. Two traps were baited with pine engraver pheromones (ipsdienol and lanierone) and one was baited with a pine tree kairomone ($\alpha$-pinene). All baits were supplied by Phero Tech Inc. (Delta, British Columbia). We emptied traps weekly.

To sample beetles arriving at host trees, we suspended transparent acrylic window traps over felled pine logs in each thinned plot and its external control plot. In 1996, four logs were placed in each plot at two sites. In 1997, four new logs were placed in each plot at all four sites (in addition to the four added in the previous year at two sites). All logs were 2 m long, and their diameter was 16.57 ± 0.60 cm. Logs were baited with ipsdienol and lanierone (Phero Tech Inc.), and were placed at least 20 m from each other and from funnel traps to ensure independent catches. One acrylic window trap (20 × 30 cm) with a collecting funnel was suspended over each log in 1997 and 1998. We emptied traps weekly.

Beetles forming breeding aggregations that we encountered while conducting coarse woody debris transects were sampled. A 15-cm$^2$ area of bark was removed from pieces of debris that showed signs of beetle activity (apparent from frass piles on the bark surface or entrance holes). We collected, identified, and counted all beetles from the 15-cm$^2$ area.

Our measure of beetle abundance was the total number captured over the entire season in each year. However, differences in sampling periods among years made comparisons of the absolute number of beetles captured over time inappropriate. In addition, one site was a year behind the others in terms of time of thinning. Therefore, we focussed on comparing thinned plots with their matched controls before combining the data from all years. To do this, we standardized the number of individuals of a given species at each stand and for each year within a site. We calculated the standardized number of individuals, $Z_{ij}$, using $Z_{ij} = (X_{ij} - \mu_j)/\sigma_j$, where $X_{ij}$ is the actual number of individuals of that species captured in stand $i$ within site $j$, $\mu_j$ is the mean number of individuals of that species in all of the stands at site $j$, and $\sigma_j$ is the standard deviation of the number of individuals of that species in all of the stands at site $j$ (Zar 1984).

To describe the diversity of bark beetle species, we used Shannon's $H$ diversity index ($H = -\Sigma(p_i)(\ln p_i)$, where $p_i$ is the proportion of all individuals that belong to species $i$). This index takes into account both species richness (number of species) and evenness and makes no assumptions about the underlying distribution of species' abundances (Hayek and Buzas 1997). In our data set, it was also strongly related to two other commonly used measures of diversity, Simpson's lambda and species richness calculated using rarefaction (e.g., $R^2 = 0.904$ and $0.900$, respectively, for pheromone trap data). We calculated Shannon's $H$ separately for all pheromone traps (using the mean of the two traps per stand), for kairomone traps, and for window traps over logs of a given age for each stand in each year (stand-year). The same community of beetles are potentially attracted to a given trap type, thereby ensuring that Shannon's $H$ reflects actual differences in species richness and evenness.

**Statistical analyses**

Analyses were conducted using JMP® version 4.0 software (SAS Institute Inc. 2000). Data were transformed to meet assumptions of tests where necessary. Simple means ± SE are reported.

To compare microclimate among stand types despite daily variation in weather, we calculated the difference in temperature and wind at each plot from the mean of these values for all plots at a site for each sample date. The mean of these residuals over all sample dates within a year was then determined for each plot. We analyzed the effect of stand type on microclimate in each year after thinning using Kruskal–Wallis tests, because the data did not meet the assumptions of parametric tests.

Our analyses of the input of fresh coarse woody debris, beetle abundance, and beetle diversity were similar in structure. For each of these dependent variables, we used analysis of variance (ANOVA) with stand type and time since thinning as main effects, blocked by site as the fixed effect. The interaction between stand type and time since thinning was also included in initial models to determine if the effect of thinning changed over time but was removed if not significant. Analyses of window trap data differed slightly from the other data, because log age was also a variable. To focus on the effects of stand type and time since thinning for the window trap data, we standardized the numbers of beetles caught within each site in each year and within each log age. We retained site and log age in the models to control for any effects these might have on differences due to stand type and time since thinning, but because of standardization their own significance is not of interest in these analyses. We also repeated these analyses with site as a random variable, to address the repeated sampling of sites over years, using the restricted maximum likelihood (REML) procedure (SAS Institute Inc. 2000). However, this iterative procedure did not always converge, meaning that the results could be unreliable. Nevertheless, in all cases the results of REML models closely mirrored the results from our standard ANOVA models, with all conclusions unchanged. Therefore, we present only the ANOVA results.

To determine the environmental variable(s) responsible for the effects of stand type and time since thinning on the abundance and diversity of beetles captured in the three types of traps, we further analyzed these as a function of tree density, the current amount of fresh coarse woody debris, the amount of fresh coarse woody debris in the previous year (a potential source of beetles), mean maximum temperature for the sampling season, and mean wind speed for the sampling season. For the first year after thinning, the amount of fresh coarse woody debris in the previous year was estimated by averaging the current amount of fresh coarse woody debris in control plots over the duration of the study (mean 0.86 m$^3$/ha). We used multiple regression to examine the contributions of each environmental variable controlling for all the others. We also used backward stepwise regression to determine if the significant environmental variables were changed by the removal of nonsignificant variables ($P > 0.05$ to remove). However, we found that our conclusions were unaltered by using stepwise regression, and therefore, we report only the results for the full models.
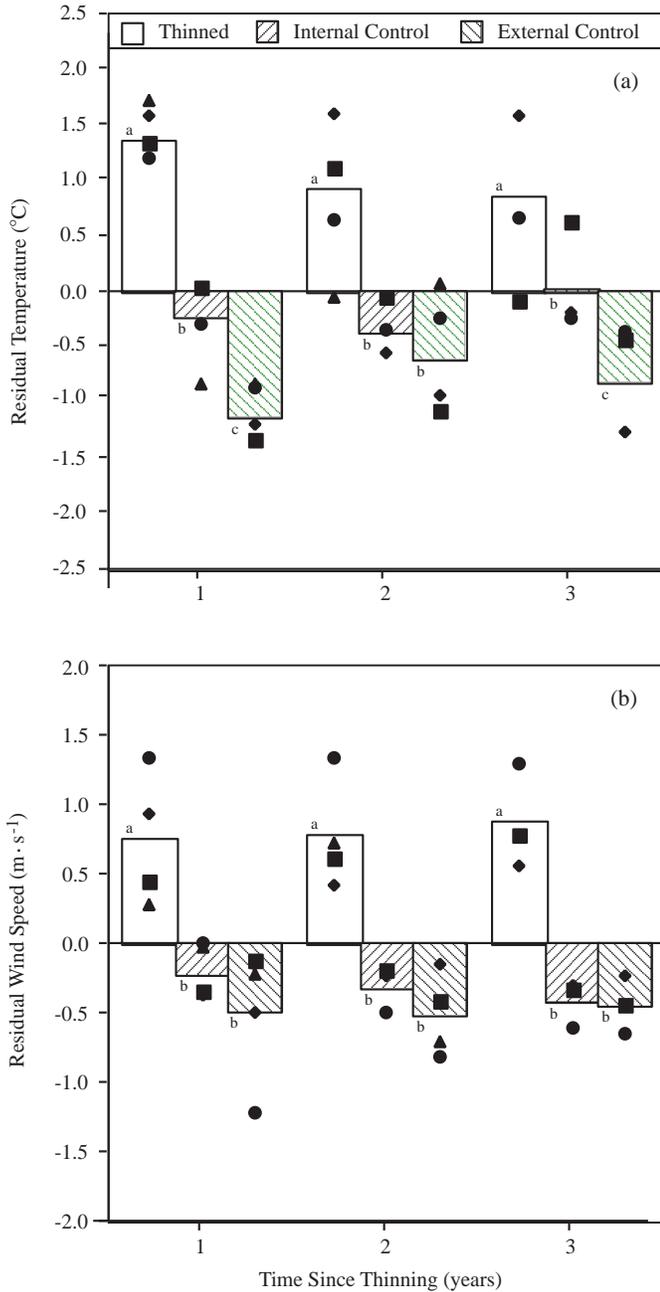
## Results

### Microclimate

There were significant differences among stand types in temperature in all 3 years after thinning (Kruskal–Wallis tests, all $P < 0.05$), with thinned stands being warmer than unthinned stands (Fig. 2a). Similarly, thinned stands were windier than unthinned stands in all 3 years (Fig. 2b, Kruskal–Wallis tests, all $P < 0.05$). Actual maximum temperatures and wind speeds are provided in Table 1.
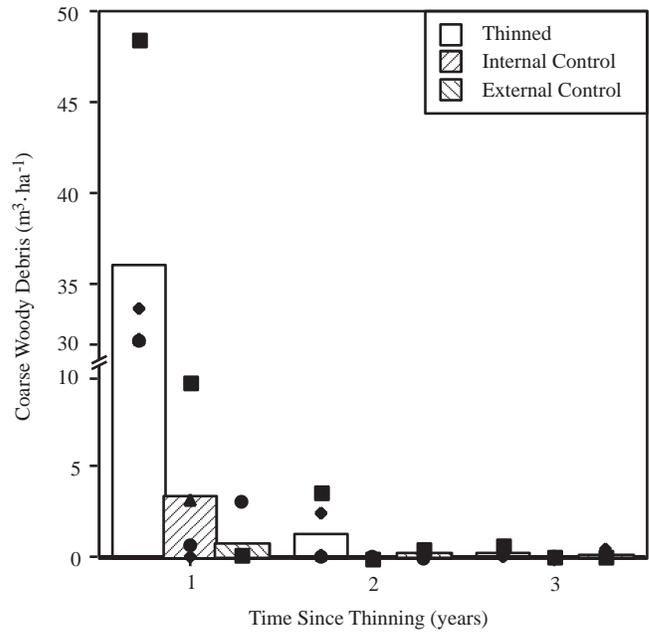
### Host availability

Thinning significantly affected fresh coarse woody debris dynamics, as indicated by a significant interaction between stand type and time since thinning ($F_{[4,20]} = 9.76$, $P <$

**Fig. 2.** (*a*) Residual maximum weekly temperatures and (*b*) residual wind speeds in thinned and unthinned stands, including internal and external controls, over time. Bars are the means for all sites, and symbols are the means for individual sites. Only three external control stands were sampled in year 2, while only three sites (thinned, internal, and external control stands) were sampled in year 3. Within years, bars with different letters are significantly different.



**Fig. 3.** Input of fresh coarse woody debris in thinned and unthinned stands over time. Bars are the means for all sites, and symbols are the means for individual sites. Note the break in the *y* axis.



0.59, $P > 0.05$). In all years, there was no site effect (all $P > 0.1$).

**Beetle abundance**

The total number of individuals captured in pheromone traps was higher in thinned stands than in the internal controls and external controls combined (Table 2). Over 90% of the individuals captured in these traps were striped ambrosia beetles and pine engravers, and therefore, we limit our analyses to these species. The standardized number of striped ambrosia beetles was higher in thinned stands than in unthinned stands for all 3 years after thinning (Fig. 4, Table 3A). Their abundance was positively related to wind speed (Table 3B). The standardized number of pine engravers was also higher in thinned stands than in unthinned stands for all 3 years after thinning (Fig. 4, Table 3A). Their presence was positively related to the current amount of fresh coarse woody debris, the amount of fresh coarse woody debris in the previous year, and wind speed (Table 3B).

For kairomone traps, the total number of individuals captured in thinned stands was lower than the number captured in internal controls but higher than in external controls (Table 2). Once again, striped ambrosia beetles and pine engravers represented over 90% of the individuals captured. Here, the abundance of both species was not significantly affected by stand type (both $P > 0.1$) or time since thinning (both $P > 0.9$). There were no relationships between their abundance and the mechanisms measured ($P > 0.1$ for all mechanisms measured for both species).

In window traps, more individuals overall were captured in thinned stands than in external controls (Table 2). Of the beetles captured in window traps, striped ambrosia beetles and pine engravers comprised 67%. The number of these

0.001). In the first year after thinning, input of fresh coarse woody debris was at least an order of magnitude greater in thinned stands than in unthinned stands (Fig. 3; comparison among treatments $F_{[2,6]} = 78.03$, $P < 0.0001$). Input of fresh coarse woody debris did not differ in thinned stands and unthinned stands in the second year after thinning (Fig. 3; $F_{[2,5]} = 1.98$, $P > 0.2$) or in the third year (Fig. 3; $F_{[2,4]} =$

**Table 1.** Maximum weekly temperatures and wind speeds in thinned and unthinned stands at each site and year after thinning.

| | | Temperature (°C) | | | | Wind (m/s) | | | |
|---|---|---|---|---|---|---|---|---|---|
| Year | Site | No. of weeks | Thinned | Internal control | External control | No. of weeks | Thinned | Internal control | External control |
| 1 | 1 | 13 | 23.5±1.5 | 22.2±1.4 | 20.8±1.4 | 4 | 0.8±0.5 | 0.05±0.03 | 0.3±0.3 |
| | 2 | 5 | 25.1±1.3 | 23.2±0.9 | 22.3±0.8 | 5 | 1.4±0.6 | 0.2±0.1 | 0.0±0.0 |
| | 3 | 10 | 24.4±1.5 | 22.9±1.9 | 22.3±1.4 | 3 | 3.0±0.4 | 1.7±1.2 | 0.5±0.3 |
| | 4 | 3 | 30.8±0.5 | 28.2±1.0 | 28.2±0.6 | 3 | 1.0±0.4 | 0.7±0.4 | 0.5±0.2 |
| 2 | 1 | 9 | 23.9±1.4 | 22.7±1.4 | 21.7±1.4 | 10 | 1.3±0.3 | 0.5±0.1 | 0.3±0.1 |
| | 2 | 14 | 24.9±1.3 | 25.8±1.0 | 22.3±1.2 | 12 | 0.8±0.2 | 0.2±0.1 | 0.3±0.1 |
| | 3 | 11 | 26.8±1.2 | 25.8±1.0 | 25.9±1.2 | 12 | 2.8±0.8 | 1.0±0.4 | 0.6±0.2 |
| | 4 | 8 | 24.1±0.9 | na | 24.2±0.8 | 8 | 2.0±0.5 | na | 0.6±0.2 |
| 3 | 1 | 5 | 25.4±1.4 | 26.1±1.4 | 25.0±1.5 | 8 | 1.4±0.3 | 0.4±0.2 | 0.2±0.1 |
| | 2 | 8 | 24.4±0.9 | 22.6±0.9 | 21.5±0.9 | 8 | 1.0±0.3 | 0.2±0.0 | 0.2±0.1 |
| | 3 | 4 | 26.5±1.4 | 25.6±1.3 | 25.4±1.5 | 8 | 2.2±0.7 | 0.3±0.2 | 0.3±0.1 |

**Note:** Values are mean ± SE. na, no data because stand was harvested prior to year 2.

two species captured depended on the age of the logs over which the window traps were suspended, as determined by comparisons within years. In 1997, traps over logs aged 2 years old caught more striped ambrosia beetles than those over 1-year-old logs (ln-transformed data; $F_{[1,42]} = 5.28$, $P < 0.03$, controlling for site and stand type (both $P > 0.3$)). However, there was no significant effect of log age in 1998 (logs aged 2 and 3 years, $P > 0.9$; stand type: $P > 0.5$, site: $P < 0.04$). Pine engravers were captured almost exclusively at freshly felled logs (age 1 year) in thinned stands, despite the presence of pine engraver pheromones on all logs. Thus, in 1997 when there were logs aged 1 and 2 years, there were significantly more pine engravers captured on 1-year-old logs ($F_{[1,42]} = 58.09$, $P < 0.0001$), while controlling for stand type ($F_{[1,42]} = 45.04$, $P < 0.0001$) and site ($F_{[3,42]} = 3.63$, $P < 0.03$). In 1998 when logs were aged 2 and 3 years, there was no effect of log age ($F_{[1,42]} = 0.44$, $P > 0.5$), while controlling for stand type and site (both $P > 0.07$).

More striped ambrosia beetles were captured in window traps in thinned stands than in external controls (Table 4A; standardized number of striped ambrosia beetles in thinned stands: $0.36 \pm 0.29$; external controls: $-0.36 \pm 0.20$; each $n = 48$ window traps). This result is initially surprising given that the overall number of striped ambrosia beetles captured in window traps was higher in external controls than in thinned stands (Table 2). However, the majority of individuals captured in external controls were the result of one trap (54 individuals). The effect of thinning on the number of striped ambrosia beetles did not vary with time since thinning (Table 4A). Overall, their numbers were positively related to the current amount of fresh coarse woody debris, temperature, and wind speed (Table 4B). Similarly, more pine engravers were captured in thinned stands than in external controls (Table 4A; standardized number of pine engravers in thinned stands: $1.02 \pm 0.50$, external controls: $-1.02 \pm 0.067$; each $n = 48$ window traps). Again, the effect of thinning on the number of pine engravers did not change detectably over time (Table 4A). Their numbers were positively related to the current amount of fresh coarse woody debris only (Table 4B).

The number of beetles encountered during coarse woody debris transects gives an estimate of the number of beetles breeding in each stand that is independent of the sampling period. Since we sampled the same lengths of transects each year, we used the number of beetles collected during these transects in our analyses. Breeding beetles were only encountered in thinned stands. Combining all such species (indicated in Table 2), the number of breeding beetles observed tended to decline with time since thinning (regression: $y = 184.2 - 58.6x$, $R^2 = 0.34$, $P < 0.06$). This trend held for four of the six species; *Orthotomicus caelatus* Eichkoff and *Polygraphus rufipennis* (Kirby) peaked in the second year after thinning. Only one species (*P. rufipennis*) was encountered breeding in the third year after thinning. Striped ambrosia beetles were encountered in the first and second years after thinning, while pine engravers were only encountered in the first year after thinning. The low numbers of beetles found precluded investigation of possible mechanisms accounting for their abundance in coarse woody debris.

### Beetle diversity

Twenty-one bark beetle species were captured in pheromone-baited funnel traps (Table 2). More species were captured in thinned stands (19) than in internal controls (13) and external controls (11) (Table 2). However, diversity of beetles captured in pheromone traps, as measured by Shannon's $H$, did not differ in thinned stands and unthinned stands in any year after thinning (Table 5A; Shannon's $H$ in thinned stands: $0.58 \pm 0.89$, $n = 11$ stand-years; internal controls: $0.48 \pm 0.13$, $n = 10$ stand-years; external controls: $0.35 \pm 0.049$, $n = 11$ stand-years). Furthermore, diversity of beetles in pheromone traps was not related to any of the features that differed between thinned and unthinned stands (Table 5B).

In kairomone-baited funnel traps, 18 species were captured (Table 2). As with the pheromone traps, more species were captured in thinned stands (16) than in internal controls (14) or external controls (10) (Table 2). Again, however, diversity of beetles captured in kairomone traps did not differ in thinned stands and unthinned stands in any year after thinning (Table 5A; Shannon's $H$ in thinned stands: $0.74 \pm 0.16$, $n = 11$ stand-years; internal controls: $0.67 \pm 0.22$, $n = 10$ stand years; external controls: $0.34 \pm 0.11$, $n = 11$ stand-years). Diversity was not related to any of the mechanisms measured (Table 5B).

**Table 2.** Total number of each species captured in pheromone, kairomone, and window traps over the course of this study.

| Species | Pheromone traps | | | Kairomone traps | | | Window traps | |
|---|---|---|---|---|---|---|---|---|
| | Thinned | Internal control | External control | Thinned | Internal control | External control | Thinned | External control |
| *Cryphalus ruficollis* | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Crypturgus borealis* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dendroctonus rufipennis* | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| *Dendroctonus valens* | 9 | 7 | 3 | 4 | 4 | 2 | 12 | 6 |
| *Dryocoetes affaber* | 15 | 6 | 2 | 2 | 2 | 1 | 10 | 5 |
| *Dryocoetes autographus* | 18 | 4 | 1 | 5 | 2 | 0 | 27 | 34 |
| *Gnathotricus* sp. | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Hylurgops rugipennis** | 88 | 13 | 7 | 60 | 23 | 5 | 93 | 65 |
| *Ips latidens* | 4 | 5 | 0 | 2 | 0 | 0 | 1 | 1 |
| *Ips mexicanus* | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Ips perroti* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Ips pini** | 5 899 | 1378 | 658 | 82 | 56 | 109 | 500 | 101 |
| *Orthotomicus caelatus** | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Othotomides lasciocarpa* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Phloeotribus annectans* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 |
| *Phloeotribus lecontei* | 3 | 4 | 1 | 1 | 4 | 2 | 0 | 0 |
| *Phloeotribus piceae* | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Pityogenes plagiatus knechteli** | 191 | 11 | 0 | 2 | 2 | 0 | 28 | 0 |
| *Pityopthorus* sp. | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polygraphus rufipennis** | 77 | 7 | 3 | 31 | 6 | 1 | 54 | 8 |
| *Pseudohylesinus* sp. | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Scierus annectans* | 1 | 4 | 2 | 3 | 4 | 1 | 0 | 1 |
| *Scolytus unispinosis* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Trypodendron lineatum** | 7 728 | 2488 | 2302 | 3196 | 4245 | 659 | 42 | 83 |
| *Xylechinus montanus* | 0 | 2 | 10 | 3 | 12 | 7 | 3 | 4 |
| Total individuals | 14 046 | 3391 | 2991 | 3397 | 4362 | 787 | 773 | 312 |
| Total species | 19 | 13 | 11 | 16 | 14 | 10 | 12 | 12 |

*Species encountered breeding in coarse woody debris.

Twelve species were captured in window traps in both thinned and external control stands for a total of 15 species (Table 2). Diversity was, however, higher in thinned stands than in unthinned stands (Table 5A; Shannon's *H* in thinned stands: $0.66 \pm 0.066$, $n = 48$ window traps; external controls: $0.40 \pm 0.062$, $n = 48$ window traps). There was no effect of time since thinning for beetles caught in window traps (Table 5A). Diversity of beetles caught in window traps was positively related to the current amount of fresh coarse woody debris and wind speed (Table 5B).

Six species of beetles were found during coarse woody debris excavations (Table 2). Their low numbers precluded reliable analyses of diversity in coarse woody debris. However, we used these data to focus our diversity analyses of trapped beetles on those species actually observed breeding in our stands. For pheromone traps, diversity for this limited data set (i.e., the six species found during coarse woody debris excavations) was higher in thinned stands than in unthinned stands (Table 6A; Shannon's *H* in thinned stands: $0.52 \pm 0.053$, $n = 11$ stand-years; internal controls: $0.19 \pm 0.044$, $n = 10$ stand-years; external controls: $0.13 \pm 0.040$, $n = 11$ stand-years) and increased over time (Table 6A; Shannon's *H* in first year after thinning: $0.21 \pm 0.06$, $n = 4$ stands; second year: $0.37 \pm 0.084$, $n = 4$ stands; third year: $0.26 \pm 0.057$, $n = 3$ stands). This diversity was positively related to the amount of fresh coarse woody debris in the pre-

**Fig. 4.** Standardized mean number (±SE) of striped ambrosia beetles and pine engravers captured in pheromone traps in the 3 years following thinning. Where error bars are not shown, they are smaller than the symbol. Solid squares, thinned stands; open triangles, internal controls; open circles, external controls.
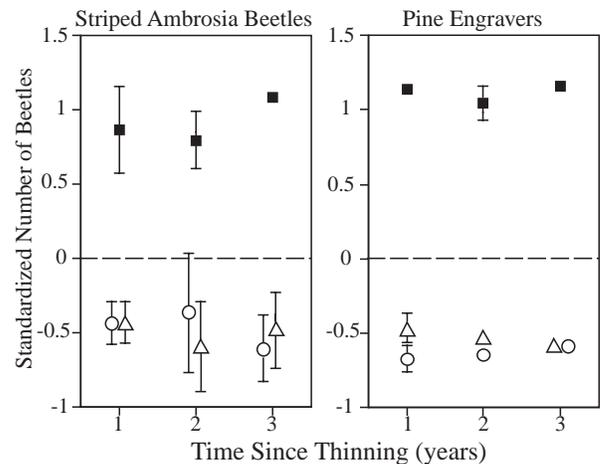


vious year (Table 6B) even though the amount of fresh coarse woody debris decreased over time (Fig. 3).

Similarly, diversity of beetles caught in kairomone traps for this limited data set was higher in thinned stands than in

**Table 3.** Standardized number of striped ambrosia beetles and pine engravers captured in pheromone traps analyzed using (A) an ANOVA examining the effects of thinning over time and (B) a multiple regression model examining the effects of environmental variables on abundance.

(A) ANOVA.

|  | Striped ambrosia beetles | | | Pine engravers | | |
|---|---|---|---|---|---|---|
|  | $F$ | df | $P$ | $F$ | df | $P$ |
| Site | 0.06 | 3, 24 | >0.9 | 0.89 | 3, 24 | >0.4 |
| Stand type | 30.46 | 2, 24 | <0.0001 | 623.69 | 2, 24 | <0.0001 |
| Time since thinning | 0.04 | 2, 24 | >0.9 | 0.49 | 2, 24 | >0.6 |

(B) Multiple regression.

|  | Striped ambrosia beetles | | | Pine engravers | | |
|---|---|---|---|---|---|---|
|  | Parameter | $F^a$ | $P$ | Parameter | $F^a$ | $P$ |
| Intercept | −0.8687 | | | −1.2702 | | |
| Tree density | −0.0000 | 0.002 | >0.9 | −0.0000 | 0.21 | >0.6 |
| Current CWD[b] | 0.0193 | 3.35 | <0.1 | 0.026 | 11.59 | <0.01 |
| Last year's CWD | 0.0125 | 1.28 | >0.2 | 0.008 | 7.73 | 0.01 |
| Temperature | 0.0148 | 0.06 | >0.8 | 0.0438 | 0.49 | >0.4 |
| Wind | 0.4182 | 4.30 | <0.05 | 0.146 | 8.86 | <0.01 |

[a]Degrees of freedom for all environmental variables were 1 and 26.
[b]CWD, coarse woody debris.

**Table 4.** Standardized number of striped ambrosia beetles and pine engravers captured in window traps analyzed using (A) an ANOVA examining the effects of thinning over time and (B) a multiple regression model examining the effects of environmental variables on abundance.

(A) ANOVA.

|  | Striped ambrosia beetles | | | Pine engravers | | |
|---|---|---|---|---|---|---|
|  | $F$ | df | $P$ | $F$ | df | $P$ |
| Site | 0.09 | 3, 56 | >0.9 | 0.56 | 3, 79 | >0.6 |
| Stand type | 4.36 | 1, 56 | <0.05 | 27.87 | 1, 79 | <0.0001 |
| Time since thinning | 0.37 | 2, 56 | >0.9 | 0.97 | 2, 79 | >0.3 |
| Log age | 0.78 | 1, 56 | >0.3 | 1.17 | 2, 79 | >0.3 |

(B) Multiple regression.

|  | Striped ambrosia beetles | | | Pine engravers | | |
|---|---|---|---|---|---|---|
|  | Parameter | $F^a$ | $P$ | Parameter | $F^b$ | $P$ |
| Intercept | 4.8946 | | | 2.0402 | | |
| Tree density | −0.0001 | 1.02 | >0.3 | −0.0001 | 1.30 | >0.2 |
| Current CWD[c] | 0.0446 | 10.99 | <0.01 | 0.0241 | 4.28 | <0.05 |
| Last year's CWD | 0.0108 | 1.87 | >0.1 | 0.0004 | 0.01 | >0.9 |
| Temperature | −0.1633 | 7.69 | <0.01 | −0.0611 | 1.95 | >0.1 |
| Wind | 0.3356 | 4.30 | <0.05 | 0.1968 | 2.49 | >0.1 |

[a]Degrees of freedom for all environmental variables were 1 and 58
[b]Degrees of freedom for all environmental variables were 1 and 82.
[c]CWD, coarse woody debris.

unthinned stands (Table 6A; Shannon's $H$ in thinned stands: 0.49 ± 0.13, $n$ = 11 stand-years; internal controls: 0.42 ± 0.14, $n$ = 10 stand-years; external controls: 0.074 ± 0.58, $n$ = 11 stand-years) and increased over time (Table 6A; $H$ in the first year after thinning: 0.25 ± 0.10, $n$ = 4 stands; second year: 0.28 ± 0.13, $n$ = 4 stands; third year: 0.48 ± 0.14, $n$ = 3 stands). However, none of the mechanisms measured explained this diversity (Table 6B).

Window trap diversity for this limited data set was also higher in thinned stands than in unthinned stands (Table 6A; Shannon's $H$ in thinned stands: 0.44 ± 0.059, $n$ = 48 window traps; external controls: 0.21 ± 0.050, $n$ = 48 window traps) but did not change over time (Table 6A). As with the full data set, window trap diversity did not depend on the age of the log that the trap was suspended over ($F_{[2,87]}$ = 0.66, $P$ > 0.5). Diversity was positively related to the current amount of fresh coarse woody debris and wind speed (Table 6B).

## Discussion

Habitat abundance is expected to positively affect species abundance (Connor and McCoy 1979). Such a relationship

**Table 5.** Diversity (Shannon's $H$) of all bark beetles captured in pheromone, kairomone, and window traps analyzed using (A) an ANOVA examining the effects of thinning over time and (B) a multiple regression model examining the effects of environmental variables on diversity.

(A) ANOVA.

| | Pheromone traps | | | Kairomone traps | | | Window traps | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F$ | df | $P$ | $F$ | df | $P$ | $F$ | df | $P$ |
| Site | 3.84 | 3, 24 | <0.05 | 1.03 | 3, 24 | >0.3 | 2.00 | 3, 87 | >0.1 |
| Stand type | 2.25 | 2, 24 | >0.1 | 1.83 | 2, 24 | >0.1 | 8.94 | 1, 87 | <0.01 |
| Time since thinning | 1.39 | 2, 24 | >0.2 | 2.62 | 2, 24 | >0.1 | 0.54 | 2, 87 | >0.5 |
| Log age | na[a] | | | na | | | 1.57 | 2, 87 | >0.2 |

(B) Multiple regression.

| | Pheromone traps | | | Kairomone traps | | | Window traps | | |
|---|---|---|---|---|---|---|---|---|---|
| | Parameter | $F^b$ | $P$ | Parameter | $F^b$ | $P$ | Parameter | $F^c$ | $P$ |
| Intercept | 0.6193 | | | –0.9676 | | | 1.1378 | | |
| Tree density | 0.0000 | 0.11 | >0.7 | 0.0001 | 0.83 | >0.3 | 0.0000 | 0.19 | >0.6 |
| Current CWD[d] | 0.0048 | 0.83 | >0.3 | 0.0118 | 1.45 | >0.2 | 0.0237 | 7.16 | <0.01 |
| Last year's CWD[d] | 0.0095 | 3.01 | <0.1 | –0.0013 | 0.01 | >0.9 | –0.0004 | 0.01 | >0.9 |
| Temperature | –0.0112 | 0.14 | >0.8 | 0.0479 | 0.73 | >0.4 | –0.0392 | 1.54 | >0.2 |
| Wind speed | –0.0149 | 0.02 | >0.7 | 0.0893 | 0.22 | >0.6 | 0.2730 | 8.35 | <0.01 |

[a]na, not applicable.
[b]Degrees of freedom for all environmental variables were 1 and 26
[c]Degrees of freedom for all environmental variables were 1 and 90.
[d]CWD, coarse woody debris.

**Table 6.** Diversity (Shannon's $H$) of bark beetles captured in pheromone, kairomone, and window traps for only those species found during coarse woody debris excavations analyzed using (A) an ANOVA examining the effects of thinning over time and (B) a multiple regression model examining the effects of environmental variables on diversity.

(A) ANOVA.

| | Pheromone traps | | | Kairomone traps | | | Window traps | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F$ | df | $P$ | $F$ | df | $P$ | $F$ | df | $P$ |
| Site | 1.18 | 3, 24 | >0.3 | 1.87 | 3, 24 | >0.1 | 0.68 | 3, 87 | >0.5 |
| Stand type | 25.07 | 2, 24 | <0.0001 | 4.71 | 2, 24 | <0.05 | 8.84 | 1, 87 | <0.01 |
| Time since thinning | 3.77 | 2, 24 | <0.05 | 3.78 | 2, 24 | <0.1 | 0.12 | 2, 87 | >0.8 |
| Log age | na[a] | | | na | | | 0.66 | 2, 87 | >0.5 |

(B) Multiple regression.

| | Pheromone traps | | | Kairomone traps | | | Window traps | | |
|---|---|---|---|---|---|---|---|---|---|
| | Parameter | $F^b$ | $P$ | Parameter | $F^b$ | $P$ | Parameter | $F^c$ | $P$ |
| Intercept | –0.7276 | | | –0.8694 | | | 0.2574 | | |
| Tree density | 0.0000 | 0.92 | >0.3 | 0.0000 | 0.07 | >0.7 | 0.0000 | 0.73 | >0.3 |
| Current CWD[d] | 0.0039 | 2.43 | >0.1 | 0.0024 | 0.12 | >0.7 | 0.0192 | 6.38 | <0.05 |
| Last year's CWD[d] | 0.0114 | 18.90 | <0.001 | 0.0012 | 0.02 | >0.8 | –0.0015 | 0.25 | >0.6 |
| Temperature | 0.032 | 4.95 | <0.05 | 0.0438 | 1.13 | >0.2 | –0.0115 | 0.18 | >0.6 |
| Wind speed | 0.0924 | 3.71 | <0.1 | 0.0642 | 0.21 | >0.6 | 0.238 | 8.61 | <0.01 |

[a]na, not applicable.
[b]Degrees of freedom for all environmental variables were 1 and 26.
[c]Degrees of freedom for all environmental variables were 1 and 90.
[d]CWD, coarse woody debris.

has been previously observed in secondary bark beetles, such that bark beetle abundance and diversity in a forest stand is determined by the amount of coarse woody debris (Vaisanen et al. 1993; Okland et al. 1996; Peltonen et al. 1998). We found that thinning resulted in a large one-time input of fresh coarse woody debris in the first year after thinning, followed by a return to preharvest input levels in the second and third years after thinning. Consequently, for most secondary bark beetles we expected that thinned stands would attract a greater abundance and diversity of beetles in the first year relative to unthinned stands. This pattern could persist in the second year after thinning as offspring from the first year that had overwintered in these stands were captured (Mason 1969). However, the abundance and diversity

of beetles in thinned stands should not have been high in the third year after thinning, because there was a limited amount of coarse woody debris in the second year after thinning to produce beetles for the third year. Striped ambrosia beetles might be expected to differ slightly from this pattern of response to coarse woody debris, since they prefer 2-year-old debris (this study; Dyer and Chapman 1965).

While there was some indication that the abundance of breeding beetles in thinned stands did decline with time since thinning, the effect of thinning on the abundance and diversity of beetles in trap catches was persistent over the 3 years following thinning. Thus, the number of striped ambrosia beetles and pine engravers captured in pheromone, kairomone, and window traps was higher in thinned stands than in unthinned stands in all 3 years after thinning. Similarly, the diversity of beetles captured in the three kinds of traps was as high or higher in thinned stands than in unthinned stands, and diversity remained constant or increased over time. Thus, although breeding habitat declined greatly over the 3 years after thinning, we were unable to detect any diminishing effect of time since thinning on the abundance and diversity of trapped beetles.

Although the difference in the amount of fresh coarse woody debris in thinned and unthinned stands appeared only in the first year after thinning, microclimate differences between thinned and unthinned stands persisted through 3 years post-thinning. Thinned stands had higher wind speeds and maximum temperatures than unthinned stands, as has been suggested in other studies of thinning (Bartos and Amman 1989; Bartos and Booth 1994). The number of striped ambrosia beetles and pine engravers captured in pheromone and window traps was positively associated with wind speeds, and the diversity of beetles captured in these traps was also positively associated with wind. These results contrast with other studies that have found negative effects of wind on bark beetle flight in pine engravers and striped ambrosia beetles over a range of similar wind speeds to those we observed (Seybert and Gara 1970; Salom and McLean 1991a, 1991b). The negative effect of wind has been attributed to the disruption of pheromone plumes, but evidence also suggests that pheromone plumes are more consistent in higher wind relative to calm conditions (Fares et al. 1980; Elkinton et al. 1987). Canopy openings, such as would be more common in thinned stands than unthinned ones, have been implicated in causing adverse pheromone turbulence, but these effects were found to be small in thinned pine stands (Schmid et al. 1992a). Thus, it could be that beetles were better able to orient to pheromones baits in thinned stands than in unthinned stands. Other physical factors that were persistently different in thinned and unthinned stands, namely temperature and tree density, appeared to be less important in accounting for the higher abundance and diversity of bark beetles in thinned stands. Temperature positively affected abundance and diversity in two analyses, while tree density never had a significantly effect.

We standardized data to compare treatments within years and then looked at whether differences persisted over time. This overcomes confounding differences among years in insect abundance, such as those due to weather and the timing of sampling with respect to the active periods of insects. If the effects of thinning were mitigated over time, the standardized number of beetles captured in thinned and unthinned stands should converge. In this study, significant differences in the standardized number of beetles captured in thinned stands and their unthinned counterparts persisted over time. However, standardization may obscure the magnitude of differences between treatments among years. Thus, it is possible that the large differences in the abundance of fresh coarse woody debris affected the absolute abundance of dispersing beetles, as suggested by some of our analyses of mechanisms affecting the number of trapped beetles and by the number of breeding beetles per hectare. Nonetheless, standardizing showed that differences between thinned and unthinned stands persisted in all 3 years after thinning and allowed reasons for these differences to be elucidated. Moreover, these results were mirrored in the diversity patterns, where standardization was not employed.

Differences in the number of beetles caught in baited traps between thinned and unthinned stands could result because of differences in the density of dispersing beetles, differences in the detectability of traps, or both. Our data cannot distinguish between these hypotheses. If the density of dispersing beetles differed, this effect would be due in part to beetles that were attracted to thinned stands from elsewhere. This is because the trap catches in thinned and unthinned stands differed in the first and third year after thinning when the abundance of breeding habitat (fresh coarse woody debris) within the stand in the previous years was the same for both types of stands. To test for differences in density, one could use passive flight intercept traps. Differences in the attraction radius of traps in thinned and unthinned stands could be assessed following the methods of Byers (1999). Regardless of the cause, the net effect is that the abundance of beetles that successfully find breeding habitat is likely to be higher in thinned stands than in unthinned stands. This was evident in our excavations of unbaited fresh coarse woody debris, where breeding beetles were only found in thinned stands in all years. Breeding densities of pine engravers were also significantly higher in baited logs in thinned stands than in unthinned stands in a separate experiment in this study area (Hindmarch and Reid 2001), reinforcing the idea that beetles are more successful in finding habitat in thinned stands.

Our finding that bark beetle abundance and diversity were higher in thinned stands than unthinned stands is opposite to the pattern that has been widely reported in the bark beetle literature. This is despite the fact that changes in wind speed and temperature were similar to other studies. One explanation for the discrepancy may be that previous work on thinning has largely focused on one primary bark beetle, mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and the measure of beetle activity has usually been tree mortality. Since tree mortality is a function of both beetle abundance and tree vigour, it is difficult to determine whether the cause of reduced tree mortality in thinned stands is due to lower beetle abundance or changes in tree vigour (Amman et al. 1988; Preisler and Mitchell 1993). However, two studies that looked directly at the abundance of mountain pine beetles in thinned and unthinned stands found fewer beetles in thinned stands than in unthinned stands (Schmitz et al. 1989; Bartos and Booth 1994), contrary to the pattern that we observed for secondary bark beetles.

Alternatively, our results may differ from those of mountain pine beetle because we focussed on secondary bark beetles whose dynamics are less influenced by tree vigour and the need for coordinated and concentrated settlement. Relatively few studies have examined the response of secondary bark beetles to thinning, and they have all examined settlement densities or tree mortality that again confound beetle abundance and host effects. However, these studies imply that the abundance of secondary bark beetles may be higher in thinned stands than in unthinned stands. For example, in thinned pine plantations in Israel, attacks by secondary bark beetles are higher in thinned stands than in unthinned stands, even in live trees that have greater vigour in thinned stands (Mendel et al. 1992). Safranyik et al. (1999) observed no difference in the percentage of trees or stumps attacked by secondary bark beetles in thinned and unthinned lodgepole pine stands, but attacks per tree were higher in thinned stands than in unthinned stands.

A final consideration is that the effects of thinning on the abundance and diversity of bark beetles may vary among habitats and geographic regions. Our study was conducted in a northern location where higher temperatures resulting from thinning may be advantageous or neutral rather than deterrents. For example, in our study area pine engravers had higher male settlement densities, attracted more mates, and had longer egg galleries in thinned stands than in unthinned stands (Hindmarch and Reid 2001). In contrast, pine engravers in Arizona had the opposite response, with these reproductive attributes negatively affected by thinning, presumably because the increased heat and drying made phloem less suitable (Villa-Castillo and Wagner 1996).

In sum, our study indicates that thinning of mature lodgepole pine stands results in an increase in the abundance and diversity of secondary bark beetles that reach breeding sites (or their trap analogues). This appears to be related to persistent microclimate differences between thinned and unthinned stands. Since the two numerically dominant beetle species, striped ambrosia beetles and pine engravers, can cause economic damage to standing and felled trees, felled trees should be removed from the stands before the breeding season of these beetles. This caution is further warranted by the observation that trees that had been growing vigorously at the time of death, such as in thinned stands, are superior breeding habitat for secondary bark beetles (Slansky and Haack 1986; Reid and Robb 1999). More generally, this study prompts caution in the use of thinning as a management tool to control bark beetles. Further work is needed to distinguish the role of physical factors influencing the abundance of beetles reaching breeding sites and the role of live tree vigour in a range of bark beetle species and geographic locations.

## Acknowledgments

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