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Interactions between fire and bark beetles in an old growth pine forest

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Abstract

Management strategies for old growth pine forests have recently begun to include prescribed burns. Fire could influence interactions between bark beetles and mature pine trees, but we cannot predict the effects because we know too little about the numeric and functional responses of bark beetle populations to fire, and because we do not know how fire affects the oleoresin defense system of pine trees. We estimated population abundance of *Ips* spp. (Coleoptera: Scolytidae), and the resin flow of mature red pines (*Pinus resinosa*), before and after a prescribed burn, inside and outside the burn, in an old growth forest at Itasca State Park, Minnesota. Following a prescribed burn in April, the local abundance of *I. pini* increased by two-fold during May, decreased by a comparable amount during 6 weeks starting in mid-July, and was otherwise unchanged. The abundance of *I. grandicollis* and *I. perroti* were unaffected, while that of a specialist predator, *Thanasimus dubius* (Coleoptera: Cleridae) increased by 30-90% during May. Many mature trees that sustained no visible crown damage from the fire were attacked by *Ips* within the scorched region of the lower bole. Oleoresin flow increased substantially in trees with scorched boles, which may limit the probability that trees will be killed by bark beetles following a ground fire. We tested whether fire increases the probability that a healthy tree will sustain bark beetle attacks by locating beetle-infested trees inside and outside of the burned area, and comparing their growth history (from growth rings) with paired, unattacked trees. Surprisingly, there was no indication of recently declining growth, or chronically slow growth, in beetle-infested trees, either inside or outside the prescribed burn. Half of the trees attacked by *Ips* in 1998 were dead in 1999 and the remainder were partly girdled by the attacks, which increases their subsequent vulnerability to fires, insects, and pathogens. *Ips* bark beetles can exert meaningful effects on the survivorship of red pine populations, and their demographic impact is probably increased by ground fires.

Keywords: fire, Itasca State Park, tree defense, Scolytidae

1. Introduction

Fire suppression has altered the structure of many forest ecosystems by disrupting patterns of disturbance and regrowth (Clark, 1990; Baker, 1992). In some forests, prescribed burns are now being implemented in an attempt to restore fire to the ecosystem and re-create natural disturbance dynamics (Weber and Taylor, 1992; Attiwill, 1994; Agee, 1996). In addition to promoting regeneration of some desirable tree species, prescribed fires may reduce pest outbreaks and have been advocated as a strategy to reduce populations of bark beetles (Coleoptera: Scolytidae); (Smith et al., 1983; Stock and Gorley, 1989; Hadley and Veblen, 1993; Mutch et al., 1993). However, fire is also thought to put trees at increased risk of insect attack due to decreased resistance (Geiszler et al., 1984). Increased tree mortality from beetle infestations has been frequently reported following fire (Dixon et al., 1984; Thomas and Agee, 1986; McCullough et al., 1998). Distinguishing between these alternative viewpoints is difficult because most of the relevant data are non-experimental and/or non-quantitative (McCullough et al., 1998). Interactions between disturbance from fire and bark beetles should be of special interest to forest managers concerned with maintaining the natural functioning of old growth pine ecosystems (Hansen and Duncan, 1954; Rasmussen et al., 1996).

We studied the effects of fire on interactions between pine trees and bark beetles in association with prescribed fires in the old growth forests at Itasca State Park in northwestern Minnesota. Immediately following fire, bark beetle populations might decrease because of beetle mortality from the fire (McCullough et al., 1998) or increase because volatiles from the fire are long range attractants to beetles and lead to recruitment of beetles from outside the burned area (Muona and Rutanen, 1994; Holsten et al., 1995; Hart, 1998; Schmitz and Blekmann, 1998). To distinguish between these two hypotheses, we used pheromone-baited funnel traps to measure beetle abundance both before and after the prescribed burn in replicated sites within and outside of the burned area. Fire could increase the risk of tree mortality from beetles by compromising tree defenses against beetles. Oleoresin, a mixture of monoterpene olefins and diterpene resin acids, is the primary defense of pines against insect pests (Berryman, 1972; Hodges et al., 1979;

Phillips and Croteau, 1999). Pine bark beetles, which bore through the tree's outer bark to feed and reproduce within the phloem, are inhibited by the viscous and potentially toxic fluid, resulting in negative relationships between resin production and beetle attack success (Coyne and Lott, 1976; Reeve et al., 1995). Most oleoresin is synthesized by specialized epithelial cells within the xylem of pine trees and stored within vertical resin ducts in the xylem and some may also be produced in bark resin canals. So oleoresin defenses could be reduced as a result of heat trauma to these tissues in the lower bole of pine trees. Alternatively, it is possible that species such as red pine (*Pinus resinosa* Aiton), which have a long evolutionary history of interactions with fire and bark beetles, respond to fire with increases in resin flow to counteract the increased risk of beetle attacks. In fact, some conifers can begin to synthesize oleoresin within phloem tissue that has been exposed to insects and pathogens (Raffa and Berryman, 1982; Lieutier et al., 1991). In some pine species, trees respond to light burning with increased resin flow (Harper, 1944; Feeney et al., 1998) yet, in other species or with more severe burns, trees respond with reduced resin flow or bark terpene contents (Harper 1944, Jakubas et al., 1994). We tested for effects of fire on the resin system of red pine by measuring resin flow in replicated trees before and after a prescribed burn, within and outside of the burned area.

The prevalent species of bark beetles feeding on pine trees in our study area are *Ips pini* (Say), *I. grandicollis* (Eichhoff), and *I. perroti* Swaine. These species usually are described as secondary insect pests that primarily invade trees that are in poor physiological condition and likely to die irrespective of beetle infestations (Rudinsky, 1962; Paine et al., 1997), although there also are reports of *Ips* killing trees (Schenk and Benjamin, 1969; Sartwell et al., 1971; Geiszler et al., 1984; Klepzig et al., 1991; Rasmussen et al., 1996; Kegley et al., 1997). We hypothesized that fire influences the attack patterns of *Ips*. If, in the absence of fire, beetles are preferentially colonizing trees that are in physiological decline, there should be a history of declining growth in attacked trees relative to nearby trees that are not attacked. If fire has the effect of exacerbating tree risks from bark beetles, then burned forests should contain a higher proportion of trees that were growing well but came under attack by beetles nonetheless. We tested these hypotheses using tree ring analyses to compare the growth history of beetle-infested trees and paired controls, inside and outside the burned area.

2. Methods
Study site
Itasca State Park, Minnesota, USA (43° 13' N, 95° 11' W) is a 20,000 ha reserve of old growth pine forest. Prescribed burns were implemented to remove understory vegetation and stimulate regeneration of red pine, which has been nearly nonexistent since the park's establishment in 1891 (Hansen and Duncan, 1954; Janssen, 1967; Frissell, 1973). The first large prescribed burn at Itasca was initiated on 20 April 1998 and included . 2200 ha. Burn management teams attempted to keep flame heights between 15 and 60 cm (B. Marty, personal communication).

2.1 Resin response to fire
We measured resin flow on ten old growth red pines that were haphazardly selected within each of twelve sites within the park (five trees of codominant crown class and five trees of intermediate crown class; total of 120 trees). Average height, diameter at breast height, basal area, percent live crown, and age of red pines at these twelve sites ranged from 23 - 32 m, 33 - 54 cm, 17 - 43 m^3 / ha, 58 - 72%, and 112 - 187 years, respectively. One site served as a baseline site and was sampled every day of resin sampling to control for day-to-day variation in resin flow when the sampling period extended over multiple days. It turned out that there was no significant day-to-day variation in resin flow so no adjustments were required.

Resin flow was measured with standard techniques (Lorio et al., 1990; Ruel et al., 1998). Trees were wounded by removing a 125 mm^2 disk of bark and phloem at 1.5 m height with a metal punch. Resin flowing from the wound was directed into a collection vial. Two measurements were made per tree on each sampling occasion. Each tree was measured in August of 1997, July of 1998 and August of 1998. Resin samples were collected after 6 h and weighed. Resin sampling protocol differed slightly in 1997 in that vials were allowed to collect resin for 24 h instead of 6 h, but repeated measurements indicated that there was little or no additional resin flow between 6 and 24 h so the effect of the protocol difference was negligible. In any case, no conclusions were affected because the analyses compared burned and unburned trees which were measured with the same protocol in both years.

Two study sites were within the area of the April 1998 prescribed burn. All ten trees at one site and five trees at the second site were damaged by the fire. Thus, the test for effects of fire on resin flow compared 15 charred trees with 105 undamaged trees. (Vagaries of the prescribed burn prevented us from having more equal numbers of charred and undamaged trees, but the treatment effects were very clear nonetheless.) For each tree that was exposed to the ground fire, we measured the height of highest bark charring (blackened outer bark) and recorded whether or not the crown had been scorched (presence of many red, yellow, or brown needles on lower branches). Statistical analyses were based on the change in resin flow from 1997 to 1998:
$$\rangle Resinflow = (Resin98)^{0.5} - (Resin97)^{0.5}$$
where Resin97 and Resin98 = average resin flow for each tree in 1997 and 1998, respectively. $\rangle Resinflow$ was calculated for each tree for both sampling dates in 1998. Square root transformations corrected for mild heteroscedastity of the data. $\rangle Resinflow$ was analyzed with an ANOVA model that included burn, date of sampling in 1998, crown class, and their interactions as fixed effects categorical variables and tree (nested within burn and crown class) as a random effect. The relationship between char height and change in resin flow was evaluated with a linear regression.

2.2. Bark beetle abundance
We used pheromone-baited funnel traps to sample abundances of three *Ips* species and their specialist predator *Thanasimus dubius* (Coleoptera: Cleridae) in 23 pine stands before and after the prescribed fire. Ten of these sampling areas were within the April 1998

prescribed burn. Each site was sampled with an array of three traps separated by . 15 m and configured as an equilateral triangle. Within a site, each trap was baited with either ipsdienol + lanierone (produced and preferred by *I. pini*), ipsenol (produced and preferred by *I. grandicollis*), or ipsdienol + ipsenol (produced and preferred by *I. perroti*). Sampling was initiated on 1 July in 1997 and on 1 May in 1998 and traps were emptied every two weeks through late September in both 1997 and 1998. Pheromone lures (Phero Tech, Delta, British Columbia) were rotated around the array each time the traps were checked to control against spurious effects of trap position. Bubble cap lures had elution rates that are recommended by Phero Tech for sampling with funnel traps (0.2 mg /d for ipsdienol or ipsenol and 0.01 mg / d for lanierone). We counted and identified the *Ips* spp. and *T. dubius* that were captured. Beetle abundance levels were analyzed with an ANOVA model that included burn, date of sampling, burn x date, and site nested in fire. Abundance data were log transformed, $\log_{10}(N + 1)$, to correct for heteroscedasticity.

2.3. Infested trees
In September 1998, we identified 41 live mature red pine that were under attack by *I. pini*, *I. grandicollis*, and/or *I. perroti*. Infested trees were located through visual examination of tree crowns for discolored needles at a distance of 20 - 50 m with good light and then inspecting the bole of candidate trees for the presence of beetles and boring dust by hand and eye at the base of the tree and with binoculars to the lower live crown. We estimate that we surveyed . 4000 trees. Cores were extracted from the nearest similarly-sized red pine to serve as a controls. Cores also were taken from 120 old growth red pine trees throughout the park to determine growth patterns in the park at large. Analyses of mounted and sanded cores were done using WinDENDRO software (Regent, V 6.0.4) to determine yearly growth.

For each infested tree, we looked for evidence of declining growth prior to infestation by plotting annual radial growth from 1935 to 1997 relative to its paired control. Statistical comparison of the populations of infested and control trees was complicated by site-specific differences in growth rates (e.g., some infested trees had systematically higher growth rates than their control tree throughout the growth record and some had systematically lower growth rates than their control trees). Under the hypothesis that declining growth predisposes trees to attack by bark beetles, we expected that there should be evidence of growth declines during the 2 - 10 years prior to infestation. To obtain the strongest possible test for such growth declines, we adjusted for differences in the growth rate of each infested tree and its control tree during the years that preceded this. Our cores went back to at least 1935 for all trees, so we arbitrarily chose 50 years from 1935 - 1984 as the standard against which to test for subsequent declines. Adjusted annual growth was calculated for each infested tree as:

$$G_{T, Y} = (GI_{T, Y} - GC_{T, Y}) - (GI_{T, 35-84} - GC_{T, 35-84})$$

where G_{TY} equals the standardized growth for infested tree T in year Y, GI_{TY} is the radial growth for infested tree T in year Y, GC_{TY} is the radial growth for control tree T in year Y, $GI_{T, 35-84}$ is the average radial growth for infested

tree T from 1935-1984 and $GC_{T, 35-84}$ is the average radial growth of control tree T from 1935-1984. If the average of $G_{T, Y}$ differs from 0, this indicates a divergence in the growth of infested vs. control trees. We tested whether fire reduced beetle preferences for declining trees by comparing $G_{T, Y}$ for trees that were and were not burned prior to infestation.

In September 1999 we revisited the infested trees that were marked in 1998 and evaluated their condition. At this time, we also recorded the number of newly infested trees that we observed while searching the same area as in 1998.

3. Results
3.1 Resin response to fire
Char heights for burn damaged trees ranged from 0.35 m to 11.54 m (mean $\pm$ SD = 4.57 $\pm$ 3.51 m). Resin flow tended to increase in trees damaged by the spring 1998 fire relative to those not damaged by the fire ($F_{1, 116}$ = 5.98, $p = 0.016$). Trees with low initial resin flow in 1997 showed the greatest increases post-burn (Fig. 1). There was no effect of crown class or crown class x burn ($F_{1, 116}$ = 0.43 and 0.28 respectively), although there was some variation among trees within crown class and burning treatments ($F_{116, 116} = 2.77$, $p < 0.0001$). There was no effect of 1998 sample date ($F_{1, 116} = 1.59$, $p = 0.21$). Among burned trees, resin flow increased approximately linearly with height of charring () $Resin = -0.20 + 0.097 \bullet CharHeight$, $r^2 = 0.26$, $p = 0.004$).

3. 2. Ips *species abundance*
We captured 3697 *I. pini*, 872 *I. grandicollis*, 408 *I. perroti*, and 1759 *T. dubius* in 1998. There was no correlation for any *Ips* species between abundance at a site in 1997 and abundance at that site in 1998 (n = 23 sites, P > 0.10 for all species). Fire damaged sites had higher abundances of *I. pini* in May, one month following the fire (Fig. 2a, fire x date interaction in Table 1). *I. pini* abundance in burned areas fell below that of unburned sites during mid-summer and was similar to unburned sites in September. Abundances of both *I. grandicollis* and *I. perroti* were similar in burned and unburned sites throughout the summer (Fig. 2b, 2c; Table 1). There was, however, a spatial correlation between years for *T. dubius* as well as an increase in abundance in burned areas (Figs. 2d, 3).

3. 3. Infested trees
In 1998, we located 41 mature red pines that were infested by bark beetles. All were of codominant crown class (none were intermediate or suppressed). Study trees were scattered along . 10 km of road system within the park. Seventeen of the infested trees were within the area burned in April 1998; char heights on these trees ranged from 0.2 to 5 m (mean $\pm$ SD = 1.83 $\pm$ 0.37 m). Only three infested study trees had sustained scorching of the live crown. The park included more infested trees than were included in the study, especially within the burned area, where many trees were attacked by bark beetles within the scorched area of the lower bole. *Ips pini* and *I. grandicollis* were the dominant insects infesting live trees. Three trees with scorched crowns were infested with *I. perroti* and we found occasional individuals of *Dendroctonus valens* LeConte, *Polygraphus rufipennis*

(Kirby), *Trypodendron lineatum* (Olivier), and *Xyleborus dispar* (Fabricius). Most beetle-infested trees had extensive recent bark punctures from woodpecker foraging (especially *Picoides arcticus* (Swainson)). We found no evidence of root or crown pathogens in any of the infested study trees, although our survey revealed two trees with declining crowns that contained no beetles and were probably afflicted with Diplodia blight (*Sphaeropsis sapinea* (Fr.) Dyko & Sutton, = *S. ellisii* = *Diplodia pinea*).

None of the individual infested trees showed evidence of declining growth in the years preceding infestation compared to their paired uninfested tree (Fig. 4 shows four representative examples). Furthermore, analyses of all 41 pairs of infested and uninfested trees revealed no significant difference in growth between infested and uninfested trees for any year from 1935 to 1997 (Fig. 5). This was true even during the years immediately preceding infestation (Fig. 5b); mean growth difference for 1985-1997 ($\pm$ SE) = 0.029 $\pm$ 0.026 mm / year, which was indistinguishable from 0 ($t = 1.12$, $p = 0.26$). Patterns were the same for trees infested following fire as for trees infested in the absence of fire (Fig. 5).

Even given the results in Figs. 4-5, beetles could still have been tending to infest trees on sites where growth rates were low relative to the rest of the forest. However, this was not true, as indicated by comparing the growth of infested trees with a different sample of control trees (120 codominant trees that were scattered throughout the park and selected at random with respect to the location of infested trees; Fig. 6). To the contrary, infested trees included some of the fastest growing trees in the park (note similarities in the right-hand tails of the two frequency distributions in Fig. 6).

Of 41 mature red pines that were infested with beetles during 1998, 21 were dead or nearly dead by the end of the next growing season. Of these, 18 appeared to have been killed by the beetles and 3 might have died anyway from the fire damage alone. Of the 17 trees that were still alive, 6 were sustaining continuing beetle attacks in 1999, and 11 were apparently free of new beetle attacks. In our judgment, some of the trees that were alive and no longer sustaining beetle attacks could survive for decades longer. In the process of revisiting infested trees that were marked in 1998, we identified 39 other mature, codominant red pines that became infested during 1999 - comparable to the 41 trees that we found in 1998.

4. Discussion

Increased resin flow following a fire may be an evolved response of red pine to the increased probability of bark beetle attack. This could be adaptive for tree populations that are regularly subjected to low, creeping ground fires that do not necessarily cause mortality, as is the case for red pine in this region (Hendee et al., 1978; Heinselman, 1981, 1983; Clark, 1990). Two other fire-adapted pine species, longleaf pine (*Pinus palustris* Miller) in southeastern U.S. and ponderosa pine (*Pinus ponderosa* Douglas) in southwestern U.S., also have been shown to respond to surface fires with increases in resin flow (Harper 1944; Feeney et al., 1998). Facultative increases in anti-herbivore defenses following fire may be part of the adaptive syndrome that characterize woody plants in fire-based ecosystems (DeBano et al., 1998). This could be further tested by comparing the responses to fire of *Pinus* species with and without an evolutionary history of frequent ground fires. An alternative hypothesis is that increased resin flow following fire is part of a generalized response of *Pinus* to wounding. Loblolly pine tends to increase resin production following mechanical wounding of the inner bark (Ruel et al., 1998). Heat trauma might trigger the same physiological response. Further data are needed to determine whether increased resin flow is a localized or whole-tree response to fire.

It is not obvious how to reconcile the increase in tree defenses with the increased abundance of *I. pini* immediately following the fire. One possibility is that *Ips* are attracted to volatiles released by pines during burning (Muona and Rutanen, 1994; Holsten et al., 1995; Hart, 1998; Schmitz and Bleckmann, 1998), which could be adaptive for *Ips* because fires frequently kill some trees outright, and recently killed trees provide high quality habitat for bark beetles (Reid and Robb, 1999). In this scenario, some beetles may be deceived into attacking trees that were charred but not killed and have high resin flow that limits reproduction by the beetles. However, this is not consistent with accounts of bark beetle infestations following fires (Amman and Ryan, 1991; Ehnström et al., 1995; Rasmussen et al., 1996). Another possibility is that resin production drops in the short term, which creates a window of opportunity for beetle colonization of the trees. (Our first resin sampling in 1998 was . 2 months after the fire.) Resin production in loblolly pine drops following lightning (Blanche et al. 1985) and during 1 - 3 days following physical wounding of the inner bark (Ruel et al., 1998). Subsequent increases in resin flow during the months following fire might account for the mid-season reduction of *I. pini* abundance within burned areas (Fig. 2a). Ehnström et al. (1995) also noted increased resistance of trees following a fire. If fires enhance beetle reproductive success, thereby increasing the local abundance of beetles, beetle attack rates of trees might remain elevated in the years following a fire, as occurred in Yellowstone National Park (Rasmussen et al., 1996). Tree susceptibility to subsequent attack could be increased by fire scars on the lower bole that facilitate fungal infection and beetle attack (Geiszler et al., 1980, 1984). Figure 3 and Table 1 clearly indicate that there was not enough direct mortality of beetles from the fire to support the use of prescribed burns as a beetle control strategy in this system (McCullough et al., 1998).

There was no evidence that *Ips* were preferentially infesting trees with declining growth. If *Ips* attacks were concentrated on trees that were destined to succumb because of drought stress, nutrient deficiencies, root pathogens, senescence or most other factors that could predispose trees to bark beetle attack (Paine et al., 1997), we would have expected some signal of declining tree growth in the years preceding attack (Hepting et al., 1945; De Kort and Baas, 1997). Instead, our data indicate that beetle attacks are random with respect to tree growth (Figs. 5-6). Apparently, *Ips* are attacking trees that would otherwise live.

It is noteworthy that *Ips* were not at epidemic levels in Itasca State Park during 1998 or 1999. Conventional

wisdom holds that *Ips* only infest healthy trees during population outbreaks (Rudinsky, 1962; Geiszler et al., 1984). However, average *Ips* captures did not exceed 47 beetles / site during any trapping period in the summer of 1998, which is less than we normally capture with the same trapping protocol at other sites (Herms et al., 1991; B. D. Ayres unpublished data). Observations in 1999 revealed that all trees attacked in 1998 had either died or sustained irreparable damage to their vascular system, lost significant portions of their crown that had been supported by the damaged vascular tissue, and were in the process of losing portions of their bark, making them more vulnerable to pathogens, fire, windstorms, and future insect attacks. Numerous, otherwise healthy, red pines were killed during the prescribed burn of April 1998 when the wood exposed by such scars was ignited.

Apparently, *Ips* are influencing the demographics of this natural red pine population. There has been virtually no recruitment of red pines at Itasca State Park within the last century (apparently as a result of fire suppression and deer browsing; Hansen and Duncan, 1954; Janssen, 1967; Frissell, 1973). If this continues, the longevity of the population is finite and depends on mortality rates. Thus, tree survivorship is of critical interest to park managers, who are mandated to "preserve intact the primeval pine forest now growing in Itasca State Park" (1891 legislation of the state of Minnesota). In two years, we found 41 and 39 newly infested trees in a survey of . 4000 trees, suggesting that the annual probability of an individual tree becoming infested is . 1%. About half of the infested trees died in the short term. With an annual mortality rate of 0.5%, and no recruitment of trees, the Itasca population of red pines would be halved by beetle attacks in 139 years. Of course red pines also die from windstorms, fires, pathogens, and lightning. If the survivorship function includes a mortality rate of 0.25% / year from these other causes, the tree population would be halved in 93 years. This model still fails to account for the increased probability of future mortality that is a legacy of surviving past beetle infestations. If the mortality rate of previously attacked trees increases to 5% per year, and the other parameters are unchanged, the tree population would be halved in 65 years. This can be contrasted to a hypothetical forest that lacks beetles (background mortality of 0.25% / year only), which would have a half life of 277 years.

These calculations are simplistic but illustrate that endemic populations of *Ips* bark beetles can have meaningful effects on the expected longevity of old growth pine forests. Furthermore, this conceptual model provides a starting point for evaluating the consequences of prescribed fire. If the objectives of prescribed fire are to preserve the red pine population, then the demographic benefits of increased regeneration must exceed the demographic costs of increased mortality risks for mature trees. These assessments should incorporate the possibility that fire increases the mortality risks from bark beetles and that sub-lethal scarring from bark beetles increases the mortality risk from subsequent fires (Linder et al. 1998).

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Table 1. Summaries of ANOVAs testing for effects of fire and date on trap captures of three species of *Ips* bark beetles and their chief predator, *Thanasimus dubius*

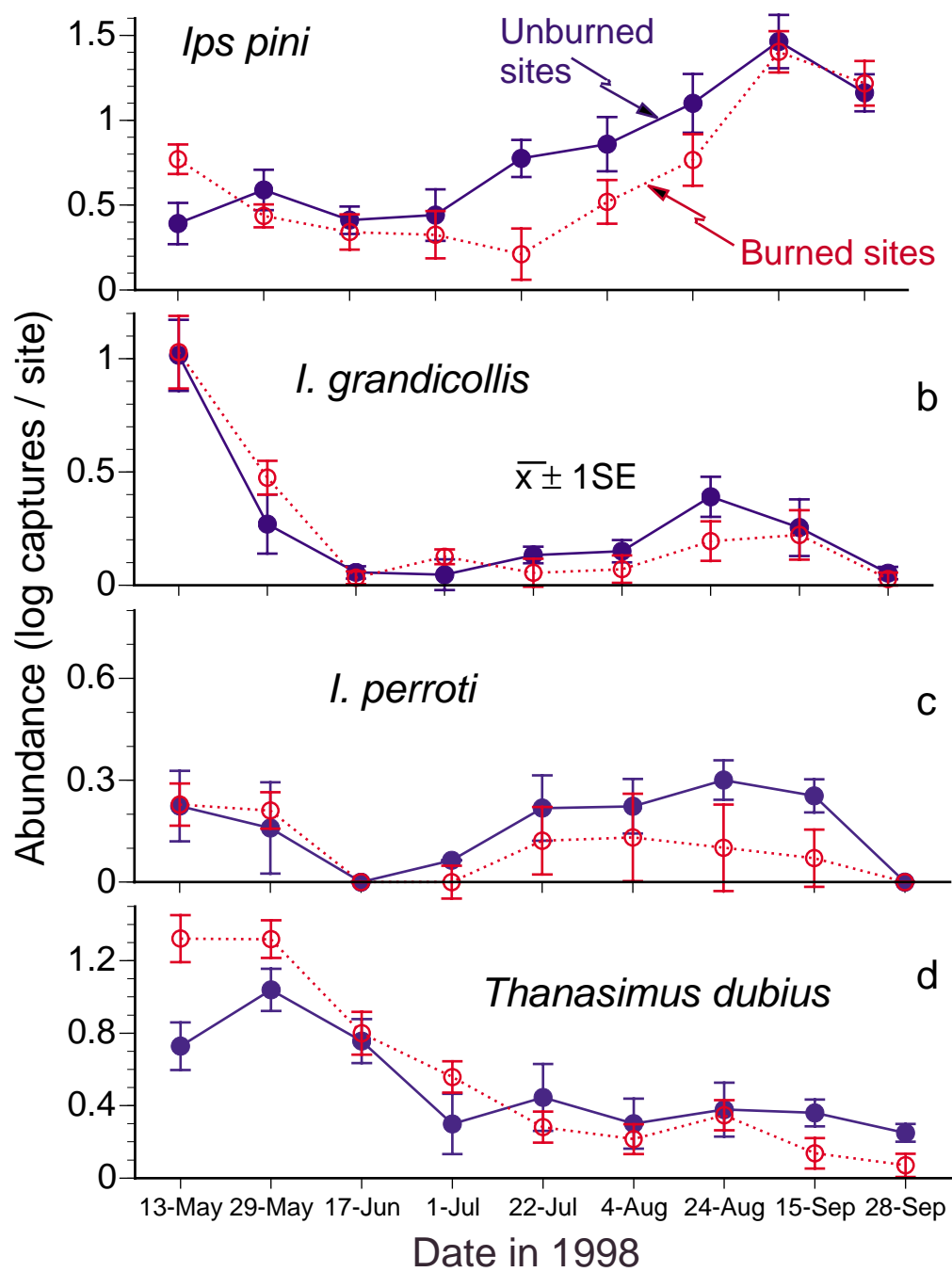| Source	df	*I. pini* MS	*I. pini* F	*I. grandicollis* MS	*I. grandicollis* F	*I. perroti* MS	*I. perroti* F	*T. dubius* MS	*T. dubius* F
Fire	1	1.075	1.76	0.014	0.09	0.249	1.50	0.181	0.32
Date	8	3.733	19.78[***]	2.571	25.75[***]	0.219	2.65[**]	3.623	30.80[***]
Fire x Date	8	0.481	2.55[*]	0.0831	0.83	0.051	0.61	0.492	4.18[***]
Site(Fire)	26	0.611	3.24[***]	0.160	1.60[**]	0.166	2.02[**]	0.570	4.85[***]
Error	208	0.189		0.100		0.083		0.118	

[*] $p < 0.05$; [**] $p < 0.01$; [***] $p < 0.001$

Figure legends

Fig. 1. Resin flow in 1998 vs. 1997 for mature red pines that were and were not exposed to prescribed fires in the spring of 1998. Dotted line and solid line indicate regressions for burned trees and control trees, respectively. Trees exposed to ground fire had significantly elevated resin flow by mid summer of 1998 compared to trees that did not experience a fire.

Fig. 2. Abundance of *Ips* bark beetles and their specialist predator, *Thanasimus dubius*, at sites within old-growth pine forests that were and were not exposed to a prescribed fire.

Fig. 3. Abundance in 1998 vs. 1997 of the bark beetle predator, *Thanasimus dubius*, at sites that were and were not burned in April 1998 (fire effect: $F_{1, 20} = 6.94$, $p = 0.016$; covariation with abundance in 1997: $F_{1, 20} = 5.24$, $p = 0.033$).

Fig. 4. Examples of growth histories in four *Pinus resinosa* infested with *Ips* bark beetles in 1998 compared to paired uninfested control trees.

Fig. 5. Mean growth difference between *Pinus resinosa* infested with bark beetles in 1998 and their paired uninfested control trees from 1935-1980 (upper) and from 1980-1997 (lower).

Fig. 6. Average growth rates during 50 years (1935-1984) for trees infested by *Ips* in 1998 compared to a sample of trees not infested by *Ips.*
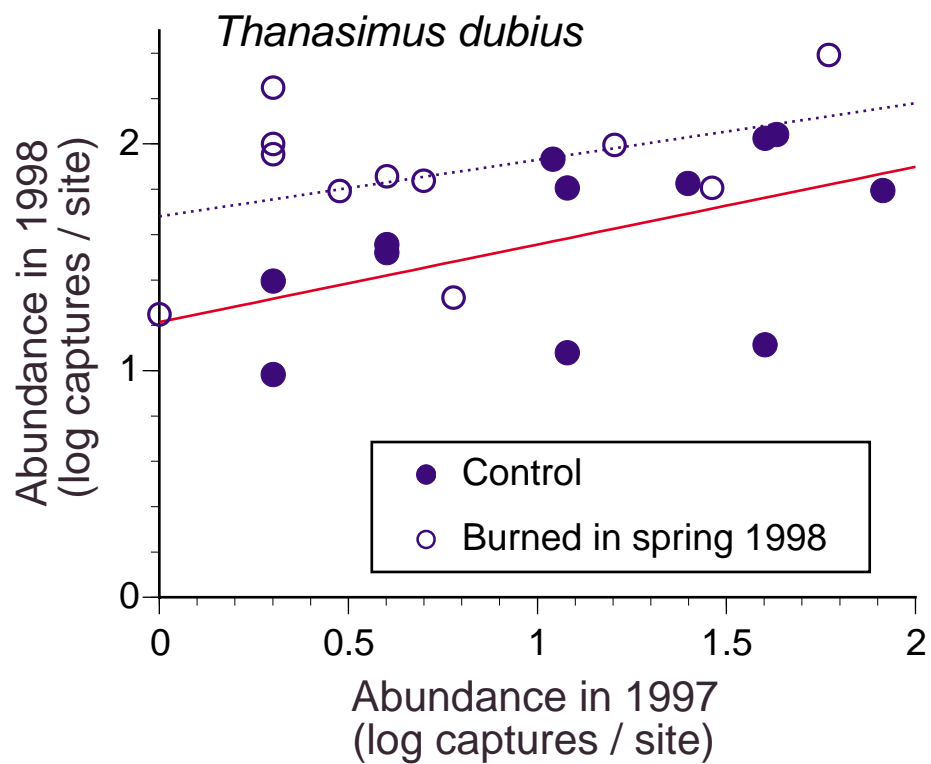
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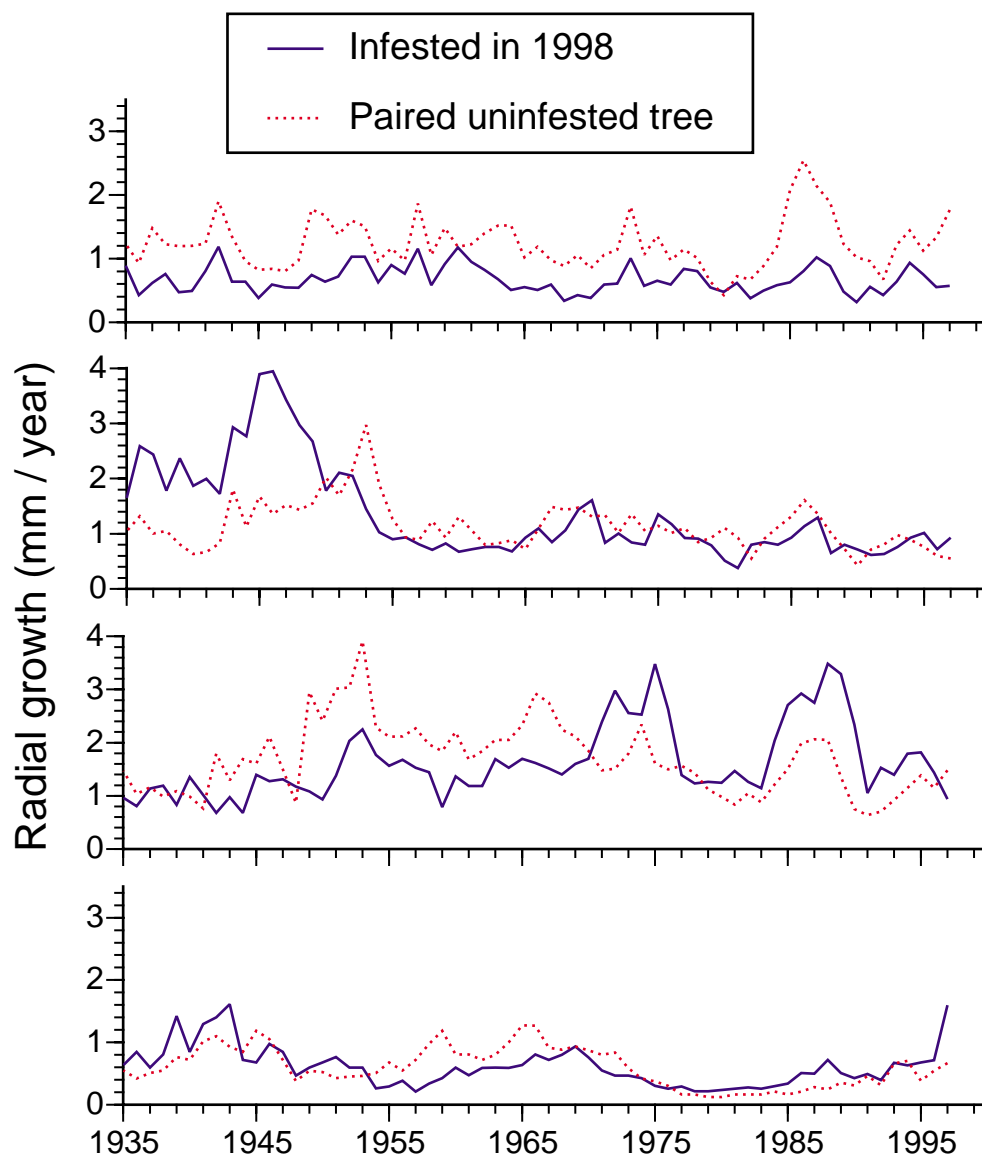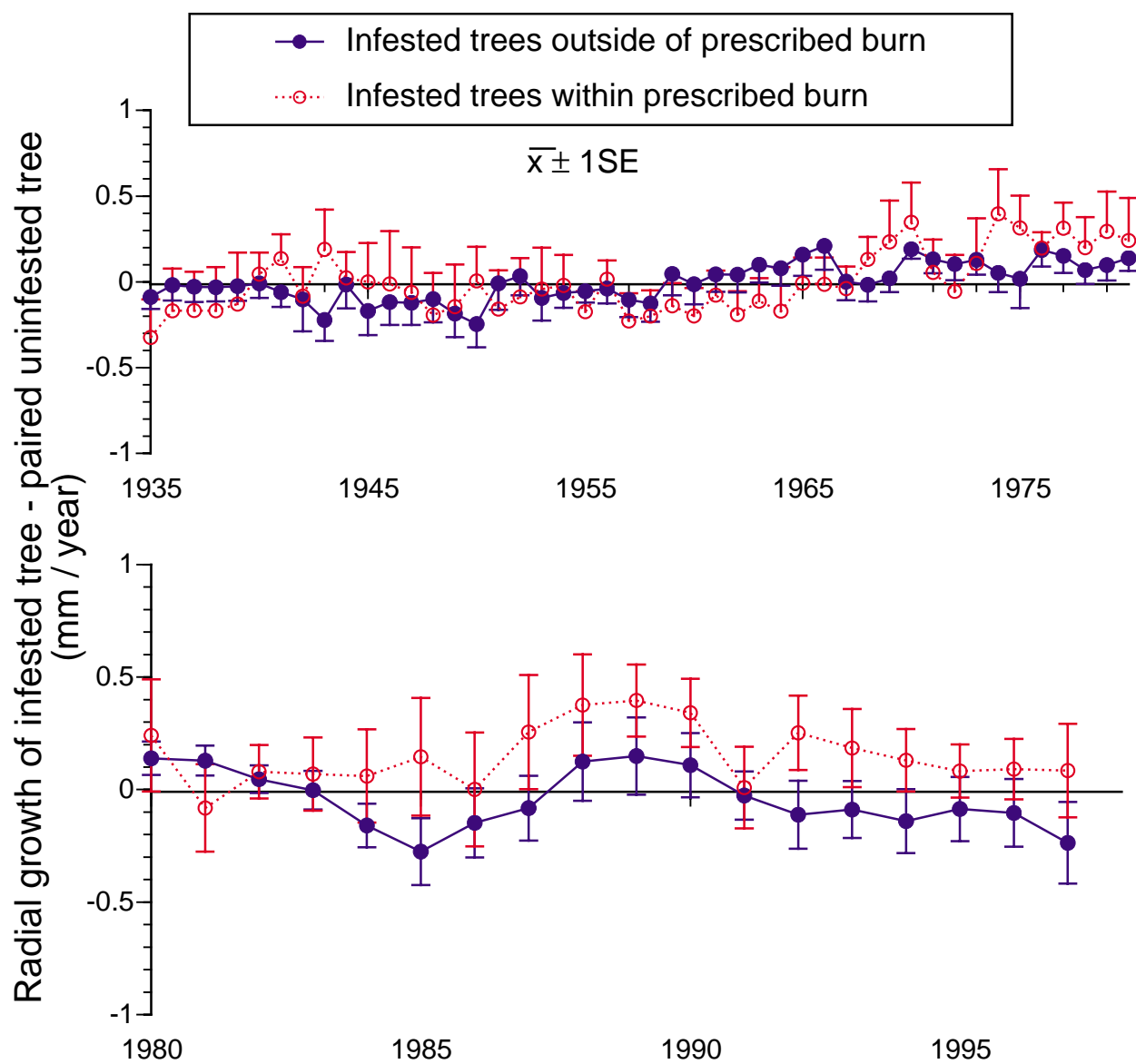
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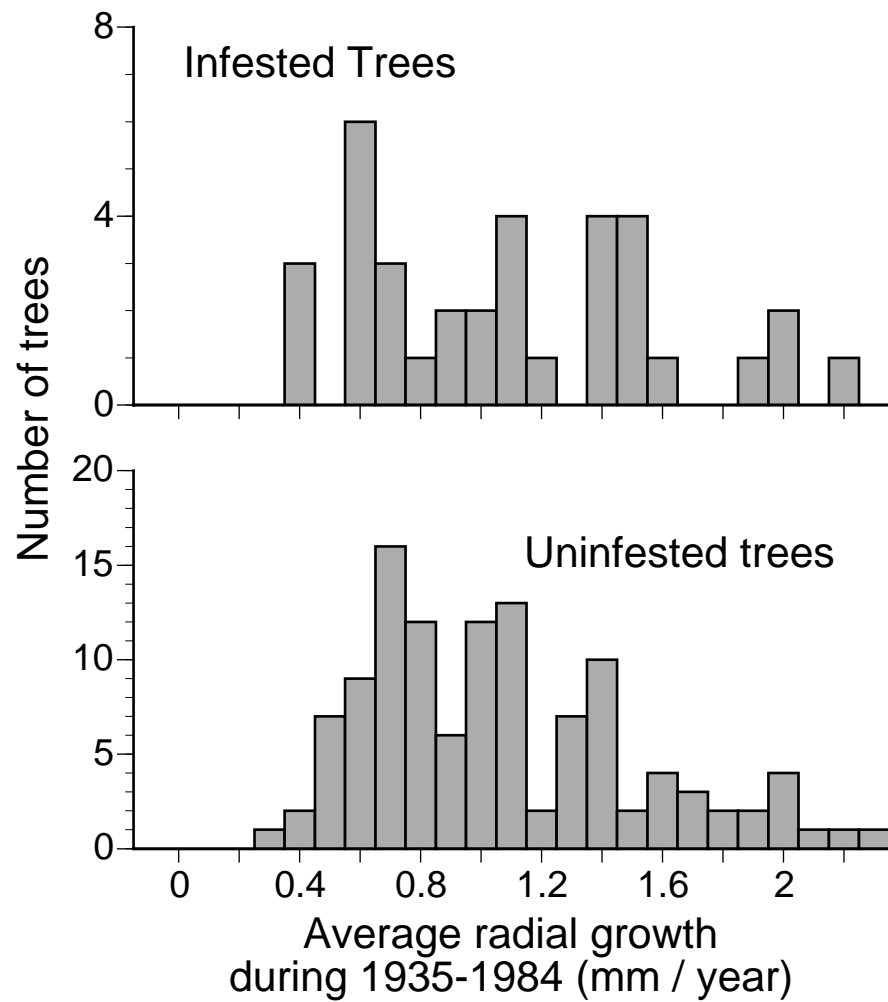
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