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Can spruce beetle (*Dendroctonus rufipennis* Kirky) pheromone trap catches or stand conditions predict Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) tree mortality in Colorado?

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Abstract

1 Bark beetles (Coleoptera: Curculionidae: Scolytinae) can cause extensive tree mortality in forests dominated by their hosts. Among these, the spruce beetle (*Dendroctonus rufipennis*) is one of the most important beetles in western North America causing Engelmann spruce (*Picea engelmannii*) tree mortality.

2 Although pheromone traps with attractants are commonly used to monitor spruce beetle populations, the relationship between the numbers of beetles caught in pheromone traps and subsequent tree mortality has not been investigated adequately.

3 We used pheromone traps to catch spruce beetles in plots throughout the insect flight period, quantified subsequent tree mortality, and modelled spruce tree mortality as a function of spruce beetle trap catches and stand conditions.

4 The number of beetles caught was not different between years. It was also positively associated with tree mortality, as was the amount of available host. The year of sampling was significant in all models as a result of different mortality levels between years.

5 We conclude that, although the models had good fit, the difference in mortality between the years with a similar beetle catch negates reliable estimates of tree mortality across years. Managers and forest health specialists will be better served by continued monitoring of spruce beetle populations with pheromone traps and the use of stand variables to identify susceptible stands.

Keywords Bark beetles, disturbance, forest insects, Scolytinae.

Introduction

In recent decades, coniferous forests in western North America have experienced extensive tree mortality caused by various bark beetles (Raffa *et al.*, 2008). One of the most notable is the spruce beetle (SB) (*Dendroctonus rufipennis* Kirby), which is widely distributed in North America, from Alaska east to Newfoundland and south to Arizona and New Mexico in the west and to Michigan and Pennsylvania in the east (Wood, 1982b). This insect utilizes various species of *Picea* as hosts for habitat, food and reproduction and, in the interior western U.S.A., its primary host is Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). In Alaska, the preferred hosts are Sitka spruce [*Picea sitchensis* (Bong.) Carr.] and white spruce [*Picea glauca* (Moench) Voss]. Bark beetles are natural and integral components of forest ecosystems and contribute to regulating forest composition and structure (Dymerski *et al.*, 2001; Kayes & Tinker, 2012). Associated tree mortality can result in a number of ecological changes that can benefit the ecosystem, such as creating the small scale disturbances and coarse woody debris that characterize resilient functioning ecosystems (Harmon *et al.*, 1986; Lundquist & Negrón, 2000; Klutsch *et al.*, 2014). Under certain circumstances, eruptive populations affect large landscapes and can result in timber losses, safety hazards and changes in hydrological processes, and can also influence the dynamics of fire behaviour (Klutsch *et al.*, 2011; Pye *et al.*, 2011; Jenkins *et al.*, 2012; Mikkelson *et al.*, 2013). Spruce beetle outbreaks are driven by various factors. An abundance of large-diameter host trees needs to be available (Schmid & Frye, 1976; Dymerski *et al.*, 2001). Triggering events such as the occurrence of wind storms that result in downed trees, which are preferred by the beetles, can provide an adequate habitat for a population increase (Schmid, 1981). Climatic conditions have also been implicated with outbreaks; drought

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can result in compromised defences and warm temperatures can accelerate insect development (Werner & Holsten, 1985; Hansen *et al.*, 2001; Berg *et al.*, 2006; DeRose & Long, 2012; Hart *et al.*, 2014).

Most commonly, SB completes its life cycle in 2 years, although a 1-year life cycle occurs when relatively warm weather conditions prevail, as well as at lower elevations (Knight, 1961; Werner & Holsten, 1985; Hansen *et al.*, 2001). Completion of the life cycle in 1 year can lead to an exponential growth of populations (Hansen & Bentz, 2003), fostering an increase in the extent of outbreaks (Dyer, 1969) and elevated spruce mortality levels (Safranyik *et al.*, 1990; Berg *et al.*, 2006). Management can be futile when populations reach epidemic levels, although some strategies may be used when populations are at endemic or incipient levels to help lessen undesirable mortality when and where appropriate. Some options include the use of trap trees, the removal or debarking of infested trees, and insecticide applications (Nagel *et al.*, 1957; Bentz & Munson, 2000; Jenkins *et al.*, 2014).

Similar to other tree-killing bark beetles, the SB relies on a sophisticated chemical communication process utilizing pheromones and host compounds to facilitate mass attacks and overcome the defensive mechanisms of the tree (Wood, 1982a; Franceschi *et al.*, 2005). Pheromones are now synthesized in the laboratory and are commercially available for many species, including SB. These chemicals are used for management applications and research. For example, synthetic aggregation pheromones are used: (i) to protect trees from attacks by the western balsam bark beetle (*Dryocoetes confusus* Swaine) (Stock *et al.*, 1994) and the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) (Ross & Daterman, 1997); (ii) to predict southern pine beetle (*Dendroctonus frontalis* Zimmermann) population trends (Billings & Upton, 2010); and (iii) to study the flight periodicity of bark beetles (Hansen, 1996; Negrón *et al.*, 2011), amongst others. A common use of commercial formulations is to monitor population trends in areas of interest to inform practitioners and land managers of insect activity. An often posed question is whether the number of insects caught in pheromone traps can be used to predict tree mortality levels. Few studies have examined this relationship. In the case of high-value areas, resources could then be directed and mitigation measures planned with the aim of averting excessive SB-caused tree mortality. Infestations of SB are associated with stand conditions such as basal area, percentage host type and tree diameter (Schmid & Frye, 1976; Hansen *et al.*, 2010). In the present study, we investigated whether there is a relationship between the number of SBs caught in pheromone traps or stand conditions and SB-caused tree mortality.

Materials and methods

Study site and insect trapping

The present study was conducted at the Hahns Peak/Bears Ears Ranger District of the Medicine Bow-Routt National Forest in central Colorado during the summers of 2001 and 2002 in a spruce-subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] mixed forest. Other tree species in the area included lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) and quaking aspen (*Populus tremuloides* Michx.). The study area was north-north-east of the town of Clarke, which is located at UTM 13T, 0337812, 4508047. SB populations developed in downed trees resulting from a windstorm and later transitioned to live trees in surrounding stands; a frequent way for eruptive populations to develop (Schmid & Frye, 1977; Schmid, 1981). The windstorm occurred in 1997 and, by 2003, approximately 210 000 trees were killed in approximately 20 000 ha (Jorgensen, 2003). We established 18 study plots, each 400×400 m (16 ha); two plots were elongated but encompassed the same area and the mean $\pm$ SEM plot elevation was 2663 ± 85 m. We surveyed nine plots in 2001 and nine in 2002, although two plots that had no mortality in 2002 were not included in the analysis. Plots in 2001 were separated by a mean $\pm$ SEM distance of 3.1 ± 0.3 km and, in 2002, by 3.6 ± 2.2 km. In the central portion of each plot, five Lindgren 12-funnel pheromone traps were deployed (Phero Tech Inc./Contech Enterprises Inc., Canada). The traps comprised a series of black plastic funnels connected and arranged vertically with a collection cup at the bottom (Lindgren, 1983). Traps contained a commercial formulation of a SB attractant consisting of frontalin (release rate of 2.8 mg/day at 20 °C) and α-pinene (release rate of 1.3 mg/day at 20 °C) (Phero Tech Inc./Contech Enterprises Inc.). A small insecticide strip was placed in the collection cup to kill the beetles, as well as to prevent cannibalism and losses to predatory insects (Dichlorvos, ProZap® Insect Guard™, Durvet, Inc., Pleasantville, Iowa). Traps were hung on nonhost trees to minimize unintended beetle attacks to surrounding host trees and were at least 1 m from the bole, with the collection cups approximately 1 m from the ground. Plots were gridded using $x-y$ coordinates and traps were deployed around mid-May within the 400×400 m plot at the coordinates: 100, 100; 100, 300; 200, 200; 300, 100; and 300, 300. Therefore, perimeter traps were separated by approximately 200 m, with the centre trap approximately 140 m from these. Beetles were collected from the traps three to four times during the season depending on location, starting late spring and ending in the autumn, and the number of SBs caught determined in the laboratory. The trapping period encompassed the flight period reported for SB in the vicinity of the study area, which is from early June until early September, with peak flight occurring around the end of June (Jorgensen, 2003). We summed the number of beetles caught in all traps and dates to determine the total number of beetles caught in each plot for the season.

Mortality assessments

To quantify tree mortality caused by SBs, 12 fixed-radius subplots (0.02 ha; 8 m radius) were established in each plot after the completion of the insect flight period. Subplots were established in three transects that crossed the plot with randomly selected starting points and included four evenly-spaced subplots. For every plot tree ≥ 2.54 cm in diameter at 1.4 m above the ground (diameter at breast height; DBH), we recorded species and DBH, as well as whether the tree was alive, current year SB-killed, dead to unknown causes or older SB-killed; trees in the last two conditions were excluded from the analysis. Current year SB-killed trees had abundant fresh frass and boring residue and

Table 1 Stand characteristics, tree mortality, and mean diameters in study plots in 2001 and 2002

Stand measurement	2001 $n=9$	2002 $n=7$	P
Total basal area (m^2/ha)	41.9 (3.7)	40.2 (2.8)	0.5254
Total trees per ha	1195.2 (139.1)	1120.1 (76.4)	0.7911
Spruce basal area (m^2/ha)	20.9 (4.4)	19.9 (1.8)	0.9157
Spruce trees per ha	314.9 (66.0)	387.6 (43.5)	0.1527
% Spruce basal area	43.7 (8.3)	51.9 (4.8)	0.5254
% Spruce trees per ha	29.2 (5.3)	36.6 (3.6)	0.3408
Spruce killed basal area (m^2/ha)	13.8 (4.0)	3.2 (0.9)	0.1123
Spruce killed trees per ha	104.8 (34.6)	18.5 (5.5)	*0.0429*
% Spruce basal area killed	43.4 (8.7)	9.1 (1.4)	*0.0010*
% Spruce trees per ha killed	25.9 (6.1)	4.6 (1.2)	*0.0059*
All species DBH (cm)	17.9 (0.7)	17.6 (0.6)	0.7508
Spruce DBH (cm)	24.0 (1.8)	22.1 (1.2)	0.4587
Spruce DBH killed (cm)	41.3 (2.1)	45.0 (3.4)	0.5966

Probabilities in italics indicate significant differences, Wilcoxon rank sum test at $P<0.05$. Routt National Forest, Colorado, 2001–2002. DBH, diameter at breast height.

fresh pitch tubes. With these data, we calculated plot basal area and tree density; spruce basal area, tree density, and percentage thereof; beetle-killed spruce basal area, tree density, and percentage thereof; and mean DBH for all species combined, for spruce and beetle-killed spruce. A few trees in the vicinity of traps were attacked by spillover beetles, which would have reduced the trap catch, although this was a rare event and did not result in any trees being killed.

Statistical analysis

We compared the mean number of beetles caught from June through September across the study plots in 2001–2002 using a Kruskal–Wallis test. We compared plot variables across plots between years with a Wilcoxon rank sum test. We modelled the percentage of spruce basal area killed and the percentage of tree density killed by beetles using the total number of beetles, spruce basal area and tree density, percentage spruce basal area and percentage spruce tree density, and mean spruce DBH as independent variables with year as a covariate and a beta distribution using mixed general linear models (SAS Institute, 2012). We checked for correlations between spruce beetle catches and stand variables by year and repeated the modelling adding each stand variable to the spruce beetle catch (i.e. two independent variables per run). Model fit was assessed by the deviance (best when close to 1) and by calculating a correlation coefficient between observed means of tree mortality predictors and the predicted means. The number of spruce trees > 27.9 cm DBH has been associated with the level of tree mortality in spruce (Hansen *et al.*, 2010) and so we repeated all modelling including only trees of this size.

Results

Most plot conditions were similar between the years (Table 1). Engelmann spruce comprised approximately one-half of the basal area and approximately one-third of the trees in the plots in both years. Percentage spruce basal area killed, percentage tree density killed and tree density killed by SB were significantly higher in plots sampled in 2001 compared with 2002 and there were no differences in the rest of the variables examined.

The total number of beetles caught across all plots in 2001 was 25 057 and ranged from 842 to 7151 with a mean ± SEM of 2784.1 ± 656.3 ($n=9$). For 2002, the total number of beetles across all plots was 29 432 and ranged from 2112 to 6853 with a mean of 4204.6 ± 553.0 ($n=7$). The mean number of beetles caught across all plots was not different between years (Kruskal–Wallis test, chi-square = 2.4, d.f. = 1, $P=0.12$). The number of beetles caught, spruce basal area and percentage spruce basal area were positively related to the percentage of basal area killed by SB (Fig. 1 and Table 2). We observed the same with the percentage tree density killed; the number of beetles caught, spruce tree density and percentage spruce tree density were positively correlated (Fig. 2 and Table 2). In all cases, relationships were strongly influenced by years as indicated by significant P-values and little to no overlap in the 95% confidence bands. All models had good fit as indicated by their low deviance and high correlation coefficient between the observed and predicted values. Modelling including only spruces > 27.9 cm did not change the results and therefore is not presented for brevity. Correlation coefficients (r, P-value) indicated that, in 2000, spruce beetle catch was positively correlated with spruce basal area (0.79, 0.01), spruce tree density (0.87, 0.002), percentage spruce basal area (0.77, 0.02) and percentage spruce tree density (0.77, 0.02) and, in 2000, with spruce basal area (0.86, 0.01) and tree density (0.78, 0.04); catches were not correlated with mean spruce diameter in either year. Adding a stand condition variable to the spruce beetle catch did not improve models over those with spruce beetle catch only. In all cases, stand variables were not significant (not shown).

Discussion

The data obtained in the present study indicate that there is a significant positive relationship between the number of SBs caught during the yearly flight period and the percentage spruce basal area and percentage tree density killed that same year. This was also true for spruce basal area, spruce tree density and percentage thereof. Relationships were, however, strongly influenced by year of sampling as a result of higher mortality levels observed in 2001 compared with 2002. This suggests that, in the present study, the relationship between beetles caught in pheromone traps, spruce basal area or spruce tree density or percent thereof with tree mortality, although positive and significant, was variable as a result of other factors between years. The relationships therefore would not provide reliable estimates of tree mortality across years.

The higher mortality levels observed in the plots studied in 2001 is difficult to explain considering that stand conditions and the number of beetles caught were not different between the years. It is possible that trees in plots examined in 2001 were under more stress than those examined in 2002 and, as a result, less beetles may have been required to kill trees in 2001 because of compromised defences (Raffa & Berryman, 1983). However,

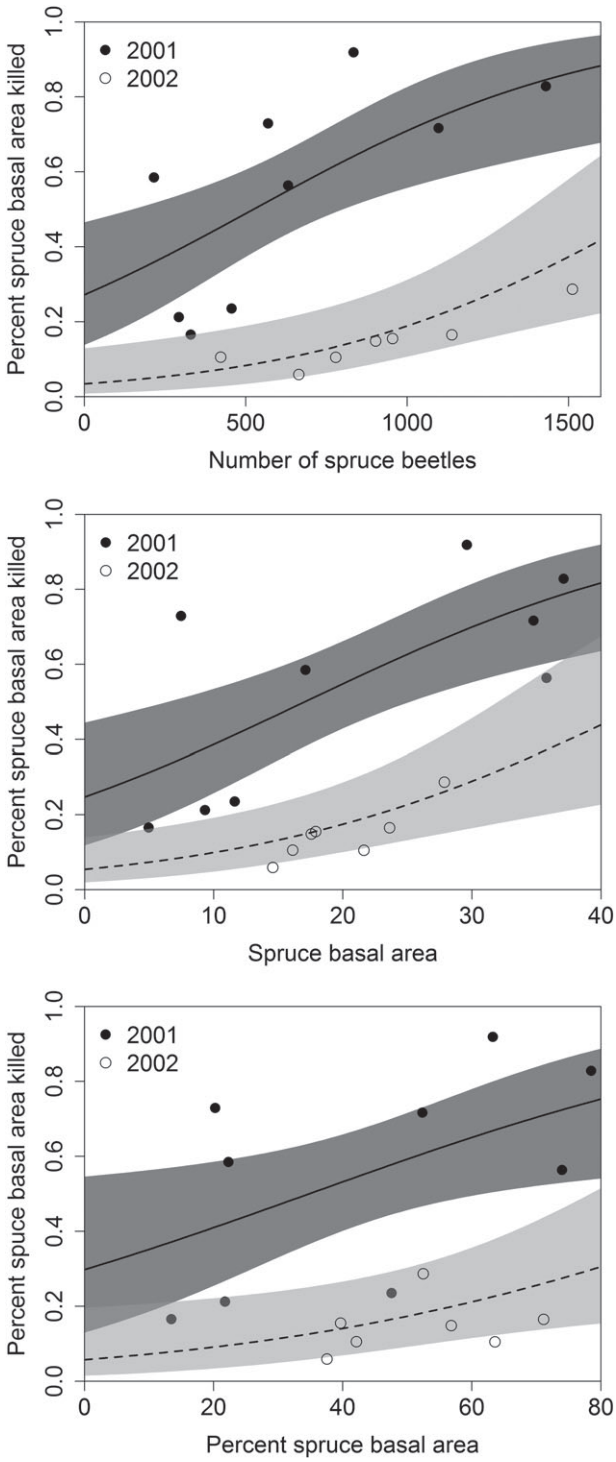

Figure 1 Models for estimating percentage *Picea engelmannii* basal area killed by *Dendroctonus rufipennis* as a function of number of spruce beetles caught in pheromone traps; spruce basal area; and percentage spruce basal area. The solid line indicates model prediction for 2001 and the dashed line is for 2002. Shading represents the 95% confidence interval and dots represent actual observations. Routt National Forest, Colorado, 2001–2002.

Table 2 Significance of effects and model fit for estimating percentage of *Picea engelmannii* basal area and percentage tree density killed by *Dendroctonus rufipennis* as a function of the number of beetles caught in pheromone traps, spruce basal area, spruce tree density, and percentage thereof

Variable	*P*	Year *P*	Deviance	Correlation
Response = Percentage basal area killed				
Number of beetles	0.0304	0.0006	1.1	0.82
Spruce basal area	0.0032	0.0004	1.3	0.86
% Spruce basal area	0.0256	0.0006	1.3	0.80
Response = Percentage trees per ha killed				
Number of beetles	0.0780	0.0015	1.4	0.70
Spruce trees/ ha	0.0232	0.0008	1.2	0.76
% Spruce trees/ha	0.0393	0.0010	1.2	0.77

All models show good fit. Year *P* is the significance of year effect. Correlation coefficients are between observed and predicted values of the predictor variables and were significant in all cases ($P < 0.001$). Routt National Forest, Colorado, 2001–2002.

plots were under similar environmental conditions during the study years. The Palmer Drought Severity index for the study area was from −3 to −4 from March to September in 2001 and below −4 for the same time period in 2002 (NOAA, National Centers for Environmental Information; www.ncdc.noaa.gov, accessed December 2016). This suggests a severe to extreme drought, being more pronounced in 2002 instead, which is the year with less mortality.

Studies addressing the relationship between bark beetles caught in pheromone traps and mortality levels have had variable results. Hansen *et al.* (2006) working with SB in Utah measured the number of trees attacked in plots where a single 16-funnel Lindgren pheromone trap was deployed using the same attractant as that employed in the present study. Three different block sizes were surveyed around the trap, comprising 1, 4 and 10 ha, and a significant relationship was observed between the numbers of beetles caught during the insect flight period and the number of attacked trees in all three block sizes, although with high variation; the models were considered as having poor fit. Working with the European spruce bark beetle [*Ips typographus* (L.)], Weslien *et al.* (1989) sampled forest districts in Norway, Sweden, Finland, and Denmark; districts ranged in area from 1000 to 9000 ha and were widely separated within each country. A strong correlation was reported across all sites between the numbers of beetles and tree mortality for the duration of the yearly flight period. Also working with the European spruce bark beetle in north-eastern Italy, Faccoli and Stergulc (2004) monitored populations with pheromone traps and evaluated tree mortality over a 7-year period. Forty traps were used over a 1200 ha and a positive relationship was reported between the number of beetles caught per trap and tree mortality. Hayes *et al.* (2008) trapped five species of *Dendroctonus* and five species of *Ips* using clusters of three pheromone traps in 26 sites in northern Arizona and examined the relationship between insect catches and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) mortality. No relationship was reported between trap catches and host tree mortality within a 1 ha area around the traps. Working with western pine beetle [*Dendroctonus brevicomis* (LeConte)] in ponderosa pine in California, Hayes *et al.*

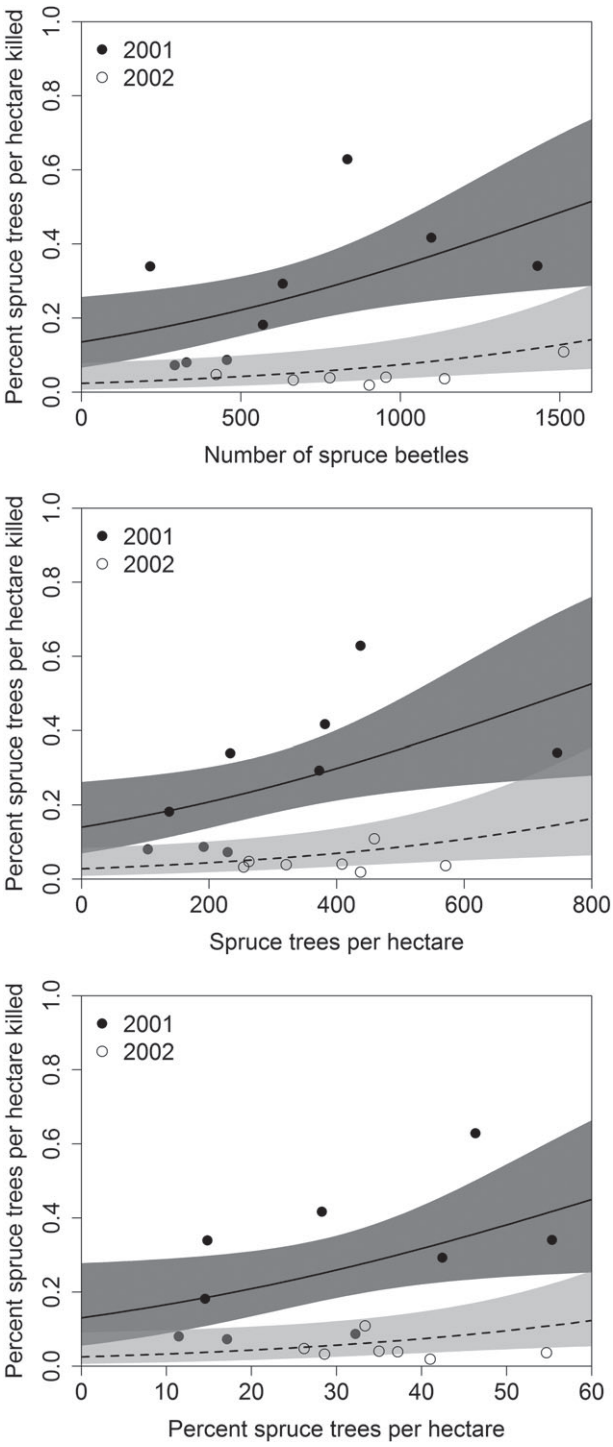

Figure 2 Models for estimating percentage *Picea engelmannii* trees per hectare killed by *Dendroctonus rufipennis* as a function of number of spruce beetles caught in pheromone traps; spruce trees per hectare; and percentage spruce trees per hectare. The solid line indicates model prediction for 2001 and the dashed line is for 2002. Shading represents the 95% confidence interval and dots represent actual observations. Routt National Forest, Colorado, 2001–2002.

(2009) examined the relationship at two scales (i.e. stand and forest) by establishing sites with a single 16-funnel Lindgren funnel trap in five National Forests in a north–south gradient across the state. A 2-ha area was surveyed around the trap location for tree mortality and few relationships were reported between beetle catches and tree mortality at either scale.

Differences in mortality levels in stands with the same number of beetles could be the result of various factors. The number of beetles caught in a pheromone trap can be influenced by many factors, including the type and number of funnels, location of the trap, stand conditions in the proximity of the traps, environmental conditions such as temperature and wind speed and direction, pheromone release rate and competition with natural pheromone sources, amongst others. For example, in a study by Miller and Crowe (2009), 16-funnel Lindgren traps caught significantly more *Xyleborus* spp. bark beetles compared with eight-funnel traps; no differences were observed with various other species. The geographical variation in how the same insect species may respond to the pheromone components can also influence beetle catch in traps. Hofstetter *et al.* (2008) indicated that, in Arizona, the western pine beetle is more attracted to traps where the monoterpene component of the attractant is replaced with α-pinene instead of myrcene, the monoterpene in the commercial formulation. The number of beetles required to kill a tree will also vary depending on host vigour and the condition of tree defensive mechanisms (Raffa & Berryman, 1983; Waring & Pitman, 1985). This suggests that, when trees in a stand become more stressed, less beetles (i.e. a smaller population) could cause more mortality than a larger population where trees are more vigourous.

The effective range of a pheromone trap (i.e. the distance where the trap remains attractive to beetles) affects trapping efficiency and could influence results based on how far apart traps are located. Traps separated by a distance larger than its range of efficiency are assumed to be independent, which means the traps sample discrete portions of the beetle population. Hansen *et al.* (2006) suggested that this distance may be species and pheromone-dependent. For SB, Shore *et al.* (1990), estimated this distance to be approximately 25 m, whereas Hansen *et al.* (2006) caught marked beetles up to 100 m away. Dodds and Ross (2002) conducted a mark–recapture study with the Douglas-fir beetle and most beetles caught by pheromone traps were within 200 m. Hansen *et al.* (2006) separated traps by 800 m, whereas our traps were separated approximately 200 m apart, suggesting that, in both studies, beetle catch in traps may have been independent of one another. However, it is unknown how the difference in trapping distances or trap effective range may have affected the results. For example, if traps in the present study were attracting beetles from more than 200 m, we could have been collecting beetles from areas outside the study plot.

The relationship between bark beetle trap catches and tree mortality can be also expressed in terms of a threshold that may be related to tree mortality. Considering the many factors discussed that influence trap catches, this may offer a more realistic application. For example, Hansen *et al.* (2006) used classification trees and identified relationships that distinguish endemic and epidemic population phases. An endemic phase was characterized as having less than two trees per ha attacked by beetles compared with an epidemic phase characterized by

two or more trees per ha attacked. At the 10-ha plot size in the study by Hansen *et al.* (2006), a season-long beetle catch of more than 842 beetles classifies the stand as being in an epidemic phase; less beetles would classify the stand to be in an endemic phase. Similarly, Faccoli and Stergulc (2004) reported mean trap catches of the European spruce bark beetle up to approximately 20 000 beetles per trap for the trapping season. Based on their calculated relationship between beetles caught to tree mortality, they suggested that a catch of 8000 beetles represents a volume loss of less than 100 m^3, which they consider acceptable. Weslien (1992) indicated that with yearly trap catches of less than 10 000 European spruce bark beetles, forest districts would have low tree mortality but, with more than 10 000 beetles, mortality could be either low or high.

In the present study, we observed a significant relationship between spruce basal area and percentage spruce with percentage spruce basal area killed and with spruce tree density and percentage spruce tree density with percentage spruce density killed, although the relationships were influenced by year. Hansen *et al.* (2010) indicated that stand density index, spruce basal area and the number of spruce trees larger than 27.9 cm were correlated with SB-caused tree mortality, although the relationships were not strong. Tree mortality caused by bark beetles is strongly influenced by stand conditions and the relationship is documented for various bark beetles in western North America (Fettig *et al.*, 2007). SB exhibits preference for slow growing trees associated with increased basal area (Hard *et al.*, 1983; Hard, 1985; Holsten *et al.*, 1995). Johnson *et al.* (2014) indicated that SB-caused tree mortality increases with tree diameter and basal area and that stand density reduction as a result of patch cuts can reduce mortality of the larger trees. Regarding the potential for having an outbreak in a spruce stand (*sensu* probability of infestation; Negrón & Popp, 2004), Schmid and Frye (1976) indicated that Engelmann spruce stands growing on well-drained sites with mean DBH among spruces larger than 25.4 cm being greater than 40.6 cm (i.e. large-diameter trees), basal areas greater than 34.3 m^2/ha, and proportions of spruce greater than 65% are more susceptible to SB attack. However, based on our findings, further data are needed to adequately evaluate the relationship between stand conditions and tree mortality in spruce.

As indicated by Weslien (1992), for a relationship to be useful, it needs to be robust, such that it is based on several years of information and covers a range of conditions, resulting in it being useful as a predictive tool. We agree with the assessment by Hayes *et al.* (2009) that sampling for a number of years and over a large area may yield stronger relationships between beetle catches and tree mortality. For example, Faccoli and Stergulc (2004) reported a strong relationship based on 7 years of sampling over a 1200-ha area and the work of Weslien *et al.* (1989) was based on 2 years but included 12 sites over a very large area.

Continuing the research to improve and develop the relationship between beetle catches and tree mortality for SB and other bark beetles in North America could result in useful tools for land managers and practitioners, although the work required will be laborious, expensive and likely require refinement of consistent and reliable trapping protocols. Obtaining an understanding of the forest conditions that foster an increased probability of infestation and extent of mortality in spruce needs further research. Until then, land managers and practitioners may be better served by focusing on identifying susceptible areas based on the available information with respect to stand conditions and using pheromone trapping as a way of keeping abreast of population trends and detecting incipient populations of bark beetles.

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