

Evaluation of funnel traps for estimating tree mortality and associated population phase of spruce beetle in Utah

E. Matthew Hansen, Barbara J. Bentz, A. Steven Munson, James C. Vandygriff, and David L. Turner

Abstract: Although funnel traps are routinely used to manage bark beetles, little is known regarding the relationship between trap captures and tree mortality near the trap. We conducted a 4 year study in Utah to examine the correlation between funnel-trap captures of spruce beetle (*Dendroctonus rufipennis* Kirby) and mortality of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) within a 10 ha block of the trap. Using recursive partitioning tree analyses, rules were developed for predicting spruce mortality and associated levels of beetle population phase (endemic or epidemic), in the current year and subsequent year, for a given level of trap captures. Although model predictions of infested-stem counts had large variances, our results suggest that funnel-trap captures can be reliably used to estimate relative levels of tree mortality, expressed as spruce beetle population phase. Classification-tree analyses indicate that captures of ~842 spruce beetles during a season (late May to mid-August) from a single funnel trap represent a threshold between endemic (<2 mass-attacked stems/ha) and epidemic conditions (≥ 2 mass-attacked stems/ha) for either the current or the subsequent year relative to deployment of the funnel trap. Likewise, a lack of infested hosts within 10 m of a funnel trap, also known as spillover, was associated with endemic conditions, whereas trees attacked near the trap correlated with epidemic conditions.

Résumé : Bien que les pièges en entonnoir soient couramment utilisés pour la gestion des scolytes, la relation entre les captures dans les pièges et la mortalité des arbres près des pièges est peu connue. Nous avons réalisé une étude d'une durée de quatre ans en Utah pour déterminer le degré de corrélation entre les captures de dendroctone de l'épinette (*Dendroctonus rufipennis* Kirby) dans les pièges en entonnoir et la mortalité de l'épinette d'Engelmann (*Picea engelmannii* Parry ex Engelm.) à l'intérieur d'un bloc de 10 ha autour du piège. À l'aide d'analyses récursives de partitionnement des arbres, des règles ont été développées pour prédire la mortalité de l'épinette et les niveaux correspondants de population du dendroctone (endémique ou épidémique), dans l'année en cours et l'année suivante, pour un niveau donné de captures dans les pièges. Malgré la forte variation des prédictions du nombre de tiges infestées générées par le modèle, nos résultats indiquent que les captures dans les pièges en entonnoir peuvent être utilisées de manière fiable pour estimer les niveaux relatifs de mortalité des arbres, exprimés en fonction des phases de population du dendroctone de l'épinette. Les analyses de classification des arbres indiquent que la capture de ~842 dendroctones de l'épinette pendant une saison (fin mai à mi-août) dans une seule trappe en entonnoir représente un seuil entre des conditions endémiques (attaque massive de <2 tiges/ha) et épidémiques (attaque massive de ≥ 2 tiges/ha), soit pour l'année en cours, soit pour l'année suivant l'installation du piège en entonnoir. De la même façon, l'absence d'hôtes infestés à moins de 10 m d'un piège en entonnoir, aussi appelé débordement, est associée à des conditions endémiques tandis que la présence d'arbres attaqués près d'un piège est corrélée avec des conditions épidémiques.

[Traduit par la Rédaction]

Introduction

Pheromone-baited multiple funnel traps (Lindgren 1983), hereinafter referred to as funnel traps, have become a widely used tool for monitoring and managing bark beetle (Coleoptera: Curculionidae, Scolytinae) populations. Synthetic aggregation pheromones, which are placed in a trap, are commercially available for many bark beetle species

(Skillen et al. 1997). These pheromones are very effective at attracting adult beetles to a funnel trap (Borden 1995), although the response can vary depending on such factors as (i) pheromone constituents, release rates, and chirality (Borden et al. 1987), or (ii) intraspecific geographic variance (Borden et al. 1996; Dahlsten et al. 2004). Management uses of pheromones and funnel traps include beetle containment and concentration (Gray and Borden 1989; Vandygriff et al.

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Table 1. Specifications of the two-component spruce lures (PheroTech, Inc., Delta, British Columbia) used in funnel traps.

	Frontalin	α -Pinene
Device	400 μ L Eppendorf® centrifuge tube	1.8 mL Eppendorf® centrifuge tube
Release rate	2.8 mg/day at 20 °C	1.3 mg/day at 20 °C
Enantiomer ratio	Racemic	+5/-95
Purity	>99%	>99%

2000), beetle suppression and mass trapping (Hansen et al. 2006; Laidlaw et al. 2003; Ross and Daterman 1997; Raty et al. 1995), forecasting infestation trends (Billings 1988), stand and individual-tree protection (Bentz et al. 2005; Kegley and Gibson 2004; Ross et al. 1996; Ross and Daterman 1995), and characterization of beetle-flight timing and patterns (Peck et al. 1997; Hansen 1996).

A potential use of funnel traps that has received little attention is using trap captures to estimate the tree mortality in a given area or the size of a local beetle population. One problem is determining the effective sampling area of a trap or series of traps (Byers et al. 1989). Using marked beetles that were released from specific points, Turchin and Odendaal (1996) estimated the effective sampling radius of a trap for the southern pine beetle, *Dendroctonus frontalis* Zimmermann, to be about 18 m. In a mark-recapture experiment, Dodds and Ross (2002) collected Douglas-fir beetles, *Dendroctonus pseudotsugae* Hopkins, from as far away as 400 m, although about 90% of recaptured beetles were from distances of 200 m or less. Weslien and Lindelow (1990) recaptured about 8% of marked European spruce bark beetles, *Ips typographus* L., in baited drainpipe traps at a distance of 100 m from release sites, and recaptured 2% at distances of 1.2–1.6 km. These results indicate that although sampling range is a function of distance to the trap, the nature of the relationship may be species- and (or) pheromone-dependent. Nevertheless, quantification of funnel-trap sampling range is complex. No similar research has been conducted for the spruce beetle (*Dendroctonus rufipennis* Kirby), although Shore et al. (1990) estimated an effective range of about 25 m for the attractant spruce beetle semiochemical bait. Hansen and Bentz (2003) trapped marked spruce beetles up to 100 m from a funnel trap, although their study was not focused on assessing sampling range.

Trap catch will also be affected by a complex variety of factors, including topography, stand density, wind direction and strength, temperature, and stand composition (Schmid et al. 1992; Salom and McLean 1991). For example, Bentz and Munson (2000) observed disproportionate spruce beetle catches in a series of funnel traps, most likely because of differences in local terrain features and prevailing wind direction. Furthermore, there is anecdotal evidence that natural pheromone/kairomone sources influence captures of mountain pine beetles (*Dendroctonus ponderosae* Hopkins) in synthetically baited funnel traps (Bentz 2006). Because of these difficulties, few efforts have been made to estimate population levels or host mortality using trap-catch data. Billings (1988) developed a system for using information on catches from pheromone-baited traps, including clerid beetles (*Thanasimus dubius* Fabr.) known to prey on bark beetles, to forecast trends in southern pine beetle infestations,

though not tree mortality. Scandinavian researchers have found strong correlations ($R^2 = 0.64\text{--}0.91$) between catches of European spruce bark beetles from baited drainpipe traps and numbers of infested stems along clear-cut edges (Weslien et al. 1989; Hubertz et al. 1991).

We know that funnel traps are efficient for catching spruce beetles (Ross et al. 2005; Bentz and Munson 2000; Werner and Holsten 1995; Borden et al. 1996) and have been used extensively to monitor their flight periodicity. It is not understood, however, what a specific number of trapped spruce beetles indicates in terms of either tree mortality or population trend. For example, are 500 trapped spruce beetles indicative of endemic or epidemic populations? Or how many infested trees are likely to be associated with that level of trap catch? Using a commercially available two-component spruce beetle lure, our goal was to develop rules that can be used to predict current- and subsequent-year mortality of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) caused by spruce beetles, based on funnel-trap catches. Ancillary data evaluated included stand conditions, spruce beetle population phase, clerid beetle counts, air temperature, and topographic variables. Estimates of tree mortality or beetle population phase obtained using funnel-trap captures will provide resource specialists with additional decision-making information for forest management. Specific objectives of the study were to (i) quantify the relationship between funnel-trap catches and spruce beetle-caused tree mortality in the vicinity of the trap, and (ii) quantify the relationship between year-to-year trends in spruce beetle-caused tree mortality and year-to-year trends in funnel-trap catches.

Materials and methods

Plot selection and survey

Areas were selected to represent a range of spruce beetle population phases. Using aerial detection survey (ADS) maps (developed by USDA Forest Service, Forest Health Protection; <http://www.fs.fed.us/r1-r4/spf/fhp/aerial/index.html>) and ocular estimates, spruce stands in central and southern Utah were classified as being in the endemic, building, or epidemic phase. Extrapolating from the definitions of Bentz and Munson (2000), areas were partitioned as follows: endemic phase: <1 stem/ha; building phase: 1–5 stems/ha; and epidemic phase: >5 stems/ha.

Within each area, four plots were installed, each with a centrally located 16 unit funnel trap baited with a two-component spruce beetle lure (Table 1). To prevent full elution of α -pinene before the end of spruce beetle flight, α -pinene tubes were replaced in midsummer. To facilitate weekly trap collections, road access was a location criterion, the require-

ment being that plots be spaced at >800 m (i.e., we assume that there is no trap-to-trap influence at this distance). Population-phase areas were at least 5 km apart. Traps were hung on non-host trees, with the trap cup about 1.5 m above ground level, and positioned so as not to contact a bole (>0.25 m gap). Plastic strips impregnated with pesticide (dichlorovinyl dimethyl phosphate) were placed in the trap cups to prevent loss of captured beetles to predators. Traps were checked weekly from the time of installation (late May or early June) through mid-August — the typical flight period of the spruce beetle. All specimens from a trap cup were placed in labeled bags and transported to our laboratory, where spruce beetles were tallied. Clerid beetles (e.g., *Thanasimus* spp. and *Enoclerus* spp.), important predators that respond to spruce beetle pheromones, were also tallied although not identified to species. Air temperature was recorded (Onset Corp., Bourne, Massachusetts) at one plot within each area.

Following spruce beetle flight (i.e., late summer or early fall), a 100% ground survey of spruce within each study block was conducted. We surveyed a range of block sizes, centered on each trap, which enabled testing of response differences with increasing distance to the trap. During the initial year of the study, block sizes were restricted to 1 and 4 ha. We added a third size, 10 ha, in subsequent years as additional survey personnel became available. All infested spruce were tallied according to attack status — (i) mass attack: a successful attack, i.e., spruce beetle brood present around the entire tree circumference; (ii) strip attack: a successful attack on some portion of the bole; (iii) fill-in attack: a tree that was strip-attacked in the previous year was currently attacked on the remaining bole faces; or (iv) pitch out: an unsuccessful attack (pitch tubes present, possibly with egg galleries, but without living brood) — and by year of attack — (i) current-year attack: boring dust and immature brood, occasionally pitch tubes, present on an otherwise green-needled tree; (ii) previous-year attack: symptoms range from fading needles to some or most needles fallen; live beetles may still be present, especially at the root collar (Hansen and Bentz 2003); (iii) second-year attack: fine twigs attached, most or all needles fallen, no live brood present; or (iv) older attack: no needles, some or many fine twigs missing.²

For each infested stem, diameter at breast height (DBH) was measured using a Biltmore stick. Stand characteristics were estimated with nine variable-radius plots (BAF 20) on a 100 m grid centered on each trap. Measurements included species, attack status (spruce only), and DBH of each sample tree. Elevation, slope, aspect, and topographic position were also recorded at each variable-radius plot. Stand summaries (e.g., basal area, number of trees per acre, and stand-density index for all species and individual species) were calculated using the FINDIT program (Bentz 2000). Annual ADS data were used to estimate spruce beetle population pressure around each plot per year.

Plots were originally established in May 2001 on the Manti-LaSal and Fishlake National Forests, Utah. The three population phases were represented on each forest, totalling

24 plots. Where possible, traps were set up at the same sites during subsequent years: 2002, 2003, and 2004. Many original (2001) plots were abandoned because of logging or near-complete loss of live hosts. Where this occurred, replacement plots were selected (Table 2). In 2004, four of the building-phase plots were located on the Dixie National Forest after suitable areas could no longer be found on the Manti-La Sal National Forest. Because we were able to determine 2001 attacks using stems classified as sustaining previous-year attacks in the 2002 surveys, 2001 plots repeated in 2002 effectively represent a 10 ha survey rather than the 4 ha blocks originally surveyed.

Analyses

Relationship between funnel-trap catches and tree mortality

Although all attacked spruce were classified by status, we concentrated on mass-attack tree count as the response variable because our objective was to predict spruce beetle-caused tree mortality. Spruce beetle population phase (endemic, building, or epidemic), calculated from post-beetle-flight ground surveys rather than classified using ADS maps and walk-through assessments, was also used as a response variable. Response variables were calculated for the current and subsequent year relative to the time of trap captures (e.g., stem mortality or population phase in 2001 and 2002 was dependent upon funnel-trap catch in 2001). Additionally, our data collection allowed for analyses at three spatial scales (1, 4, and 10 ha). Data from three plots for a single year were discarded because the funnel trap had fallen to the ground, resulting in incomplete beetle capture data.

Exploratory data analyses were conducted using least-squares regression (PROC REG; SAS Institute Inc., Cary, North Carolina). We also used mixed models (PROC GLIMMIX; SAS Institute Inc.), which can use a Poisson distribution for count data, as well as random effects and repeated measures. Model fit for the 4 ha blocks was intermediate with respect to that for the 1 and 10 ha blocks, with no apparent interpretive gain from the analyses. Therefore, final analyses did not consider the 4 ha block size.

Recursive partitioning trees (*R*; www.r-project.org) were used to develop rules for determining relative levels of spruce mortality for a given level of trap catch. These models use recursive binary partitioning to split a data set into increasingly similar subsets (Therneau and Atkinson 1997). We used regression trees (ANOVA methods) when the response variable was expressed as stem count, whereas we used classification trees when the response variable was expressed as population phase. The minimum parent- and terminal-node sizes were specified as 20 and 10, respectively. Goodness-of-fit was evaluated using the “xerror” term (also known as cross-validation error; one minus xerror is analogous to R^2 in least-squares regression) and cross-validation classification probability tables (classification trees only).

In addition to beetle captures, predictor variables (covariates) explored included (i) stand characters (e.g., number of live trees per acre, live basal area, live host quadratic mean diam-

²Note that these characters may apply only to our area. For example, on Lutz spruce on the Kenai Peninsula, Alaska, most needles fall by the end of the summer in which the trees are attacked.

Table 2. Locations, relative spruce beetle pressure, and maximum survey areas of plots used to determine the correlation between funnel-trap captures of spruce beetles and spruce mortality (all plots are in Utah).

Plot	Latitude	Longitude	Elevation (m)	Estimated spruce beetle population phase*	Maximum area surveyed (ha)			
					2001	2002	2003	2004
Manti-LaSal National Forest								
Flat Canyon 1	39°38'N	111°15'W	2730	Endemic	4	10	10	10
Flat Canyon 2	39°38'N	111°16'W	2740	Endemic	4	10	10	10
Flat Canyon 3	39°39'N	111°16'W	2730	Endemic	— [†]	— [†]	— [†]	— [†]
Flat Canyon 4	39°39'N	111°16'W	2780	Endemic	1	— [†]	— [†]	— [†]
Flat Canyon 5	39°41'N	111°13'W	2870	Endemic	—	10	10	10
Flat Canyon 6	39°40'N	111°13'W	2750	Building	—	10	10	10
Huntington Reservoir 1	39°35'N	111°16'W	2760	Building	4	10	10	— [‡]
Huntington Reservoir 2	39°33'N	111°16'W	2730	Building	4	10	10	— [‡]
Huntington Reservoir 3	39°31'N	111°15'W	2670	Building	4	10	10	— [‡]
Huntington Reservoir 4	39°36'N	111°13'W	2740	Building	4	10	— [†]	— [†]
Huntington Reservoir 5	39°31'N	111°15'W	2790	Building	—	—	10	10
Oak Creek 1	39°26'N	111°22'W	2930	Epidemic	4	10	— [‡]	— [‡]
Oak Creek 2	39°26'N	111°22'W	2860	Epidemic	4	10	— [‡]	— [‡]
Oak Creek 3	39°26'N	111°23'W	2830	Epidemic	4	10	—	— [‡]
Oak Creek 4	39°26'N	111°23'W	2780	Epidemic	4	10	— [‡]	— [‡]
Huntington Canyon 1	39°33'N	111°10'W	2560	Endemic	—	—	4	4
Huntington Canyon 2	39°33'N	111°10'W	2550	Endemic	—	—	4	4
Huntington Canyon 3	39°34'N	111°10'W	2580	Endemic	—	—	4	4
Huntington Canyon 4	39°35'N	111°10'W	2600	Endemic	—	—	4	— [§]
Fishlake National Forest								
Anderson Meadows 1	38°13'N	112°26'W	2940	Epidemic	4	10	10	10
Anderson Meadows 2	38°12'N	112°25'W	2950	Epidemic	4	10	10	10
Anderson Meadows 3	38°13'N	112°25'W	2950	Epidemic	4	10	10	10
Anderson Meadows 4	38°12'N	112°25'W	2920	Epidemic	4	10	10	10
Puffer Lake 1	38°18'N	112°22'W	2960	Building	4	10	10	10
Puffer Lake 2	38°18'N	112°22'W	2980	Building	4	10	10	10
Puffer Lake 3	38°19'N	112°21'W	3060	Building	4	10	10	10
Puffer Lake 4	38°18'N	112°22'W	2980	Building	4	10	10	10
Big John Flat 1	38°21'N	112°24'W	3030	Endemic	4	10	10	10
Big John Flat 2	38°20'N	112°23'W	3050	Endemic	4	10	10	10
Big John Flat 3	38°20'N	112°24'W	3060	Endemic	4	10	10	10
Big John Flat 4	38°21'N	112°24'W	3030	Endemic	4	10	10	10
Dixie National Forest								
Griffin Top 1	38°13'N	112°26'W	2940	Building	—	—	—	10
Griffin Top 2	38°12'N	112°25'W	2950	Building	—	—	—	10
Griffin Top 3	38°13'N	112°25'W	2950	Building	—	—	—	10
Griffin Top 4	38°12'N	112°25'W	2920	Building	—	—	—	10

Note: For 2001 plots repeated in 2002, measurements of 2001 attacks within 10 ha blocks were identified as previous-year attacks in the 2002 surveys, so the survey area for these plots in 2001 was effectively 10 ha.

*Classified during plot selection; the phase may have changed in subsequent years (e.g., Huntington Reservoir plots were in the epidemic phase by 2003).

[†]The plot was lost to logging. In the case of Flat Canyon 4, the 1 ha block was surveyed, while the 4 ha block was lost.

[‡]The plot was abandoned because of near-complete loss of the susceptible host.

[§]The plot was abandoned for logistical reasons.

eter, live stand density index, and spruce beetle risk rating; Schmid and Frye 1976); (ii) clerid beetle counts and the proportion of spruce beetles to spruce beetles plus clerid beetles in the traps (Billings 1988); (iii) temperature variables (e.g., average temperature in June through August, cu-

mulative days above 16 °C); (iv) physiographic variables (topographic class, aspect); (v) spillover (presence/absence of currently infested stems within 10 m of the trap); and (vi) ADS stem-mortality counts within 1 and 3 km of funnel traps.

Relationship between year-to-year trends in spruce beetle-caused tree mortality and funnel-trap catches

Least-squares regression (PROC REG; SAS Institute Inc.) was used to quantify the relationship between year-to-year trends in spruce beetle-caused tree mortality and year-to-year trends in funnel-trap catches. For each site that had two or more years of data, trends (expressed as ratios) were calculated as

$$[1] \quad \text{Ratio}_{\text{stem}} = \text{stem count}_{t-1} / \text{stem count}_t$$

$$[2] \quad \text{Ratio}_{\text{catch}} = \text{trap catch}_{t-1} / \text{trap catch}_t$$

where t is the survey year (stem-count ratios were calculated using data from 10 ha blocks). To avoid problems with zero values, we added 0.1 to each observation before calculating the ratio. The resulting ratios were log-transformed, for both stem counts and beetle captures, to meet normality assumptions. Finally, the log-transformed ratios of mass-attacked-stem counts were regressed against the log-transformed ratios of beetle captures.

Results

Current-year predictions

Stem mortality

Plotting mass-attacked stem counts against beetle captures indicates a positive correlation, although the relationship has substantial variance (Fig. 1). Regression-tree analysis using current-year mass-attacked stem counts within 10 ha blocks as the response variable resulted in a tree with two terminal nodes, splitting on the variable "SBPROP", which is the ratio of spruce beetles trapped to spruce beetles plus clerid beetles trapped. All other predictor variables were pruned (xerror = 0.702; Fig. 2a). The tree produced for 1 ha blocks also had two terminal nodes, splitting on the variable SPILL, which is presence/absence of infested trees, or "spillover", within 10 m of the trap (xerror = 0.626; Fig. 2b). Results from preliminary linear regression and mixed models (not shown) had comparable model fit and standard errors.

Spruce beetle population phase

Classification-tree analysis using spruce beetle population phase, as measured by the postflight surveys, within 10 ha blocks as the response variable resulted in a tree with two terminal nodes, splitting on the variable SB, which is total seasonal spruce beetle captures. All other variables were pruned (xerror = 0.636; Fig. 3a, Table 3). The cross-validation classification table indicates that the model was unable to distinguish the building population phase. The lack of a terminal node for the building phase probably results from the overlap between the range of spruce beetle captures in plots measured as being in the building and epidemic phases (Fig. 4), and the minimum terminal node size requirement (10), which is nearly the same as the number of building-phase observations (11). The tree produced for 1 ha blocks also had two terminal nodes, splitting on the variable SPILL (xerror = 0.250; Fig. 3b, Table 3). Again the model did not distinguish the building phase, although it correctly classified the endemic- and epidemic-phase observations in nearly all cases.

Because the building phase cannot be distinguished with our data, we reclassified the data into either endemic or epidemic phases. After reviewing the data, we noted that plots that did not exceed 2 infested trees/ha in any single year were relatively unaffected by spruce beetles at the end of the study. Thus, we redefined the endemic phase as <2 infested trees/ha and the epidemic phase as ≥ 2 infested trees/ha. Using two levels of population phase as the response variable produced trees identical to those developed using three levels of population phase (Fig. 3a); this is true for the 10 ha (xerror = 0.233; Table 3) and 1 ha blocks (xerror = 0.135; Table 3). The threshold for distinguishing the endemic (<2 mass-attacked stems/ha) and epidemic phases (≥ 2 mass-attacked stems/ha) in 10 ha blocks is about 842 spruce beetles captured in a single funnel trap during a flight season.

Subsequent-year predictions

Stem mortality

Modeling mass-attacked stem counts in the subsequent year relative to trap capture data for 10 ha blocks resulted in a regression tree with two terminal nodes, splitting on SB (xerror = 0.798; Fig 5a). In 1 ha blocks, the tree for subsequent-year mortality also split on SB but at a lower value (xerror = 0.983; Fig 5b). Because the xerror term is relative to a tree with a single terminal node, the 1 ha block model is <2% better than the null model. Note that model fit is reduced relative to models that use current-year mortality.

Spruce beetle population phase

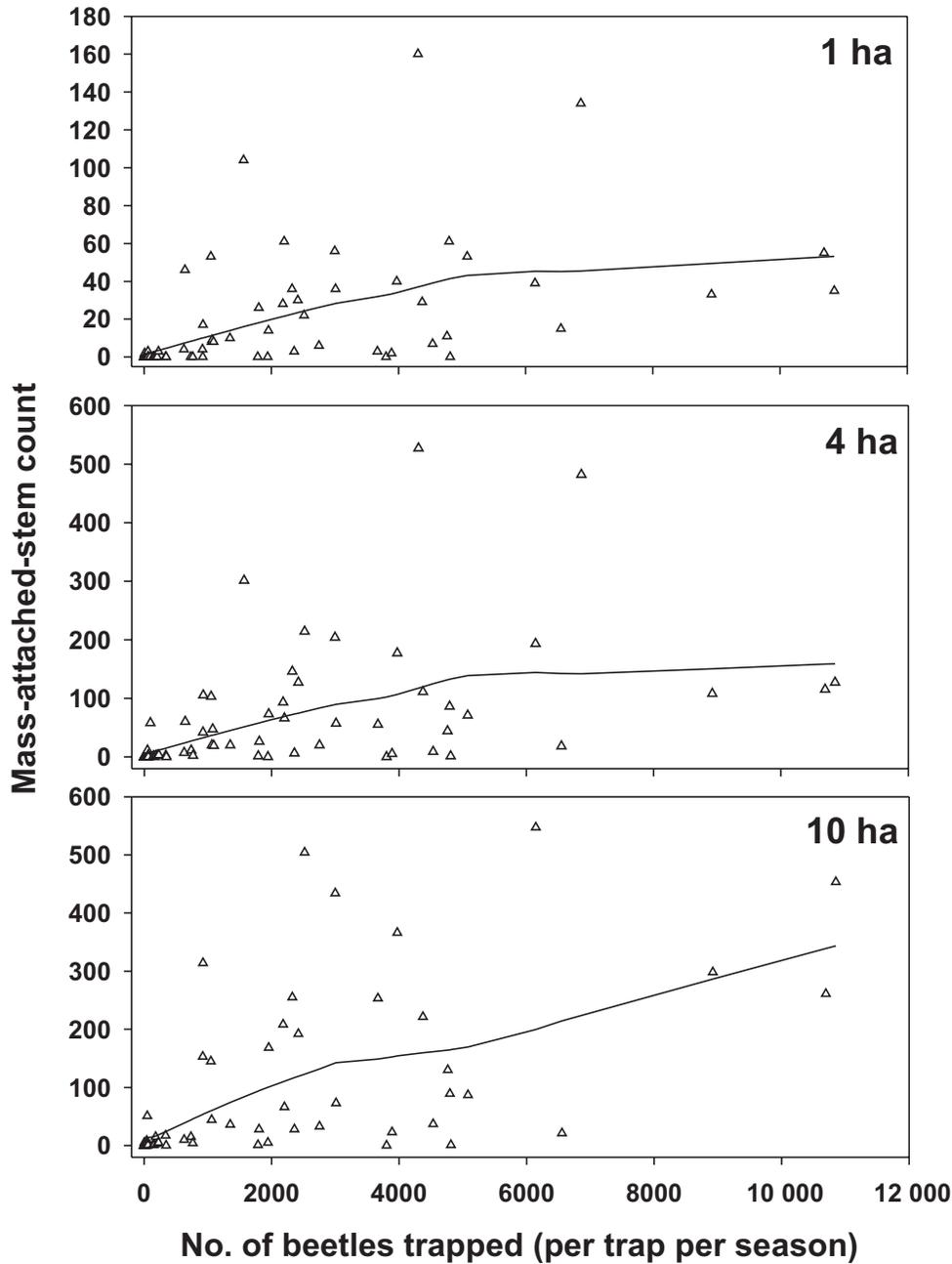
Based on the results of the current-year-model predictions, we only considered two levels of population phase, endemic and epidemic, for modeling subsequent-year spruce beetle population phase using funnel-trap captures. The classification trees for 10 and 1 ha blocks split on SB at the same value as the tree predicting current-year population phase for 10 ha blocks (see Fig. 3a). The model fit for 10 ha blocks (xerror = 0.211; Table 3) is comparable to that for the current-year population phase, but 1 ha blocks had a slightly poorer fit than the current-year population phase for the same-size block (xerror = 0.292; Table 3).

We also considered modeling the spruce beetle population phase 2 years subsequent to the observed trap catch, but lacked observations, given the minimum terminal node size constraints. Nevertheless, exploratory analysis suggested little, if any, improvement in model fit compared with the null model, even when modeling the population phase with two levels. There appears to be little relationship between trap catch and nearby host mortality 2 years subsequent to trap-catch observation.

Trends in mortality and trap captures

Comparing the trends, or ratios, of year-to-year stem mortality and spruce beetle captures in least-squares regression models, a significant positive correlation was detected ($t_1 = 2.50$, $p = 0.0157$, $R_{\text{adj}}^2 = 0.0899$). When the data were analyzed by population phase, the relationship was significant for the endemic phase ($t_1 = 2.12$, $p = 0.0416$, $R_{\text{adj}}^2 = 0.0933$) but not for the epidemic phase ($t_1 = 0.22$, $p = 0.8298$; Fig. 6). The relationship for endemic-phase plots is

Fig. 1. Scatter plots, with lowess-smoothed curves, of current-year mass-attacked spruce stems against funnel-trap captures of beetles in 1, 4, and 10 ha blocks on plots on the Dixie, Fishlake, and Manti-La Sal National Forests, Utah, in 2001–2004. Note that “lowess” is a locally weighted regression wherein each point along the curve is obtained from a regression of data points close to the curve point, with the closest points more heavily weighted (SigmaPlot 2004, Systat Software, Inc., Richmond, California).



$$[3] \quad \text{Log}(\text{stem mortality ratio}_{10 \text{ ha}}) = 0.2878 + 0.4214[\text{log}(\text{beetle capture ratio})]$$

Discussion

Predicting stem mortality

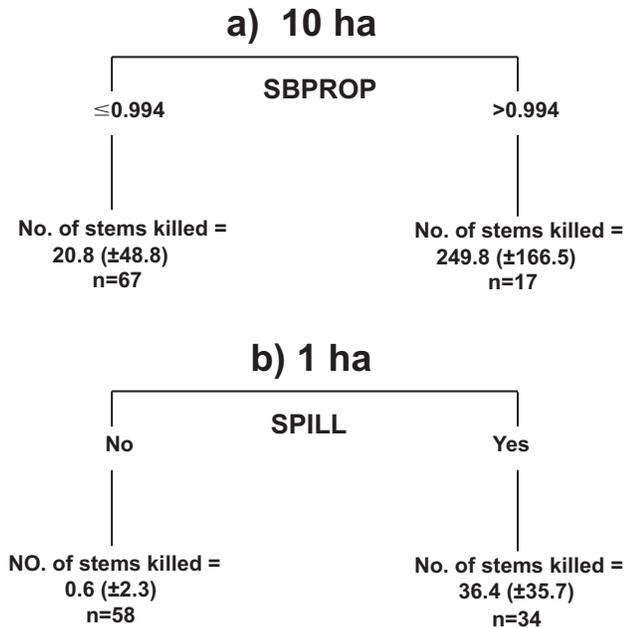
Although we found a significant relationship between spruce beetle trap captures and the number of mass-attacked spruce trees in the vicinity of a funnel trap, the relationship was highly variable. Model fit was relatively poor, explain-

ing about 30%–38% of the variance in the data when current-year mortality was considered. Model fit was even poorer when mortality in the year subsequent to trap deployment was analyzed. Moreover, the error terms, and thus prediction intervals, were so large that predictions were nearly meaningless.

The large variance found among funnel-trap captures and the number of mass-attacked spruce trees is most likely a result of complex interactions between stand structure, weather, topography, and natural sources of primary and secondary attraction (Schmid et al. 1992; Salom and McLean

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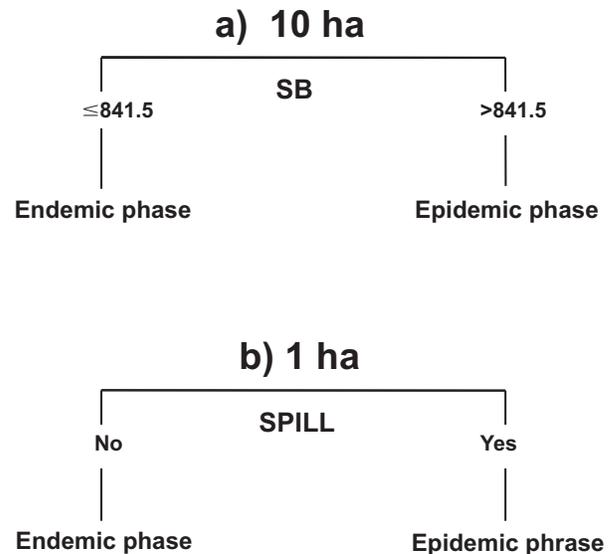
Fig. 2. Regression trees for estimating numbers of current-year mass-attacked Engelmann spruce stems (average \pm SEM) within 10 ha (a) and 1 ha (b) blocks. SBPROP is the ratio of spruce beetles trapped to spruce beetles plus clerids trapped; SPILL is absence/presence of currently infested hosts within 10 m of the funnel trap.



1991; Bentz 2006). We expected to find significant correlations with at least some of the covariates tested, e.g., physiographic class, stand characteristics, or temperature; the lack of correlation may reflect a deficiency of replicates, given the number of possible interactions. The increasing variance in observed stem mortality with increasing funnel-trap captures is similar to results from Weslien (1992), who explored the use of European spruce bark beetle baited drain-pipe captures in Scandinavia to forecast associated Norway spruce mortality along forest edges. Weslien (1992) determined that relatively low captures of European spruce bark beetles were always associated with low host mortality the following year, but higher capture levels were associated with variable amounts of mortality, either high or low. In contrast, however, our data show that relatively high funnel-trap captures are nearly always related to high amounts of mortality, i.e., relative *levels* of mortality are highly predictable even if estimates of infested-stem numbers have large prediction intervals.

Large prediction intervals aside, we found it intriguing that the ratio of spruce beetles trapped to spruce beetles plus clerid beetles trapped (SBPROP) was the best predictor of current-year infested-stem counts in 10 ha blocks. This is similar to results from Billings (1988), where southern pine beetle infestation trends were successfully modeled on the basis of (i) southern pine beetle captures and (ii) the ratio of southern pine beetles to southern pine beetles plus clerid beetles. Billings' (1988) trapping results, however, show a relatively linear relationship between southern pine beetle captures and the proportion of southern pine beetle, whereas the analogous relationship in our data can be described as

Fig. 3. Classification trees for estimating current-year spruce beetle population phases within 10 ha (a) and 1 ha (b) blocks. SB is total seasonal spruce beetle captures; SPILL is absence/presence of currently infested hosts within 10 m of the funnel trap. These trees are representative of results using two levels (endemic phase: < 2 mass-attacked stems/ha; epidemic phase: ≥ 2 mass-attacked stems/ha) or three levels (endemic phase: < 1 mass-attacked stems/ha; building phase: 1–5 mass-attacked stems/ha; epidemic phase: ≥ 5 mass-attacked stems/ha) of population phase. Note that a applies to results from 10 and 1 ha blocks using *subsequent*-year population phase (two levels).



exponential (i.e., low levels of spruce beetle captures were associated with low to high proportions of spruce beetles to spruce plus clerid beetles, SBPROP, but high levels of spruce beetle captures were associated only with high proportions of spruce beetles). Spruce beetles in epidemic areas outnumbered clerid beetles by two or more orders of magnitude. As Furniss and Carolin (1977) noted, the spruce beetle "outruns its natural controls" during outbreaks. In our study, clerid beetles appeared to be less important relative to Billings' (1988) model of the trend in southern pine beetle infestation.

Predicting the spruce beetle population phase

In contrast to our finding that funnel-trap captures cannot be used to accurately predict the number of infested spruce stems, we found that they can be reliably used to predict the spruce beetle population phase, a relative measure of host-tree mortality. Total seasonal spruce beetle captures (SB) was the most important variable in several classification trees, involving current- and subsequent-year population phases as well as the 1 and 10 ha blocks. For several of these models, the threshold distinguishing the endemic (< 2 mass-attacked stems/ha) and epidemic phases (≥ 2 mass-attacked stems/ha) is about 842 beetles captured during a flight season from a single funnel trap. The presence of spillover attacks near a funnel trap also distinguished the epidemic phase, provided that susceptible hosts were within 10 m of the funnel trap. These classification trees fit the data better than the regression trees, explaining 71%–87% of the variance when the response was two levels of population phase. Additionally, the

Table 3. Cross-validation classification probability tables from various classification trees.

Actual population phase	Predicted population phase			No. of observations
	Building	Endemic	Epidemic	
10 ha blocks using three levels of current-year population phase (84 observations)				
Building	0.000	0.636	0.364	11
Endemic	0.000	0.882	0.118	51
Epidemic	0.000	0.182	0.818	22
1 ha blocks using three levels of current-year population phase (92 observations)				
Building	0.000	0.556	0.444	9
Endemic	0.000	1.000	0.000	52
Epidemic	0.000	0.032	0.968	31
10 ha blocks using two levels of current-year population phase (84 observations)				
Endemic	—	0.926	0.074	54
Epidemic	—	0.100	0.900	30
1 ha blocks using two levels of current-year population phase (92 observations)				
Endemic	—	0.982	0.018	55
Epidemic	—	0.108	0.892	37
10 ha blocks using two levels of subsequent-year population phase (57 observations)				
Endemic	—	0.895	0.105	38
Epidemic	—	0.105	0.895	19
1 ha blocks using two levels of subsequent-year population phase (60 observations)				
Endemic	—	0.944	0.056	36
Epidemic	—	0.208	0.792	24

cross-validation tables indicate correct classifications in most cases, generally better than 90%.

Our results suggest that the spruce beetle is generally either in epidemic status, infesting numerous live trees, or endemic status with very few infested stems. This corresponds to our field observations suggesting that currently attacked trees within a spruce stand tend to be either rare or abundant. Based on our collective experience, intermediate or building levels of mortality are not common, and when they are encountered, the local spruce beetle population either builds or collapses within a year or two. Changes in infestation levels better represent a state-change phenomenon than a gradient.

Because we found significant relationships between funnel-trap captures and population phase for 1, 4, and 10 ha blocks, we wondered if areas larger than 10 ha might have similar correlations. Our data cannot, however, be used to determine the scale beyond which the correlation diminishes. We considered using ADS data for classifying the response variable but these data are prone to spatial inaccuracies, and especially, ambiguity in timing of host death (Harris and Dawson 1979). By contrast, our ground surveys are highly accurate, although multiple ground surveys become more impractical to conduct in areas larger than 10 ha.

Some of the most conspicuous misclassifications in our analyses were at sites with relatively high funnel-trap captures and relatively low current-year host mortality. For example, the Huntington Reservoir 2 funnel trap caught 3803 beetles in 2001 and yet no infested spruce stems were found during the fall survey. In this case, spruce beetles were lo-

cally abundant, as evidenced by ADS maps and ground observations, just not within the 10 ha block. Trees began to become infested at this site the following year, with extensive host mortality in 2003. Therefore, very high trap catches (e.g., >2000) almost certainly indicate high host-mortality levels, in either the current or the subsequent year. Another type of outlier is exemplified by the Anderson Meadows 3 site, where, in 2001, 51 stems were mass-attacked within 10 ha of the trap but only 48 spruce beetles were captured that year. In this case, poor trap placement could be a cause of the relatively low captures because the trap was placed away from contiguous spruce and in an area of aspen/spruce/fir mix, with very few large-diameter spruce (>40 cm DBH) within 50 m of the trap. The semiochemical diversity resulting from the mixed stand may have reduced local bark beetle abundance because of non-host-tree olfactory cues (Zhang and Schlyter 2004).

Trends in mortality and trap captures

Year-to-year trends in stem mortality rates and funnel-trap captures, like those in mass-attack-stem counts, were significantly related, yet highly variable. Among endemic-phase plots, an increasing trend in spruce beetle captures was correlated with an increasing trend in spruce mortality surrounding the funnel trap, although the opposite trend was also observed. Conversely, no significant correlation was detected between funnel trap capture trends and mortality trends among epidemic-phase plots. Funnel-trap captures are therefore not a precise predictor of the trend in the number of

Fig. 4. Spruce beetle captures by population phase, classified using the number of mass-attacked stems (current year) within 10 ha blocks ($n = 11$ for the endemic phase (<1 infested stems/ha); $n = 51$ for the building phase (1–5 infested stems/ha); $n = 22$ for the epidemic phase (>5 infested stems/ha). Values are shown as the median (solid line within the 25th/75th percentile box), 10th/90th percentiles (whiskers), and outliers.

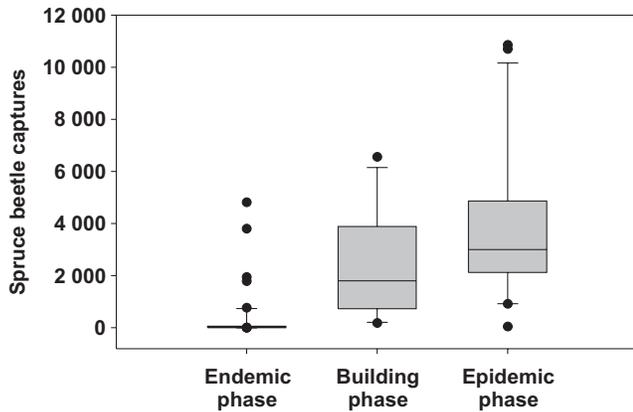
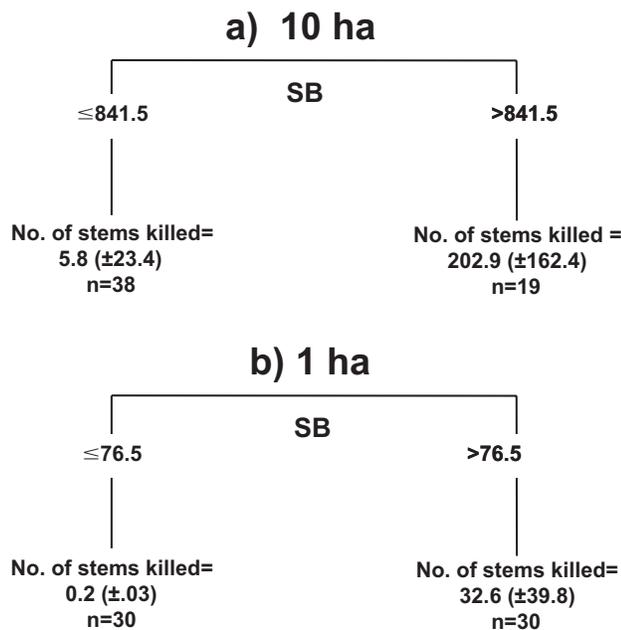


Fig. 5. Regression trees for estimating numbers of subsequent-year mass-attacked Engelmann spruce (average \pm SEM) within 10 ha (a) and 1 ha (b) blocks. SB is total seasonal spruce beetle captures.

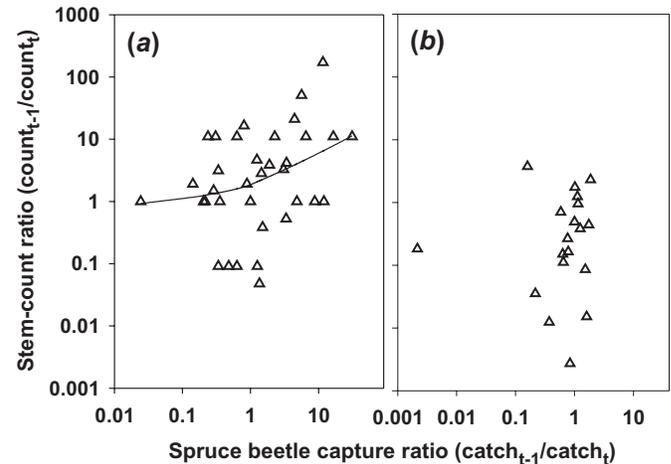


mass-attacked spruce trees in the vicinity of the trap. This is especially true when populations are at epidemic levels.

Applications

Managers have previously deployed funnel traps in spruce systems to detect spruce beetles or monitor their flight periodicity. Our results indicate that spruce beetle population phase can also be inferred from trap-catch information and used as a relative measure of host-tree mortality. Because spruce beetles respond well to the two-component lure in Utah, Colorado, and Wyoming (Hansen et al. 2006), we believe that our results can be applied to Engelmann spruce

Fig. 6. Year-to-year trends (ratios) of spruce mortality plotted against year-to-year trends in spruce beetle captures by population phase, where t is the survey year (stem counts are from 10 ha blocks). Least-squares regressions showed significant relationships for the endemic phase (a) (shown with lowess-smoothed curve) but not for the epidemic phase alone (b). Note that both axes are in log scale.



systems throughout the central and southern Rocky Mountains. Assuming the use of equivalent traps and lures, managers and entomologists can use our results as a guide for predicting the relative severity of spruce mortality for a given level of spruce captures. For example, a capture total of 200 spruce beetles without spillover into nearby trees suggests the endemic phase (i.e., few, if any, trees within 10 ha will be infested in the current or subsequent year), whereas capture of 1000 spruce beetles or spillover near the trap suggests the epidemic phase in the subsequent, if not the current, year (i.e., substantial host mortality within a 10 ha area). For managers to use the rules developed herein, trap deployments should follow our protocols. To reduce the likelihood of misclassifying population phase over the landscape of interest, we recommend multiple deployments of single funnel traps. Funnel traps should be spaced at least 800 m apart, placed within spruce stands but away from susceptible material, and suspended with the trap cup about 1.5 m above ground level. Managers should be prepared for the possibility of spillover (Borden 1989). A final caveat is that spruce beetles in Alaska, British Columbia, and Alberta have been shown to respond differentially to synthetic-lure combinations (Borden et al. 1996). Thus, our results will need to be verified or recalibrated for other regions or for other lure/trap types. These results will allow managers to extract additional information from routinely deployed funnel traps. Predictions of relative mortality levels will aid forest planning, inform suppression actions, and allow silvicultural treatments to be prioritized.

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