Timber harvest interacts with broad-scale forest mortality to affect site occupancy dynamics of a vertebrate seed predator

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ABSTRACT

Extensive ecological disturbances can interact with spatial heterogeneity produced by previous disturbances, influencing responses of vertebrates to environmental change. Recent and ongoing outbreaks of bark beetles (including *Dendroctonus* spp. and *Dryocoetes confusus)* in the Rocky Mountains produced an opportunity to investigate effects of broad-scale tree mortality on an important seed predator in Nearctic coniferous forests, the red squirrel (*Tamiasciurus hudsonicus*), and to evaluate whether those effects interact with forest heterogeneity produced by previous timber harvest. Our study characterized site occupancy dynamics for red squirrels in relation to patch-cutting, a type of group-selection cut, and the bark-beetle outbreak, and evaluated whether patch cutting influenced subsequent effects of bark beetles on these squirrels. We used multi-season occupancy models and covariates for harvest- and outbreak-related habitat characteristics to describe extinction and colonization rates of red squirrels over a 27-yr period in Wyoming, USA. We observed effects of year, patch-cutting, and the bark beetle outbreak on the probability of detecting a red squirrel. We observed a negative association between local extinction rate and increasing snag density, but only to a threshold of 5 snags/0.04 ha. Local colonization rate was positively associated with the basal area of live trees. Annual site occupancy varied across years (range pre-harvest: 0.76–0.89; post-harvest: 0.84–0.99), and was lowest (0.70–0.72) during the two years sampling occurred approximately 14 years after the bark beetle outbreaks began. Tree mortality was lowest near patch cuts; this pattern was especially pronounced for mature trees (>30 cm diameter at breast height), which tend to produce the most cones and would likely contribute the most to red squirrel survival. Strong habitat effects on occupancy dynamics suggest that previously-harvested areas may provide refugia for red squirrels in post-outbreak forests. Our results support managing for uneven-aged stands of mixed species composition in subalpine forests of the Rocky Mountains.

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1. Introduction

Many ecological processes respond to spatial heterogeneity (Pickett and Cadenasso, 1995). Heterogeneity is at least partly due to disturbance history; multiple disturbance types (e.g., fire and insect outbreak) interact with each other and abiotic factors to produce landscape mosaics (Veblen et al., 1994). Spatial patterns produced by previous disturbances can influence the response of a system to subsequent ones, but the direction and magnitude of these effects are unclear from scarce empirical evidence (Turner, 2010).

Broad-scale, severe disturbances are common in subalpine forests of the Rocky Mountains, and interactions among disturbances of several types are well-documented in this system (Veblen et al., 1994; Bigler et al., 2005). Recently, coniferous forests in western North America have experienced large-scale mortality caused by synchronized extensive outbreaks of several species of bark beetle (Raffa et al., 2008; Bentz et al., 2010). High mortality has affected millions of hectares (Meddens et al., 2012). Because bark beetle behavior and demography are related to, among other factors, structure and composition of forests (Fettig et al., 2007), beetle-caused mortality has the potential to interact with previous timber harvest. The severity of forest insect outbreaks might be moderated by some timber harvest regimes if they reduce tree density, release trees from competition, or result in younger stands (Fettig et al., 2007; 2014). However, the efficacy of tree harvest as a

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means to reduce beetle-caused mortality has also been disputed (Six et al., 2014).

We have some knowledge of how various disturbances interact to influence vegetation patterns, but, seldom know the consequences for higher trophic levels. For consumers such as mammals, this knowledge gap is significant because some of them perform important ecological functions. The red squirrel (Tamiasciurus hudsonicus) is a coniferous-forest obligate that reaches densities of up to 6.0 individuals/ha (Rusch and Reeder, 1978), and typically associates with mature, seed-producing trees. The species is considered a keystone taxon in Rocky Mountain forests (Pearson and Ruggiero, 2001; Smith et al., 2003), because of its roles as ecological engineer, predator, and prey. Red squirrel consumption of tree buds, young tree stems, and seeds significantly influences lodgepole pine (Pinus contorta) reproduction and rates of stand-level cone serotiny (Benkman and Siepielski, 2004; Talluto and Benkman, 2013). Further, predation of bird nests by red squirrels is believed to influence canopy-nesting bird communities in conifer forests (Siepielski, 2006). Red squirrels are prey for the Northern Goshawk (Accipiter gentilis; Squires, 2000), martens (Martes spp.; Buskirk and MacDonald, 1984), Canada lynx (Lynx canadensis; Koehler and Aubry, 1994), and the Great Gray Owl (Strix nebulosa; Schauffert et al., 2002). Squirrel food caches and associated deposits of cone bracts, called middens, are exploited by various mammals, including bears (Mattson and Reinhardt, 1997), other small mammals and martens (Pearson and Ruggiero, 2001). Thus, many of the features of late-successional Rocky Mountain subalpine forests, from perspectives of conifer life history and wildlife habitat, are mediated over ecological and evolutionary time scales by red squirrels.

Here, we report site-occupancy dynamics in relation to forest stand characteristics for a population of red squirrels in south-central Wyoming, USA. Changes in vital rates of red squirrel populations can be indicated by local extinction and colonization events, two of the mechanisms by which species respond to disturbance (Hansen et al., 2001). The bark beetle outbreak allowed us to evaluate effects of tree mortality on red squirrel site occupancy, and to determine whether site occupancy dynamics differed between sites with vs. without previous timber harvest. We expected altered forest characteristics resulting from timber harvest and bark beetle outbreaks to influence the abundance and distribution of red squirrels. We predicted that a harvested watershed would show reduced red squirrel occupancy in the three years of study following cutting because of the removal of cone-producing trees and destruction of middens. Because beetle kill is concentrated in large-diameter conifers, we expected that regenerating lodgepole pine would not be killed outright by beetles, and that any indirect effect of beetles on red squirrels in the harvested watershed would be mitigated by changes in habitat due to timber harvest. Density of snags, basal area of live trees, and canopy cover might predict the occurrence of red squirrels; we tested the predictive power of these habitat variables.

2. Materials and methods

2.1. Study site

Beginning around 1996, populations of multiple species of bark beetle erupted in Colorado and Wyoming (Harris et al., 2001). Since around 2005, beetle populations have been at epidemic levels in most conifer forests of Wyoming. By 2012, over 17,000 km^2 of pine (Pinus spp.) − dominated forests in the region had been affected, and mortality rates approach 100% for lodgepole pine and Engelmann spruce > 30 cm in diameter at breast height (dbh) in forests of south-central Wyoming (Harris, 2013; see Johnson et al., 2014 for details regarding the outbreak). This outbreak affected an historical study site (Coon Creek) where timber harvest and its effects

on vertebrates were studied during 1985–96. The data from before and after cutting—but before the beetle outbreak—provided an opportunity to evaluate possible interactions between beetle-caused tree mortality and previous timber harvest, along with the demographic response of an ecologically important vertebrate that is closely associated with large-diameter conifers.

We previously reported that large diameter (>50-cm-dbh) lodgepole pine (Pinus contorta) and Engelmann spruce (Picea engelmannii) located near areas harvested 15–20 years earlier had higher probabilities of survival after the bark-beetle outbreak than farther from harvested patches. However, in areas at least 15 m away from areas previously harvested, mortality was higher for lodgepole pine in smaller size classes, suggesting that landscape pattern created by pre-outbreak harvest and its effects on stand structure may influence bark beetle activity (Johnson et al., 2014).

Red squirrel populations were sampled in two adjacent watersheds in the Sierra Madre Mountains of south-central Wyoming (Fig. 1). Elevations of both watersheds range from 2682 to 3322 m. Mean annual precipitation was 87 cm, 70% of which fell as snow (Troendle et al., 2001). Snow cover typically lasted from late September to late June. At the beginning of the study, forest cover was 60% lodgepole pine; the other 40% was mixed Engelmann spruce and subalpine fir (Abies lasiocarpa). Seventy percent of the forest was characterized as mature in 1985 (Raphael, 1988).

2.2. Sampling design

The two watersheds studied were the upper East Fork of the Encampment River (East Fork; 908 ha) and Coon Creek (1673 ha; Fig. 1). These watersheds were the site of an experiment during 1985–1996 designed to evaluate whether patch-cutting, a type of group selection cut, could increase water yield at the watershed scale (Troendle et al., 2001). Coon Creek, the harvested watershed, received 240 patch cuts (mean area: 1.5 ha; range: 0.1–7.0 ha). A 985-ha area was designated as the portion to be sampled to evaluate wildlife and vegetation responses; this area received 155 patch cuts and a system of access roads (total length = 31.5 km in sampling area, 44.1 km on entire watershed; Fig. 1). The pre-harvest period was 1985–90, harvest occurred from 1990–92, and the post-harvest period was 1993–96. East Fork, the control
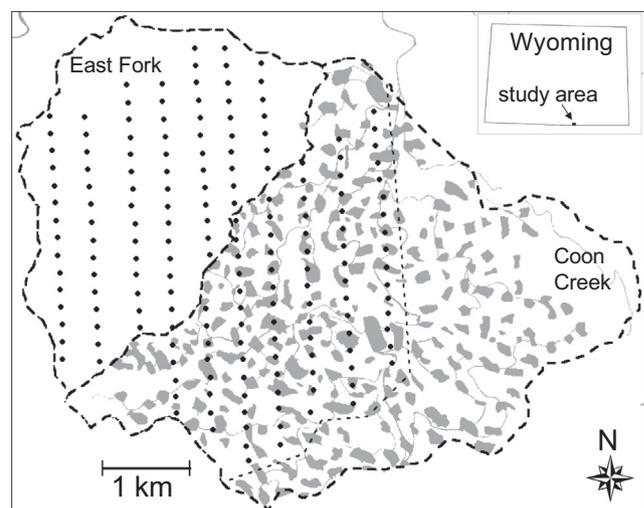

Fig. 1. Boundaries (thick dashed line) for control (East Fork) and harvested (Coon Creek) watersheds in south-central Wyoming, USA. The thin dashed line delineates the portion of Coon Creek used to evaluate squirrel responses to patch-cutting. Gray areas indicate patch cuts and roads. Black dots represent location of sampling points (n = 180), which are 200 m apart on the north–south axis and 400 m apart on the east–west axis.

watershed, remained uncut and free of roads (Fig. 1). The areas compared between the two watersheds were similar in basal area for each cover type, canopy cover, tree height, and old-growth score at the beginning of the study (Raphael, 1987). About 3.2% of the areas of both watersheds were natural openings; after harvest, 23% of the harvested watershed (22% of the sampled area) was in patch cuts. Cover types were cut in proportions similar to those available (χ^2 Goodness of fit = 5.2, d.f. = 4, P = 0.26), and 70% of the patch cuts occurred in areas dominated by lodgepole pine where mean dbh > 41 cm (USFS, E. O'Doherty, unpublished data). Within patch cuts, most trees > 15 cm were removed, but some advanced regeneration was retained, resulting in post cutting densities < 10 trees/ha (Hayward et al., 1999).

2.3. Site occupancy sampling

The sampling units for occupancy modeling were permanent points sampled repeatedly for red squirrels during 1985–1996, then in 2011–2012. In each watershed, 90 permanent sampling points were established in 1985 prior to harvesting. Sampling points were established using systematic 200-m spacing from a random start. Points were fixed along transect lines that ran north–south and were 400 m apart (Fig. 1). The roughly circular territorial home ranges of red squirrels have been reported to be 0.24–0.98 ha in area (Steele, 1998). Red squirrels were sampled during 5–6 standardized point count surveys conducted each summer from mid-June to late July. During each survey, an observer walked to the sampling point, waited silently for 1 min, then recorded the number of red squirrels seen or heard within 100 m of the point during a 10-min period. Surveys began within 30 min of dawn and were completed before 11:00 MST.

2.4. Habitat sampling

Vegetation surveys were conducted in 1985 (pre-harvest), 1992 (post-harvest), 2011, and 2012 (both years representing post-out-break conditions) at the same permanent sampling points where red squirrels were surveyed. Observers measured a distance of 11.3 m and 15 m from each point in four cardinal directions and marked the boundaries of the nested circular plots with survey flags. In the harvested watershed observers recorded whether any part of the 15-m-radius plot fell within a patch cut; if so, the plot was designated a "cut" plot; if not the plot was designated as "uncut". Part of the plots designated as "cut" often included portions that were not cut, but lie adjacent to a cut. Thus, we also quantified habitat characteristics (snag density, basal area, and canopy cover) to describe each plot using continuous variables. All plots within the control watershed were designated as "control" plots. All vegetation data were collected within the boundaries of the 11.3-m-radius (0.04-ha) plot (Fig. 1).

To estimate snag density, observers counted all dead trees ⩾20 cm dbh and ⩾1.8 m tall. Trees were considered dead if <50% of needles were green and the tree was in any stage of decomposition but still standing. Stand basal area was estimated separately for live and dead trees of each species using a wedge prism relascope and a basal area factor of 10. Canopy cover was measured by taking the average of four readings (one in each cardinal direction) at the boundary of each plot using a spherical densiometer.

2.5. Statistical analysis

From our multiple surveys within each year, we created encounter histories for red squirrels at each sampling point during the study period. Each encounter history represented detections during 83 visits to each of 180 sampling points (sites) during the entire sampling period. We tested for effects of attributes associated with timber harvest and beetle-kill on site occupancy dynamics by estimating extinction and colonization as a function of timber harvest (control, uncut, and cut), time, and habitat covariates.

We modeled site occupancy using multiple-season probabilistic models developed by MacKenzie et al. (2003, 2006). These models use maximum likelihood estimation to estimate probability of site occupancy when detection probabilities are <1, and allow incorporation of effects of time, group, and habitat variables (MacKenzie et al., 2002). Our study included 14 years and 5–6 visits within each year. Sites were assumed open to changes in occupancy status among years, but closed to changes among visits within a year. Lack of closure among visits within a year was possible; however, red squirrels are territorial throughout the year and do not hibernate, so individuals present should have been available for detection during all surveys within a year. Using these models, we estimated the probability of site occupancy (ψ_1) for the initial year, extinction probability (ε) and colonization probability (γ) for each interval between year i and year $i + 1$ (i.e., conditional on status in year i), corrected for the probability of detection (ρ_{tj}) given presence in each survey (j) within a year (t). Estimates of annual site occupancy were derived using the following equation from MacKenzie et al. (2003):

$$\hat{\psi}_t = \hat{\psi}_{t-1}(1 - \hat{\varepsilon}_{t-1}) + (1 - \hat{\psi}_{t-1})\hat{\gamma}_{t-1}.$$

We used a multi-stage approach to model site occupancy of red squirrels, similar to that of Olson et al. (2005) and Dugger et al. (2011). First, we modeled detection probability by evaluating constant, annual, and timber harvest effects. During this stage of modeling, we held site occupancy, extinction, and colonization in their fully-parameterized forms (time × plot type [control, cut, or uncut]) to account for maximum variation not associated with detection probability. We included models where detection probability varied before and after timber harvest at sampling points where cutting did and did not occur, and before and after the bark beetle epidemic. Once the best structure for ρ_{tj} was identified, it was retained and used for the remainder of the modeling process. We then evaluated time and timber harvest effects on extinction and colonization probabilities. Exploratory data analysis suggested initial site occupancy was similar among control, cut, and uncut sites; thus, we held site occupancy constant during the second stage of modeling. The best model from this stage was retained for the final stage, where habitat covariates were added to test for effects of snag density, live basal area, and canopy cover. Candidate models that included habitat covariates were based on predicted relationships between habitat variables and red squirrel occupancy informed from relationships reported in the peer-reviewed literature (Koprowski, 2005; Zugmeyer and Koprowski, 2009; Patterson and Malcolm, 2010). Threshold responses to covariates were identified by first evaluating the range of observed values for a particular covariate, and then examining responses over that range. Cut points were then chosen that corresponded to nonlinearities in the responses. For example, the range of values for snags for all plots was 0–23, and we tested for thresholds at values of 5 and 15; the range of values for live basal area was 0–62, and we tested for thresholds at 10, 20 and 40. All models were executed using Program MARK (White and Burnham, 1999). We used Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) for model selection at each stage of the modeling process (Burnham and Anderson, 2002). Whether 95% confidence intervals for slope coefficients overlapped zero was considered when evaluating the importance of variables in competing models (<2 AIC$_c$). All parameter estimates are presented as mean ± 1 standard error.

3. Results

3.1. Habitat characteristics

We reported earlier (Johnson et al., 2014) that timber harvest and bark beetle activity substantially altered forest characteristics, potentially affecting habitat for red squirrels. Timber harvest reduced canopy cover by 65.4 ± 3.0% at cut plots; however, from post-harvest to post-outbreak, canopy cover at cut plots recovered, increasing by 65.8 ± 2.3%. Canopy cover increased over the entire study period (pre-harvest to post-outbreak) in control plots (by 21.5 ± 2.3%) and uncut plots in the harvested watershed (by 17.7 ± 3.0%). Harvest did not affect snag density (for all tree species combined), but bark beetle activity increased density of snags from a mean of 2.0 snags/0.04 ha pre-harvest to a mean of 7.5 snags/ 0.04 ha post-outbreak at control plots and from 1.9 snags/0.04 ha to 8.4 snags/0.04 ha at uncut plots in the harvested watershed. Snag density was not substantially changed at cut plots in the harvested watershed, and was estimated at 1.9 snags/0.04 ha pre-harvest and 0.9 snags/0.04 ha post-outbreak. The beetle outbreak resulted in high mortality of lodgepole pine and Engelmann spruce, and moderate mortality of subalpine fir (Johnson et al., 2014). The total amount of live basal area (TLBA: all three conifer species) was similar before and after harvest in the control watershed, and at points that were not cut in the harvested watershed. At points that were cut, TLBA decreased from 30.1 ± 1.4 to 14.4 ± 2.1 m²/ha from pre-harvest to post-harvest. After the outbreak, TLBA was reduced to <10 m²/ha for control, cut, and uncut points (Fig. 2).

3.2. Red squirrel detection probabilities

Over 14 years, we detected red squirrels on 8901 occasions (59.6% of all visits to all sampling points). Of those, 3708 (41.7%) occurred in the harvested watershed and 5193 (58.3%) in the control. In the harvested watershed, mean number of detections per year pre-harvest was 183.4 ± 29.1, post-harvest was 372.9 ± 70.7, and post-outbreak was 90.5 ± 33.5. In the control watershed, mean number of detections across all sampling points per year pre-harvest was 233.4 ± 24.6, post-harvest was 549.4 ± 78.8, and post-outbreak was 90.0 ± 42.0. Probability of detection varied among control, cut, and uncut points and years (see Table S1 in Supporting
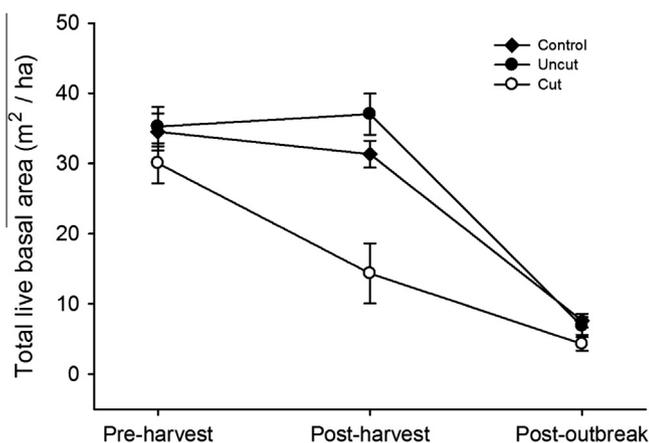
Information), but was consistently < 0.8 (see Fig. S1 in Supporting Information). There was strong support for variation in detection probabilities among years and among control, cut, and uncut points (w_i = 1.0). In the control watershed, detection probabilities ranged from 0.15 ± 0.03 to 0.75 ± 0.02 and were highest during post-harvest years and lowest during post-outbreak years. In the harvested watershed, detection probabilities at plots that were cut ranged from 0.19 ± 0.03 to 0.62 ± 0.03 and were highest during post-harvest years and lowest during a pre-harvest year although there was considerable overlap in confidence intervals with post-harvest and post-outbreak years. Similarly, detection probabilities at uncut plots in the harvested watershed ranged from 0.13 ± 0.03 to 0.66 ± 0.03 and were highest during post-harvest years and lowest during a pre-harvest year, but confidence intervals overlapped with post-outbreak years (Fig. S1).

3.3. Occupancy parameters

3.3.1. Harvest and time effects

We found support for an effect of year on extinction and colonization rates of red squirrels; the effect was similar across control, cut, and uncut plots. Our top model garnered strong support as it accounted for 89% of AIC$_c$ weight (Table 1) and was eight times more likely than the second-best model.

3.3.2. Habitat correlates

Snag density most strongly affected extinction probabilities for red squirrels, and the relationship included a threshold effect of snag density values (Table 2). This effect was well-supported inasmuch as all five best models included a threshold effect of snag density (Table 2). Extinction probabilities decreased with increasing snag density at the 0.04-ha scale, but only until density reached 5 snags/0.04 ha (β = −0.22 ± 0.06, 95% CI = −0.33 to −0.11; Table 2, Fig. 3). Live basal area most strongly affected colonization probabilities, and an effect of live basal area was included in three of four best models (Table 2). Colonization probabilities increased with increasing live basal area (β = 0.03 ± 0.02, 0.001–0.06; Fig. 4). This model had an AIC$_c$ weight of 0.55 and was almost 3 times more likely than the second-best model. The latter model (<2 delta AIC$_c$) did not include an effect of any habitat covariate on colonization probabilities (Table 2). Extinction and colonization probability as well as habitat covariate values varied widely from before to after the beetle outbreak; thus, we present the two time periods separately. Mean annual site occupancy was generally high before the beetle outbreak, but was highest during and immediately after patch-cutting occurred in the harvested watershed (Fig. 5). During two years after the beetle outbreak, site occupancy was lower and more variable (Fig. 5).

4. Discussion

Our retrospective study took advantage of a natural experiment: a broad-scale bark beetle epidemic that began after timber harvest and continues in the Rocky Mountains in 2015. The strong, positive effect of live basal area on colonization rates suggests that broad-scale tree mortality interacts with previous timber harvest— in our case patch-cutting—to influence site occupancy dynamics for an important vertebrate interactor, the red squirrel. Large (>30-cm-dbh) trees, which typically produce the most cones, near (≤15 m) patch cuts had higher probabilities of surviving the beetle outbreak than similarly-sized trees farther from patch cuts (Johnson et al., 2014). Regeneration within patch cuts generally resulted in smaller trees than the size class typically preferred by bark beetles, and mortality in these young patch cut plots was lower than at uncut plots in the harvested and control watersheds

Fig. 2. Changes in live basal area for lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) combined at two watersheds in south-central Wyoming, USA. Data were collected before (pre-harvest: 1985) and after patch-cutting (post-harvest: 1992) occurred in the harvested watershed, and after outbreaks of bark beetles in the Rocky Mountains (post-outbreak: 2011). Sampling points in the harvested watershed that fell between patch cuts are labeled "uncut", and points that fell within 15 m of a patch cut are labeled "cut".

Table 1

Model selection results for models relating year, patch-cutting, and bark beetle activity to extinction (ε) and colonization (γ) probabilities for red squirrels in south-central Wyoming, USA (1985–1996, 2011–2012; K = number of parameters and w = Akaike weight). Year, cutting, and beetle effects were added to a base model that included a constant probability of initial site occupancy [$\psi(.)$] and the best detection probability structure [p (trt × yr)].

ε[a]	γ[a]	ΔAIC_c[b]	K	w	Deviance
yr	yr	0.00	69	0.89	17155.10
yr(beetle.)	yr*harv (beetle.)	4.26	72	0.11	17153.01
yr*harv(beetle)	yr*harv(beetle)	10.04	77	0.01	17148.17
yr(beetle.)	yr*harv + beetle	10.94	73	0.00	17157.57
yr*harv(cut = uncut)	yr*harv(cut = uncut)	17.88	87	0.00	17134.63
yr*harv(uncut = control)	yr*harv(uncut = control)	28.14	95	0.00	17127.66
yr*post-harv	yr*post-harv	28.33	97	0.00	17123.52
yr*harv(pre-1990.: cut = uncut)	yr*harv(pre-1990.: cut = uncut)	33.10	79	0.00	17166.96
yr*harv(pre-1990.)	yr*harv(pre-1990.)	33.65	77	0.00	17171.77
yr*harv(pre-1992.:beetle.)	yr*harv(pre-1992.:beetle.)	39.44	69	0.00	17194.54
yr*harv(pre-1992.)	yr*harv(pre-1992.)	46.87	75	0.00	17189.25
year*harv	year*harv	55.50	119	0.00	17102.64

[a] yr = year-specific variation; harv = variation among control, cut, and uncut plots; beetle = effect of beetle kill differed among control, cut, and uncut plots; beetle. = effect of beetle kill was similar between 2011 and 2012; post-harv = cutting effect only after 1990; pre-1990 cut = uncut = control; pre-1990. = constant before 1990 (beginning of harvest), yr*harv effects after 1990; pre-1992. = constant before 1992 (end of harvest), yr*harv effects after 1992.

[b] Minimum AIC_c = 17297.04.

Table 2

Model selection results for models relating habitat characteristics to extinction (ε) and colonization (γ) probabilities of red squirrels in south-central Wyoming, USA (1985–1996, 2011–2012; K = number of parameters and w = Akaike weight). Habitat characteristics were added to a base model containing year effects on extinction and colonization rates, constant probabilities of initial site occupancy [$\psi(.)$] and the best detection probability structure [p (trt × yr)].

ε[a]	γ[a]	ΔAIC_c[b]	K	w	Deviance
yr + snag(T_5)	yr + liveBA	0.00	83	0.55	16988.20
yr + snag(T_5)	yr	1.99	82	0.20	16992.33
yr + snag(T_5)	yr + liveBA(T_{20})	3.46	83	0.10	16991.66
yr + snag(T_5)	yr + liveBA(T_{10})	3.95	83	0.08	16992.15
yr + snag(T_5)	yr + canopy cover	4.03	83	0.07	16992.23
yr + snag(T_{15})	yr + liveBA	13.07	83	0.00	17001.27
yr	yr + liveBA	13.74	82	0.00	17004.08
yr + liveBA(T_{20})	yr + liveBA	15.43	83	0.00	17003.63
yr + snag	yr	15.48	82	0.00	17005.82
yr + snag^2	yr + liveBA	15.69	83	0.00	17003.89
yr + liveBA(T_{20})	yr	17.67	82	0.00	17008.01
yr + liveBA	yr	18.30	82	0.00	17008.64
yr	yr + canopy cover	18.33	82	0.00	17008.67
yr + liveBA(T_{40})	yr	18.34	82	0.00	17008.68
yr + canopy cover	yr	18.35	82	0.00	17008.69
yr	yr + snag	18.40	82	0.00	17008.73

[a] yr = year-specific variation; snag = total (all tree species) density of snags $\geqslant$ 20 cm dbh and 1.8 m tall; liveBA = total (all tree species) amount of live basal area (expressed as m^2 per 0.04 ha); (T_i) = minimum threshold values for the preceding habitat covariate.

[b] Minimum AIC_c = 17159.92.

Fig. 3. Mean probability of local extinction (ε) of red squirrels as a function of snag density during 1985–1996 (before a bark beetle outbreak) and 2011–2012 (after the bark beetle outbreak) at 90 sampling points in each of two watersheds in south-central Wyoming, USA. Snag density at the study site ranged from 0–11 snags/0.04 ha before the outbreak and from 0–23 snags/0.04 ha after the outbreak. Estimates were generated from the best model [$\psi(.)$, ε(yr + snagT_5), γ(yr + liveBA), p(trt × yr)]. See Tables 1 and 2 for abbreviations.

(Johnson et al., 2014). Areas near patch cuts thus had a higher probability of extinction (due to removal of snags) and lower probability of colonization (due to decreased live basal area) shortly after cutting, but regeneration within patch cuts appeared to serve as refugia after the beetle outbreak began.

Estimates of detection probability varied strongly across time and control, cut, and uncut plots—from 0.13 to 0.75—showing that detection probability should be considered when inferring abundance of red squirrels. The probability of detection generally increased across both watersheds after harvest, and may have been caused simply by increased activity of individuals displaced from patch-cut areas prospecting for new territories. However, plots that were cut tended to have lower detection rates than control plots until the post-outbreak time period. Similarity in detection probabilities among control, cut, and uncut plots after the bark beetle outbreak suggests that tree mortality swamped any effects of previous harvesting and had a homogenizing and depressing effect on detection probability. Many factors may influence
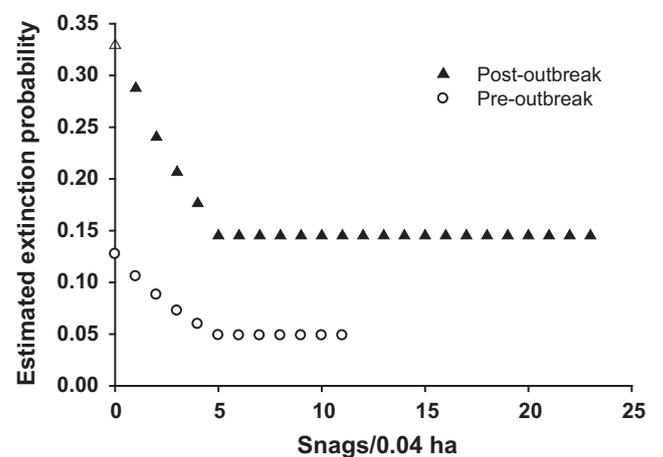
detection probability, including abundance, observer attributes, and vegetation. Further, red squirrels adjust their behavior in response to local population density, vocalizing less frequently at low densities (Dantzer et al., 2012). Most (79%) detections were by call, suggesting that decreased detection probabilities could be related to decreased population density. A similar pattern of decreased detection probability after beetle outbreak was reported in Montana (Mosher, 2011), and decreased detection during the post-outbreak time period could reflect decreased abundance even without large changes in occupancy (Royle and Nichols, 2003).

The absence of an effect of patch-cutting on site occupancy dynamics was unexpected, given previously documented responses by red squirrels. Koprowski (2005) reported reductions in red squirrel density in both clear-cuts and areas thinned to densities of 500–2304 stems/ha, although density may remain high in residual corridors between cuts. Comparing these results to those from the stage of our analysis with habitat covariates suggests our group classification (i.e. whether any part of the 0.04-ha plot was affected by patch-cutting resulting in a "cut" categorization) did not effectively characterize effects of timber harvest. Plots classified as "cut" were in some cases dominated by uncut habitat,
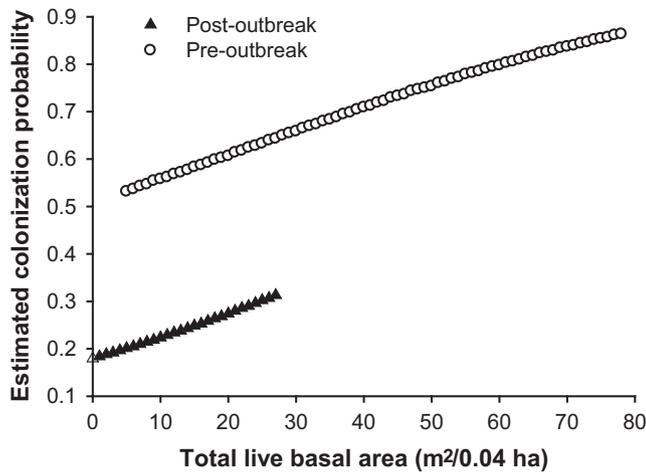
Fig. 4. Mean probability of local colonization (γ) of red squirrels as a function of total (lodgepole pine + Engelmann spruce + subalpine fir) live basal area during 1985–1996 (before a bark beetle outbreak) and 2011–2012 (after the bark beetle outbreak) at 90 sampling points in each of two watersheds in south-central Wyoming, USA. Total live basal area at the study site ranged from 0 to 79 m²/0.04 ha before the outbreak and from 0–27 m²/0.04 ha after the outbreak. Estimates were generated from the best model [$\psi(.)$, $\varepsilon(\text{yr} + \text{snagT}_5)$, $\gamma(\text{yr} + \text{liveBA})$, $p(\text{trt} \times \text{yr})$]. See Tables 1 and 2 for abbreviations.
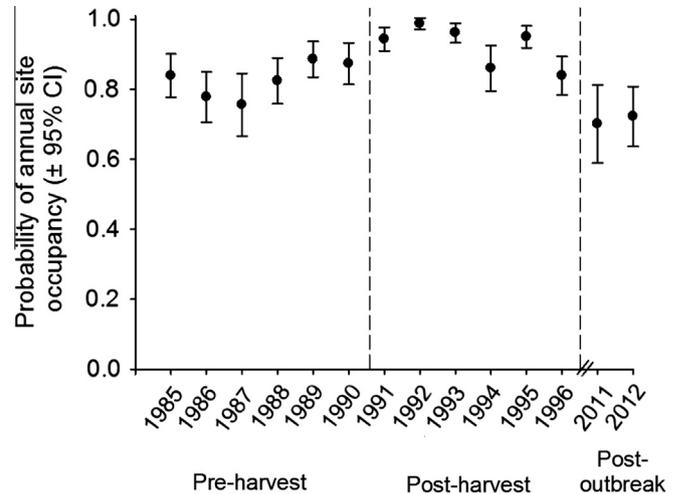

Fig. 5. Estimates of mean annual site occupancy of red squirrels at 180 sampling points in two watersheds in south-central Wyoming, USA before (pre-harvest) and after (post-harvest) patch-cutting in the harvested watershed, and after a broad-scale bark beetle outbreak (post-outbreak) in both watersheds. Estimates incorporate habitat characteristics specific to each sampling point using initial occupancy, extinction, and colonization probabilities from the best model [$\psi(.)$, $\varepsilon(\text{yr} + \text{snagT}_5)$, $\gamma(\text{yr} + \text{liveBA})$, $p(\text{trt} \times \text{yr})$]. See Tables 1 and 2 for abbreviations.

and the proportion of plots directly affected by cutting varied widely. So, while we did not detect a categorical effect using group classifications of "cut" – "uncut", we did observe large and significant effects of the specific structural attributes associated with cutting and beetles and our habitat covariates ultimately captured the expected relationship with harvest- and beetle-related changes in basal area.

Site occupancy dynamics were influenced by snag density and live basal area. Snags are important as potential nesting trees (Koprowski, 2005), and the threshold relationship with local extinction that we observed suggests that large increases in snag density beyond five snags/0.04 ha did not influence local extinction (Fig. 3). The intercept for extinction rates differed markedly from before to after the beetle outbreak, indicating additional variables may influence the probability of extinction. However, the beetle outbreak took place at a very broad spatial scale in relation to that at which we sampled, and rates of tree mortality varied spatially and with bole diameter (Johnson et al., 2014). Thus, a lack of snags in our 0.04-ha vegetation plots does not imply a lack of snags within the larger area sampled for squirrel occupancy, and the difference in spatial scale between sampling of habitat characteristics and of red squirrel occurrence may have influenced the observed change in intercepts among time periods.

The positive relationship between live basal area and colonization rate confirms documented habitat requirements for red squirrels. Dependence on conifer cones for food results in positive associations with stand density, tree size, and basal area, because these variables co-vary with seed availability (Zugmeyer and Koprowski, 2009). Red squirrels do not specifically require mature forest, but require a sufficient element of mature trees to produce seeds for food and to create cool microsites for middens (Koprowski, 2005). Regeneration in cut plots was dominated by lodgepole pine, which generally begins cone production within the first ten years, but production of cones approximating mature stand conditions is not reached in southern Wyoming until trees are ⩾17 cm dbh (50–80 yrs; Koch, 1996). Thus, re-colonization rates of plots abandoned during cutting were largely influenced by the amount of surrounding forest with mature components.

Site occupancy varied across years, and estimates after the beetle outbreak were within the range of variation of estimates for

some years before the outbreak (Fig. 5). Red squirrel populations typically vary in size across years, partially because of inter-annual variation in cone production (Gurnell, 1984; Dantzer et al., 2012). The magnitude of decrease in annual site occupancy post-outbreak was smaller than predicted; implying that red squirrels are likely to persist through at least near-term changes in structure and composition predicted for post-outbreak forests in landscapes with a diversity of tree species and tree size classes. Squirrels may be able to consume seeds from cones on dead trees if cones are serotinous. However, prevalence of serotiny was low at our study site (78% of plots containing lodgepole pine have <10% of trees characterized as serotinous, Johnson and Buskirk, unpublished data). Over the long term, food diversity provided by multiple conifer species will be important because most conifers mast every 3–6 yrs, and presence of more than one coniferous species provides more consistent cone availability (Silvertown, 1980; Hayward, 2008). Multiple species of bark beetle were active at our study site, and lodgepole pine and Engelmann spruce suffered relatively high rates of mortality (Johnson et al., 2014), suggesting that subalpine fir may be an important resource for red squirrels in the near-term. However, subalpine fir also experienced mortality (albeit lower than other conifers) attributed to western balsam bark beetle and root disease caused by *Armillaria* spp. or *Heterobasidium* spp. (Harris et al., 2001; Harris, 2012). If these or other mortality agents increase in extent or intensity before lodgepole pine or Engelmann spruce regenerate to a point of sufficient cone production, there could be additional depressing effects on red squirrel populations in the future.

The important role played by red squirrels in forest food webs suggests that reduced squirrel abundance may influence other forest species. Red squirrels are predators of juvenile snowshoe hares (O'Donoghue, 1994) and nesting birds (Willson et al., 2003), and exert substantial predation pressure on avian communities (Sieving and Willson, 1998). Thus, depressed red squirrel abundance may lead to population increases for other community members. Further, reduced seed predation by red squirrels may affect forest structure in lodgepole pine stands. Red squirrel abundance is negatively related to cone serotiny, because seed predation may overwhelm effects of fire on rates of stand-level serotiny when squirrels are relatively abundant (Benkman and

Siepielski, 2004; Talluto and Benkman, 2013). Beetle outbreaks affecting multiple tree species and resulting in prolonged reductions in red squirrel site occupancy or abundance may result in altered spatial variation and reduced intensity of seed predation. If fire-return intervals or fire intensity respond to bark beetle activity in areas of reduced seed predation, stand-level serotiny could increase. Given important effects of serotiny on post-fire stand density and community structure (Turner et al., 1997; Schoennagel et al., 2003), selection imposed by fire and reduced seed predation could influence forest characteristics across a significant proportion of western North American coniferous forest. Thus, decreased red squirrel occupancy may cause long-term changes in forest structure, in addition to those directly inflicted by tree mortality from bark beetles.

5. Conclusions

Harvested areas may become important refugia for red squirrels and other conifer seed-dependent species in coming decades as regenerating lodgepole pine matures to a point of sufficient cone production. Our results support management regimes that result in diverse tree species composition and uneven-aged stands to help mitigate demographic effects of broad-scale tree mortality on vertebrate seed predators.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.12.030.

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