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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 confuses)* 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.

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

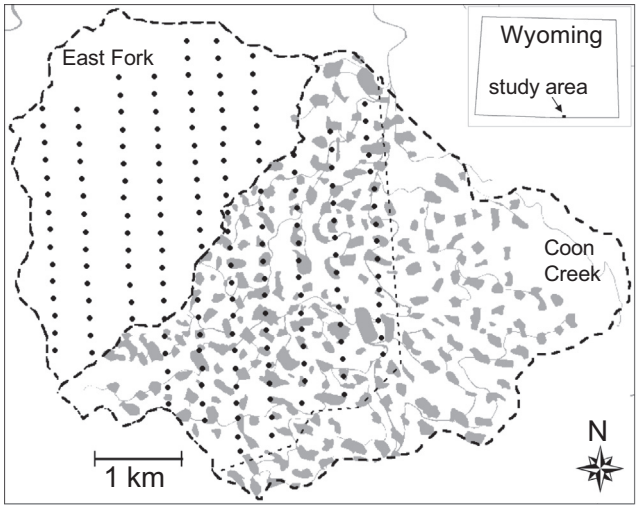

Fig. 1. Boundaries (thick dashed line) for control (East Fork) and harvested (Coon Creek) watersheds in south-central Wyoming, USA. The thin dashed line delineates the portion of Coon Creek used to evaluate squirrel responses to patch-cutting. Gray areas indicate patch cuts and roads. Black dots represent 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.