



Differential impacts of spruce beetle outbreaks on snowshoe hares and red squirrels in the southern Rocky Mountains

Jacob S. Ivan^{a,*}, Eric S. Newkirk^a, Brian D. Gerber^b

^a Colorado Parks and Wildlife, 317 W. Prospect Rd., Fort Collins, CO 80526, United States

^b University of Rhode Island, 1 Greenhouse Rd, Kingston, RI 02881, United States

ARTICLE INFO

Keywords:

Colorado

Dendroctonus rufipennis

Density

Distance sampling

Lepus americanus

Tamiasciurus hudsonicus

ABSTRACT

Spruce beetles (*Dendroctonus rufipennis*) have impacted millions of acres of Engelmann spruce (*Picea engelmannii*) – subalpine fir (*Abies lasiocarpa*) forest in North America over the past decade, resulting in the most extensive outbreak in recorded history. This dramatic alteration of forest composition and structure has precipitated numerous changes to forest ecology and ecosystem services. Among the least studied of these changes are impacts to wild mammals, including snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*). We sampled a chronosequence of spruce-fir stands along a gradient of ‘years elapsed since spruce beetle outbreak’ (YSO) in order to estimate impacts to abundance of these two species in the southern Rocky Mountains. Snowshoe hare abundance was not related to YSO, at least in the first decade post-outbreak. Instead, hare abundance during this period was positively related to horizontal cover, especially that due to stem density of small diameter subalpine fir. Notably, snowshoe hare abundance was negatively related to stem density of small diameter Engelmann spruce, suggesting that elements of horizontal cover may not be uniformly beneficial to hares. Hare abundance was also negatively related to ground cover, which could help explain the lack of relationship to YSO, assuming reduction in overstory canopy would lead to increases in ground cover. Red squirrel abundance was negatively related to YSO and outbreak severity (i.e., basal area of large diameter dead trees). This was likely due to diminished cone crops in impacted areas, which red squirrels cache and rely on heavily to sustain them through the winter. Basal area of remaining large live fir trees was not related to squirrel abundance, suggesting that regeneration of spruce and associated cone crops may be necessary for recovery of red squirrels, which may take several decades.

1. Introduction

Fire and insect outbreaks are important drivers of composition, structure, and ecological function of boreal and boreal-like subalpine forests (Gauthier et al., 2015; Payette, 1992; Raffa et al., 2008; Veblen, 2000). Effects of each have intensified in recent decades as ongoing climate change facilitates increased extent and severity of these natural disturbances (Bentz et al., 2010; Gauthier et al., 2015; Hart et al., 2017; Rocca et al., 2014; Whitman et al., 2019). Impacts are often complex and heterogeneous, but generally each results in overstory reduction and a shift in age distribution toward earlier seral stages (Payette, 1992; Rodman et al., 2022; Veblen, 2000). However, the degree of successional reset varies. Insect outbreaks typically leave non-host species in the overstory and immediately release understory due to opening of the canopy (Campbell et al., 2019; Rodman et al., 2022). Wildfire, especially

stand-replacing fire, tends to remove most or all overstory and understory which resets the stand back to an initiation stage (Agee, 1993; Schapira et al., 2021).

Timber harvest is also a significant driver of boreal and subalpine forest composition, structure, and function (Gauthier et al., 2015; Kuuluvainen and Gauthier, 2018). However the scale of disturbance from timber harvest is generally much smaller than insect outbreaks or fire (Smith, 2000). Depending on the silvicultural system, effects of harvest can resemble those observed in association with insect outbreaks (e.g., uneven-aged harvest strategies where overstory is moderately reduced in small gaps, releasing advanced regeneration), or those associated with fire (i.e., even-aged harvest where overstory is completely removed and understory is substantially reduced; Graham and Jain, 1998; Savilaakso et al., 2021). Stand-level modifications from all 3 drivers alter the mosaic of forest stands that occur across the

* Corresponding author.

E-mail address: Jake.Ivan@state.co.us (J.S. Ivan).

<https://doi.org/10.1016/j.foreco.2023.121147>

Received 14 April 2023; Received in revised form 24 May 2023; Accepted 28 May 2023

Available online 26 June 2023

0378-1127/© 2023 Colorado Parks and Wildlife.

<http://creativecommons.org/licenses/by-nc-nd/4.0/>.

Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license

landscape. Such changes to forest structure and landscape composition can have cascading effects, including impacts to the suite of wildlife that inhabits these forests.

Snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*) are considered to be keystone species in the boreal and boreal-like forest due largely to their role as primary prey for a number of predators, including species of concern, such as Canada lynx (*Lynx canadensis*; Armstrong et al., 2011; Hodges, 2000a, 2000b; Ivan and Shenk, 2016; Rusch and Reeder, 1978). Throughout their range, snowshoe hare density is strongly, positively associated with horizontal, or lateral cover (Nudds, 1977) within 0–2 m of the ground which affords them both hiding cover and food (Hodges, 2000a, 2000b; Holbrook et al., 2016; Ivan et al., 2014; Thomas et al., 2019). Consequently, snowshoe hare abundance generally peaks in early to mid-successional stands across their range (Hodges, 2000a, 2000b; Koehler, 1990), with a potential second peak in old forests where canopy gaps maintain dense understory patches (Hodson et al., 2011). Snowshoe hare occupancy or abundance may also be tied to overstory canopy, or vertical cover, although this relationship is weaker and not as ubiquitous (Hodson et al., 2011; St-Laurent et al., 2008; Thomas et al., 2019).

Red squirrels require cone crops for food, which are cached in mid-dens and provide a mechanism for winter survival (Armstrong et al., 2011; Kemp and Keith, 1970; Koprowski, 2005; Rusch and Reeder, 1978). They also use tree canopies for denning and as escape cover from predation (Armstrong et al., 2011; Yahner, 2003). As such, this species is generally associated with late successional forests (Fisher and Wilkinson, 2005; Kelly and Hodges, 2020; Yahner, 2003), where occupancy and abundance are positively related to tree size, basal area, and vertical cover (Holloway and Malcolm, 2006; Kelly and Hodges, 2020; Zugmeyer and Koprowski, 2009a).

Given the importance of these species in boreal and boreal-like systems, and their association with specific forest stages and structures, understanding their response to major disturbance agents is of interest. To date, researchers have considered wildfire and/or post-fire salvage impacts to red squirrels or snowshoe hares compared to control stands (Cheng et al., 2015; Hodges et al., 2009; Kelly and Hodges, 2020), impacts to snowshoe hares resulting from timber harvest and/or site preparation relative to mature stands (Ferron et al., 1998; Griffin and Mills, 2007; Newbury and Simon, 2005; Potvin et al., 2005, 1999; St-Laurent et al., 2008; Thompson et al., 1989; Thompson and Curran, 1995; Thornton et al., 2012), long-term trends in abundance of snowshoe hares and/or red squirrels in stands of fire-origin compared to those originating from clear cutting (Allard-Duchêne et al., 2014; Hodson et al., 2011), and short-term post-salvage impacts on snowshoe hare occupancy in beetle-killed stands (Thomas et al., 2019). Most of these projects focused on fire or timber harvest and occurred in Canada or near the U.S.-Canadian border. Few studies, however, have focused strictly at impacts of bark beetle outbreaks on snowshoe hares and red squirrels, especially in the Southern Rockies. Here, these species occur at the southern extent of their range in boreal-like subalpine forests comprised of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), hereafter “spruce-fir”.

Spruce beetles (*Dendroctonus rufipennis*) have impacted millions of acres of spruce-fir forest in North America over the past decade (Bentz et al., 2009). Climate-mediated stimulants to beetle development and population performance (Hansen and Bentz, 2003; Schebeck et al., 2017) combined with drought and an extensive landscape with mature forests (Fettig et al., 2007; Raffa et al., 2008) have optimally paired spruce beetle vigor with host susceptibility, promoting an epidemic (Bentz et al., 2010, 2009; DeRose et al., 2013; Temperli et al., 2015). In the Southern Rockies alone, over 7,500 km² have been impacted since 2000 (Colorado State Forest Service, 2021). Here, Ivan et al. (2018) and Latif et al. (2020) found that red squirrel occupancy and abundance declined within the first decade post outbreak in the most severely impacted stands. However, snowshoe hare occupancy remained largely unchanged, even in stands where overstory mortality exceeded 90%

(Ivan et al., 2018). Occupancy can be expected to coarsely track abundance under certain conditions (Ellis et al., 2014; Linden et al., 2017), but may be relatively insensitive to moderate changes in abundance (Ellis et al., 2014). Thus, while Ivan et al. (2018) did not find a material change in snowshoe hare occupancy due to beetle activity, important changes in snowshoe hare density could have been masked by the coarse nature of occupancy.

We measured snowshoe hare and red squirrel density along a gradient of time since spruce beetle outbreak in the San Juan Mountains of southwest Colorado. This region represents the southern tip of boreal-like forest, where recent spruce beetle outbreaks have been widespread and severe (Colorado State Forest Service, 2018), and where the two focal species serve the important role as primary prey for the southernmost population of threatened Canada lynx in North America (Devineau et al., 2010). We predicted that snowshoe hare density would increase at least moderately along the chronosequence owing to the rapid release of advanced regeneration (i.e., seedlings and saplings that were already established within the stand prior to the outbreak), and potentially due to recruitment of new saplings in post-outbreak environments. Given the expected transition of post-outbreak stands to fir dominance, and the presumed affinity of snowshoe hares for fir understory based on propensity of local lynx to select the same (Squires et al., 2020), we further predicted that snowshoe hare density would be positively related to fir understory. We predicted that red squirrel density would decline precipitously as suggested by the previous occupancy (Ivan et al., 2018) and density (Latif et al., 2020) estimates obtained across similar sites during summer.

2. Material and methods

2.1. Study area and site selection

We sampled snowshoe hare and red squirrel density in the San Juan Mountains of southwest Colorado (Fig. 1). The San Juans are an area of significant topographic relief, which produces stark changes in vegetation assemblies over short distances. Sagebrush (*Artemisia tridentata*) or oakbrush (*Quercus gambelii*) valleys (1,200–2,500 m) quickly give way to montane forest slopes (1,700–2,700 m) dominated by Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Subalpine forest, where sampling occurred for this study (2,700–3,500 m), extends above the montane zone. This boreal-like system is made up largely of spruce and fir, although large aspen (*Populus tremuloides*) patches are common where fire and other disturbance have made it viable. Blue spruce (*Picea pungens*), limber pine (*Pinus flexilis*), and bristlecone pine (*Pinus aristata*) also occur in localized areas where conditions are favorable. Lodgepole pine (*Pinus contorta*) is notably absent from the study area. Extensive alpine zones cap the subalpine forest, with peaks extending to 4200 m.

Mean July temperature on the study area in 2017 was 13.6° C; mean January temperature was – 5.5° C. Mean total precipitation was 0.72 m, most of which fell as snow during winter or came as rain during late summer monsoons. In the subalpine zone where sampling occurred, snow cover persisted from November through June, and March snow depth averaged 1.6 m (National Oceanic and Atmospheric Administration, 2020).

From among the population of subalpine forest stands (as delineated by USDA Forest Service R2VEG geodatabase) that were large enough to accommodate a sampling grid (16.5 ha), we selected $n = 15$ of these to serve as study sites. Sites were selected to control for aspect, elevation, outbreak severity (all but the control sites sustained considerable impact from beetles), management history (none), and fire history (>100 years since last fire). Sites varied in years since spruce beetle outbreak (YSO), which started in the east-central portion of the study area (approximately 11 years prior to our sampling) and progressed outward (Fig. 1). To ensure that we evenly sampled the gradient of time elapsed since outbreak, we selected replicate sites from each of 4 categories: control

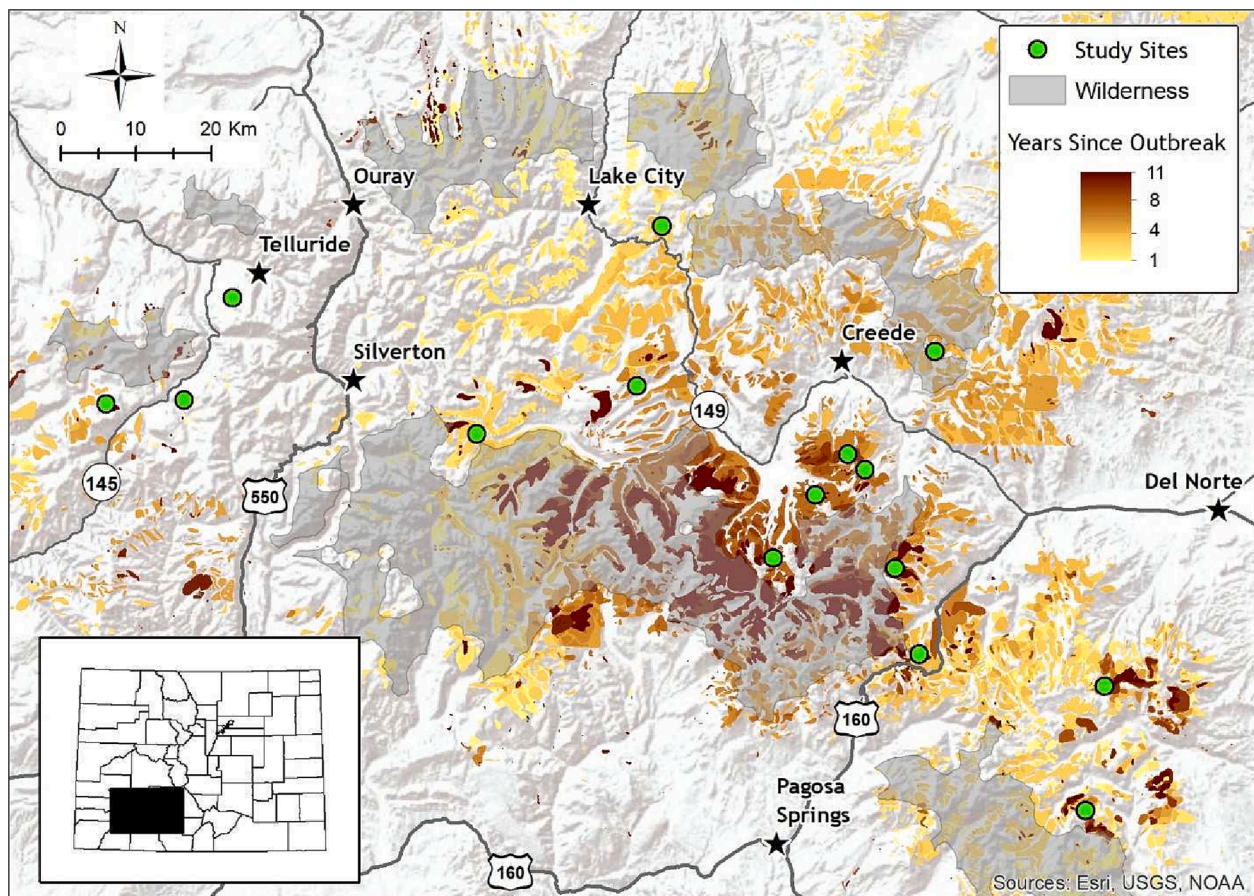


Fig. 1. Study area in southwest Colorado, USA where snowshoe hare and red squirrel densities were estimated at $n = 15$ study sites, during the 2016–17 winter.

sites to 2 years since outbreak ($n = 4$), 3–5 years since outbreak ($n = 4$), 6–8 years since outbreak ($n = 4$) and 9–11 years since outbreak ($n = 3$). Within each category, one or two of the selected sites represented drier spruce forest with little subalpine fir in the overstory or understory in order to address our secondary question regarding the importance of fir in structuring hare density. We intentionally chose sites with no history of timber management or recent fire to avoid confounding effects of those events with impacts of bark beetle outbreaks; no sites occurred in designated wilderness areas. Additionally, all sites were screened for accessibility and safety for winter sampling.

2.2. Sampling

All animal sampling occurred during winter 2016–17. At each of the 15 study sites, crews deployed a 7×12 grid (50 m spacing) of live traps (Tomahawk Model 204, Tomahawk Live Trap, Hazelhurst, Wisconsin, USA) as per Ivan et al. (2014). Traps were pre-baited (apple slice, rodent chow, hay cube) for 3 days followed by 2 nights of trapping, 1 night off, then 2 more nights of trapping. We attempted to adjust trapping sessions to avoid heavy snowfall and predation. Traps were checked once per day in early morning. Part way through the season, we modified all traps by extracting a single “intersection” of mesh in the upper corner of each trap. This allowed red squirrels and pine martens (*Martes caurina*) to escape traps unharmed, which alleviated non-target capture mortality that was observed early in the season.

Trapped hares were coaxed into a pillow case and immediately given 3 ml of pedialyte to alleviate acute capture-related stress. While physically restrained in the pillow case (no anesthesia), they were marked with a unique ear tag (Style 1005–3, National Band & Tag Company, Newport, Kentucky, USA), weighed, and then released. Additionally, to

facilitate density estimation, a sample of 5 hares at each site were fitted with a 20-g GPS/VHF collar (LiteTrack 20, Lotek, New Market, Ontario, Canada). The average time elapsed between extracting hares from traps and their release was 4 min. Hares that were re-captured on subsequent trapping events were immediately released upon confirming their identity either from the ear tag or collar frequency. Non-target species were released immediately without handling; most found their way out of the escape hatch in the corner of the trap once we made the modification.

Traps and bait were removed immediately following the last day of trapping to minimize attractive scent at the site. Collars were programmed to collect a location every hour for 7 days. Telemetry sampling began 2 days after the trapping period ended to allow individuals to return to their normal patterns of space use. Location data were remotely downloaded from collars in late winter. Animal capture and handling methods were approved by Colorado Parks and Wildlife ACUC #00–2016.

Red squirrel sampling was completed during the 3 pre-baiting days. Each morning as crews traveled the trapping grid to replenish bait, they stopped at 9 traps, systematically spaced throughout the grid 150–250 m apart, and listened for red squirrel calls for 6 min. Each observer played a recorded red squirrel call from a phone twice during the 6-minute period to elicit calls from resident individuals. We recorded the number of squirrels calling at each point along with the distance and direction to each individual, which we estimated with laser range finders. Red squirrel surveys were generally completed between one hour after sunrise and 10 am.

In addition to sampling hares and squirrels at each site, we sampled forest structure and vegetation during fall 2016. Following Squires et al. (2020), we established 15 400-m² (11.2 m radius) systematically placed

plots within each site. We quantified the diameter at breast height (dbh), species, and live-dead status of each tree > 7.6 cm dbh within the plot. We fed these data to the United States Forest Service Forest Vegetation Simulator (Dixon, 2002) to compute stem density, basal area, and canopy cover by species, size class, and live-dead status. We collected percent ground cover at 5 1-m subplots equally spaced on the N-S axis of the main plot. We measured stem density of understory trees (1–3 m in height, any dbh) in a 1-m wide strip transect along the N-S axis as well. We quantified horizontal cover from 0 to 2 m above ground by estimating visual obstruction at 10 m in the 4 cardinal directions from plot center (Nudds, 1977). We computed the mean of each vegetation characteristic at the site level, and made these site-level means available for use as covariates to explain heterogeneity in snowshoe hare or squirrel density.

2.3. Analysis

2.3.1. Snowshoe hares

We estimated snowshoe hare density for each site based on the ‘Density with Telemetry’ approach described by Ivan et al. (2013a, 2013b). Under this approach, two parameters of interest are estimated from the mark-recapture and telemetry data: individual (i) detection probability (p_i) and proportion of time on grid (\tilde{p}_i , the proportion of each individual’s activity range over the sampling period that occurs within the study site as defined by the minimum convex polygon encompassing the traps). Density (\hat{D}) is a derived parameter in which the raw count of observed individuals is simultaneously inflated to account for imperfect detection, and deflated as appropriate to reflect individuals whose activity range only partly occurs on the sampling grid. We assumed that both p_i and \tilde{p}_i were influenced by the ‘distance to edge of the grid’ (DTE) of the mean capture location for each individual, which is common with such models (Ivan et al. 2013a, 2013b). We included a random effect to account for unstructured heterogeneity in capture probability among individuals (White and Cooch, 2017). We did not fit standard spatial capture-recapture models (e.g., Borchers and Efford, 2008; Royle and Young, 2008) to our data as both current and previous trapping experiences in Colorado have indicated that the trap-revealed spatial information on hare movement is strongly biased by the presence of bait in an otherwise food-limited season (J.S. Ivan, unpublished data).

To simultaneously make inference on hare density at each site while evaluating covariates as potential drivers of hare density, we cast the ‘Density with Telemetry’ model in a hierarchical Bayesian framework. We based our analysis on Royle and Converse (2014), replacing their spatial capture-recapture structure with that of Ivan et al. (2013a). With this approach, parameter estimation was completed in a single model and uncertainty in the site-level density estimation was propagated to estimated covariate effects, albeit as predictors of latent abundance at each site.

Models were fit using Markov Chain Monte Carlo (MCMC) methods implemented in the software program JAGS (Plummer, 2017), accessed from R (R Development Core Team, 2022) using the package ‘jagsui’ (Kellner and Meredith, 2022). We used weakly informative priors for all parameters. We ran 3 chains with 20,000 iterations of burn-in, 100,000 iterations post burn-in, thinned by 4. We confirmed convergence for all parameters visually and using the criteria that the Gelman-Rubin (\hat{R}) statistic was ≤ 1.1 (Gelman and Hill, 2007). See Appendix S1 for a detailed model description. Model scripts and data files are available at <https://doi.org/10.5281/zenodo.7830032>.

We assessed 10 covariates as predictors of latent snowshoe hare abundance (and by extension, density – we use the terms roughly interchangeably hereafter) at each site. First, across the continental U.S., snowshoe hare density is widely known to be structured by horizontal cover (i.e., visual obstruction 0–2 m above ground; Hodges, 2000a; Holbrook et al., 2016; Ivan et al., 2014). Therefore, we fit a model where latent abundance was predicted by (1) horizontal cover to serve as a base

of comparison.

However, we were most interested in the potential impacts of spruce beetle outbreaks on snowshoe hare abundance. We expected the primary impact to snowshoe hare density would be via an increase in horizontal cover through time as mediated by loss of canopy with cascading positive effects on release of advanced regeneration and/or seedling establishment. Accordingly, we considered 3 main covariates of interest: We fit a binary (2) ‘beetle’ covariate (impacted or not) to determine whether snowshoe hares exhibited any generalized response to stands that had been impacted by beetles. To examine potential impacts of outbreak dynamics, we also fit (3) ‘years elapsed since outbreak’ (YSO), and (4) severity of outbreak (percent canopy mortality) as potential predictors of snowshoe hare abundance as well.

We also sought to test our hypothesis that the type of regenerating horizontal cover may be important. That is, we fit models that included (5) stem density of small diameter (7.6–12.5 cm dbh) live fir, and (6) small diameter live spruce. We also considered (7) density of understory (1–3 m in height) fir stems regardless of dbh, along with density of understory spruce (8) as slightly different measures to assess the importance of species composition in horizontal cover (correlation between small diameter stem density and understory was 0.54 for fir, 0.61 for spruce). Finally, we fit (9) percent ground cover and (10) percent canopy cover as potential predictors because these are likely to be mediated by beetle outbreaks and recent work suggests that they may be associated with snowshoe hare abundance (Hodson et al., 2011; Kelly and Hodges, 2020; Thomas et al., 2019).

All covariates were standardized before fitting to facilitate comparison among them. Because our sample size was $n = 15$ sites, we opted to restrict our analysis to univariate models. We did not fit additive combinations of any covariates, nor did we fit interaction terms. We made inference by observing magnitude and direction of coefficients (β_1 ; see Appendix S1 for details) for the covariates of interest and noting whether the effects were different from zero.

2.3.2. Red squirrels

We estimated red squirrel density using a distance sampling framework (Royle et al., 2004) adjusted for temporary emigration (Chandler et al., 2011). This model allows for the likely possibility that squirrels could move on and off plots between visits and/or refrain from calling during a given survey, making them unavailable for detection. To maintain consistency of approach, we implemented the analysis using a Bayesian hierarchical distance sampling framework (Kery and Royle, 2016a p. 483–509), although similar inference can be obtained using likelihood methods from package ‘unmarked’ (Fiske and Chandler, 2011). We chose to use 4 distance bins as a compromise between providing enough bins to fit a smooth detection function, while also ensuring a reasonable number of detections occurred in any given bin. Initial analyses using package ‘unmarked’ indicated reasonable fits to our data from both exponential and half normal curves; we elected to fit the half normal.

We estimated the density (λ) of red squirrels at a given site (along with latent abundance, see Appendix S2), the probability that an individual was available for detection during a survey (ϕ), and parameters related to detection probability. We had no reason to believe ϕ would be strongly impacted by site, YSO, or severity. Furthermore, Chandler et al. (2011) found that the model is robust to heterogeneity in ϕ . Therefore, we specified ϕ to be constant in all models. As before, we assigned weakly informative priors for all parameters and fit models using MCMC. We ran 3 chains with 50,000 iterations of burn-in, 100,000 iterations post burn-in, thinned by 10 and confirmed convergence as before. See Appendix S2 for a detailed model description. Model scripts and data files are available at <https://doi.org/10.5281/zenodo.7830032>.

As with snowshoe hares, we were most interested in whether red squirrel density would exhibit a generalized response to beetle outbreaks, or respond through time as overstory trees succumbed to beetle

attacks, or whether severity of the outbreak would be an important factor. Accordingly, we fit models that related latent squirrel abundance to a (1) beetle indicator variable, (2) YSO, and severity. We reasoned that (3) stem density of dead trees and/or (4) basal area of dead trees would be useful measures of the impacts of severity on squirrel density (as opposed to canopy cover being the mechanism by which severity would impact snowshoe hares) because these attributes should have strong associations with seed availability (Allard-Duchêne et al., 2014; Koprowski et al., 2005; Russell et al., 2010; Saab et al., 2014). Similar to the hare analysis, we also sought to tease apart the effects of dead spruce compared to live fir to determine whether surviving fir trees could serve as a buffer against the loss of large spruce at a site. Accordingly, we fit (5) basal area of large (>22.9 cm dbh) dead spruce and 6) large live fir as covariates on squirrel abundance at a site as well.

To accommodate our design in which squirrels were sampled at $n = 9$ subplots at each site, we pooled squirrel detections to the site level as is customary in distance sampling (p. 400; Kery and Royle, 2016b). As before, this left us with a modest sample size of $n = 15$ sites. Given this, we fit standardized covariates on abundance one at a time and made inference on their effect by observing the magnitude and direction of the coefficients (θ_i ; see Appendix S2 for details). We did not fit additive models, or models that included an interaction between covariates.

3. Results

3.1. Snowshoe hares

We captured 191 hares 390 times over 4,284 trap nights and collared 69 individuals. We captured 3–43 individuals per site (naïve density = 0.2–2.6 hares/ha). Traps at 6 sites were closed 1–3 nights due to presence of predators or heavy snow. Due to a software malfunction on the collars, we only recovered data from 39 of the 69 collars deployed. However, collar failure appeared arbitrary and affected each site. Furthermore, Ivan et al. (2013b) found that sampling 25% of captured individuals with telemetry devices produced density estimates that were nearly as unbiased as those obtained via telemetering 50 or 100% of captured individuals. Therefore, we were confident that use of our telemetry data would still facilitate unbiased density estimates even though we collected data on fewer individuals than we had planned.

We filtered telemetry locations to those with estimated dilution of precision < 3. Based on field testing prior to deployment, we found that this level of filtering resulted in a fix rate of 65%, and that > 95% of all retained locations were within 25 m (i.e., half the distance between traps) of truth (J. Ivan, unpublished data). We deemed this performance acceptable given that we only needed collars to determine whether individuals were on or off the 16.5-ha grid. We obtained 3–125 fixes per individual ($\bar{x} = 47$; some hares succumbed to predation shortly after marking; during the 1-week sampling period following trapping; proportion of locations within the MCP of the trapping grid ranged from 0 to 0.84 ($\bar{x} = 0.22$).

Detection, time on grid, and density estimates varied slightly (0–1.5% depending on the parameter) from model to model depending on the estimated relationship with the habitat covariate of interest. Using results from the YSO model for illustration, mean detection probability (p_i) was 0.53 (95% Bayesian Credible Interval (BCI) = [0.39, 0.62]) and mean proportion of time on grid (\tilde{p}_i) was 0.21 (95% BCI = [0.19, 0.23]). Both estimates varied positively with DTE as expected ($\hat{\alpha}_1 = 0.43$, 95% BCI = [0.11, 0.77]; ($\hat{\alpha}_3 = 0.74$, 95% BCI = [0.61, 0.87]; Appendix S1). That is, individuals captured closer to the center of the grid had a higher capture probability (presumably because they were exposed to more traps within their activity range during trapping) and were located within the MCP of the trapping grid more often once traps and bait were removed. Density estimates ranged from 0.07 to 0.68 hares/ha ($\bar{x} = 0.20$ hares/ha).

Snowshoe hare abundance was unrelated to the binary ‘beetle’

covariate ($\hat{\beta}_1 = 0.31$, 95% BCI = [-0.07, 0.72]). We also did not find evidence that snowshoe hare abundance was related to YSO or severity (Figs. 2, 3). Hare abundance was positively related to horizontal cover, stem density of small diameter fir, and stem density of understory fir. It was negatively related to stem density of small diameter spruce, ground cover, and stem density of understory spruce, although the latter overlapped zero by a small margin. Snowshoe hare abundance was unrelated to canopy cover (Fig. 3, See Appendix S3 for specific coefficient values).

3.2. Red squirrels

We recorded 45 red squirrel detections across 3 visits to 133 points (2 points were never visited due to unsafe terrain) at the 15 sites; we recorded 0–7 detections per site. From the YSO model, the probability of a squirrel being available for detection during a survey was 0.52 (95% BCI = [0.18, 0.93]) and mean density ranged from 0.8 to 7.2 squirrels/ha ($\bar{x} = 3.2$ squirrels/ha). Squirrel abundance was negatively associated with the categorical beetle variable ($\hat{\theta}_1 = -0.83$, 95% BCI = [-1.46, -0.18]) as well as YSO, and severity as measured by basal area of dead trees (Figs. 2, 4). Red squirrel abundance was estimated to decline by 84% between control sites ($\hat{n} = 18.9$ squirrels per site) and those sites impacted by beetles 11 years prior to sampling ($\hat{n} = 3.06$ squirrels per site; Fig. 2). Additionally, basal area of dead spruce was related to squirrel abundance in nearly identical fashion as basal area of dead trees in general, but squirrel density was not related to basal area of live fir. Severity measured as stem density of dead trees was unrelated to squirrel density (Fig. 4, See Appendix S3 for specific coefficient values).

4. Discussion

4.1. Snowshoe hares

Snowshoe hare density in Colorado was largely unrelated to spruce beetle outbreaks, at least in the first decade after impact. This result mirrors patterns in summer occupancy observed by Ivan et al. (2018). The lack of noticeable impact to hare density stands in stark contrast to impacts from other large-scale forest disturbances such as fire and clearcutting. Each of these disturbances tends to push hare densities to near zero immediately afterward, with a prolonged recovery in which density may not approach pre-disturbance levels for one to several decades (Allard-Duchêne et al., 2014; Kelly and Hodges, 2020). This is likely because fire and logging produce immediate, drastic impacts to all layers of forest vegetation, including the understory, which directly affects suitability of a stand to support snowshoe hares. However, bark beetle outbreaks act only on larger trees while drastic and immediate impacts to the understory are dampened or absent.

As expected, we found that snowshoe hare density was strongly, positively related to horizontal cover, a pattern that has been documented repeatedly across snowshoe hare range (Hodges, 2000a, 2000b; Holbrook et al., 2016; Ivan et al., 2014). However, we anticipated that canopy reduction induced by beetle outbreaks would enhance horizontal cover over time and we would therefore observe increasing hare density following the outbreak. A linear regression of horizontal cover vs. YSO indicated that horizontal cover did indeed increase after outbreaks ($\beta_{YSO} = 1.1$, SE = 0.05, $p = 0.048$), yet we did not observe a concomitant increase in hare abundance. Notably, understory and stem density of small diameter spruce and fir did not increase after outbreaks as expected (regressions of these covariates on YSO were not significant, $p > 0.25$). Perhaps increases in horizontal cover after beetle outbreaks were driven by increased ground cover (which was negatively related to hare abundance) or increased downfall, but these components of horizontal cover are not as important as conifer understory and small trees, which did not respond as expected.

We found that stem density of small diameter fir and stem density of understory fir were as strongly, positively associated with snowshoe

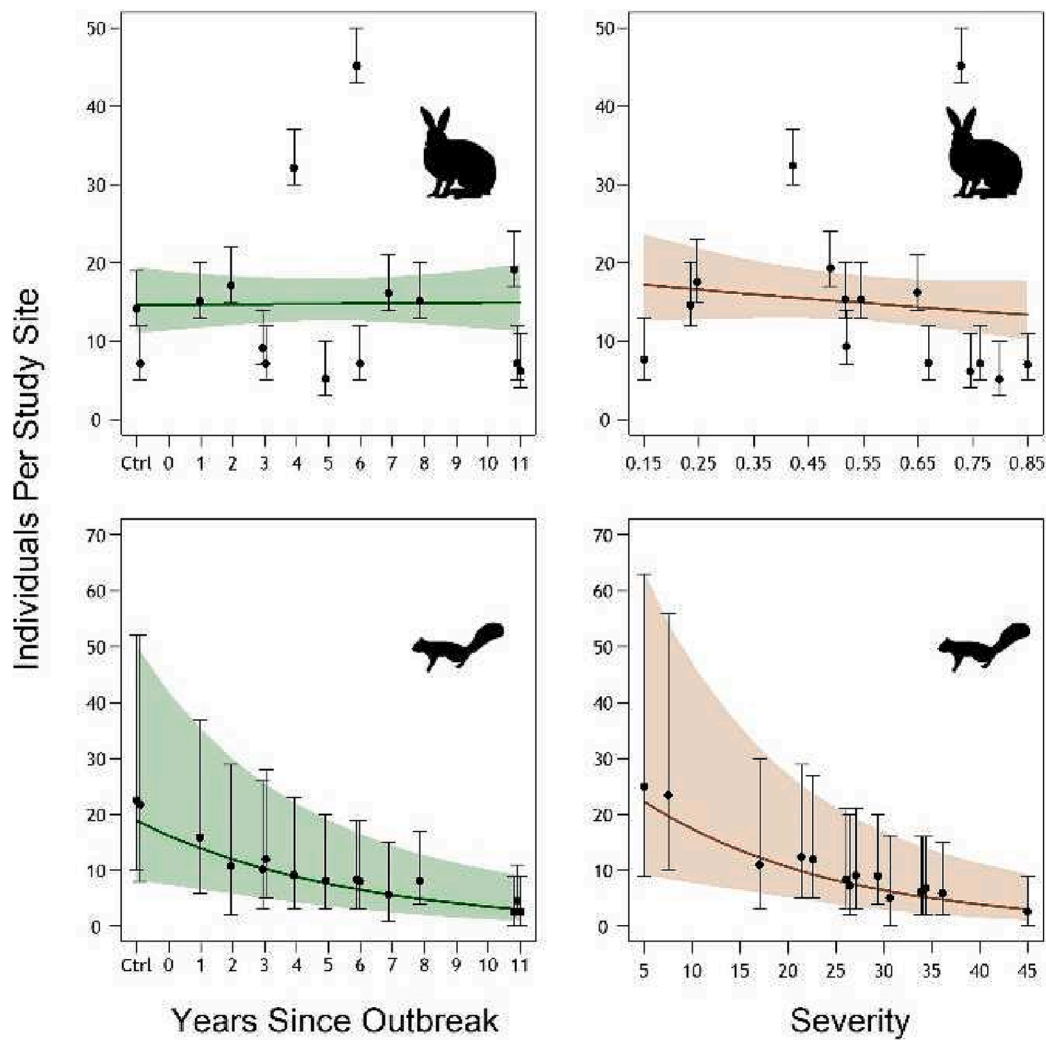


Fig. 2. Relationship between snowshoe hare (top panels) or red squirrel (bottom panels) abundance and (1) years elapsed since spruce beetle outbreak (left), or (2) severity of the outbreak (right) in southwest Colorado, USA 2016–17. Severity was measured by percent canopy mortality for snowshoe hares and basal area of dead trees (m^2/ha) for red squirrels. Shaded areas indicate 95% Bayesian credible intervals.

hare abundance as the generalized aggregate horizontal cover variable. Additionally, stem density of small diameter and understory spruce were negatively associated with hare abundance. These relationships further suggest that components of horizontal cover may not be homogeneous in their importance to snowshoe hares. In fact, they indicate that fir understory and stem density of small diameter fir may be primary drivers of hare abundance in this system. This finding aligns with concurrent Canada lynx research in roughly the same study area. Squires et al. (2020) reported that most individual lynx chose movement paths that traversed areas with abundant subalpine fir in the subcanopy. Given the strong association between Canada lynx and snowshoe hares (Koehler and Aubry, 1994), it seems likely that selection patterns exhibited by lynx are reflections of snowshoe hare distribution within their home range.

If hare abundance in the Southern Rockies is indeed driven by small diameter and understory fir, then perhaps our prediction of a positive response to spruce beetle outbreaks is still possible, if not a few decades away. In examining a 1940s spruce beetle outbreak in Colorado, Veblen et al. (1991) found that regeneration of seedlings was slow. Even 50 years post outbreak, seedlings established after the outbreak were generally < 20 cm tall. Similarly, Baker and Veblen (1990), found evidence that release and accelerated growth of advanced regeneration was still ongoing 40 years following spruce beetle outbreaks in western

Colorado. Thus, snowshoe hares may yet exhibit a positive response to beetle outbreaks, but such a response may take much longer to observe than the 11-year chronosequence currently available.

Our finding that snowshoe hare density in Colorado was negatively related to percent ground cover aligns with recent work in British Columbia (Kelly and Hodges, 2020) and Yukon Territory (Thomas et al., 2019). Similarly, Ivan et al. (2018) found bare ground to be positively related to snowshoe hare occupancy in Colorado. Thomas et al. (2019) suggested that avoidance of areas with heavy ground cover (i.e., food resources) represented a tradeoff – forgoing areas rich in food resources in favor of selecting areas with better cover attributes. In our system, the fresh ground cover growing post-beetles was quite dense, and in most places much taller than a hare. Thus, lack of cover seems like an insufficient explanation for avoidance. We suggest that very dense forbs, as tall or taller than a hare, may impede locomotion. Alternatively, perhaps dense ground cover is simply an indicator for lack of conifer regeneration, or even serves as an impediment to it. We did not find a positive relationship between snowshoe hare density and canopy cover in contrast to recent work in boreal Canada (Hodson et al., 2011; Thomas et al., 2019).

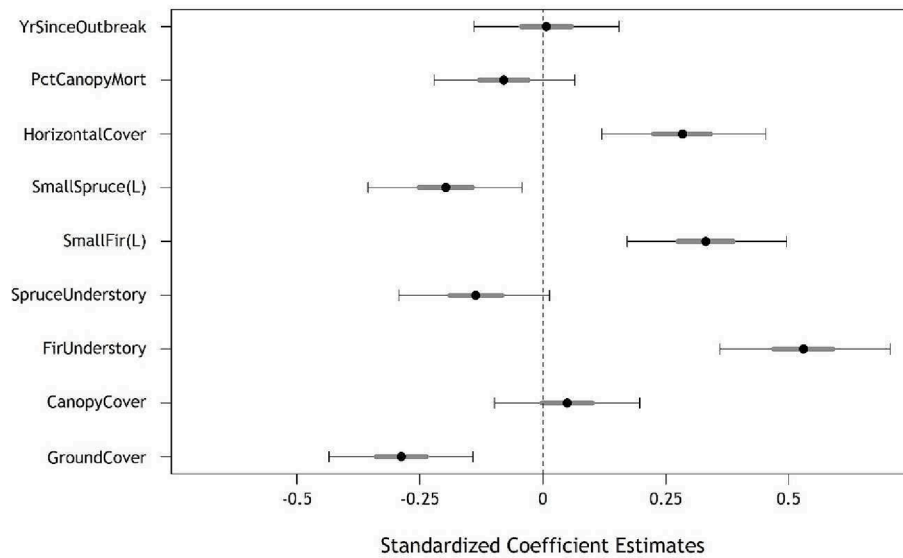


Fig. 3. Standardized coefficients ($\hat{\beta}_1$) for the relationship between snowshoe hare abundance and various outbreak and habitat-related variables, including 50% (gray) and 95% (whiskers) Bayesian credible intervals. Small spruce or fir indicates stem density of live trees 7.6–12.5 cm. Spruce or fir understory indicates stem density, regardless of dbh, of trees that were considered part of the understory (1–3 m in height).

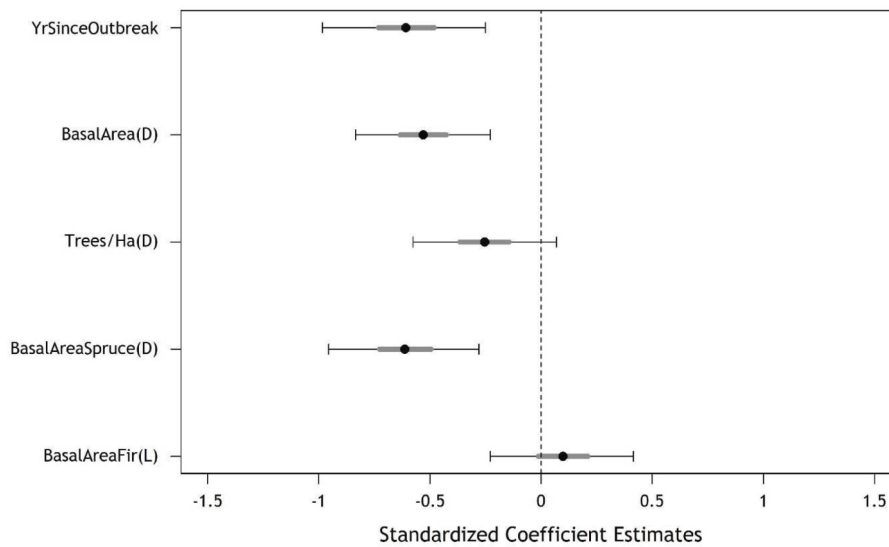


Fig. 4. Standardized coefficients ($\hat{\theta}_1$) for the relationship between red squirrel abundance and various outbreak and habitat-related variables, including 50% (gray) and 95% (whiskers) Bayesian credible intervals. “L” indicates live trees; “D” indicates dead trees. Basal areas for large dead spruce and large live fir were for trees > 23 cm dbh.

4.2. Red squirrels

The generally negative response of red squirrels to spruce beetle outbreak, their decreased density with years since outbreak, and the negative relationship between squirrel density and outbreak severity all followed our a priori hypotheses. The response we observed as a function of YSO was nearly identical to that described by [Latif et al. \(2020; Appendix S2\)](#) using similarly collected data over a larger area of Colorado during summer. Furthermore, our results track severe declines observed in Mt. Graham red squirrel abundance following beetle outbreaks in high elevation spruce-fir forests in Arizona ([Koprowski et al., 2005](#)). There, red squirrel occupancy declined in parallel with declines in individual survival and seed counts, suggesting that the loss of cone crops is indeed a major mechanism driving responses in demography and other state variables ([Koprowski et al., 2005; Zugmeyer and](#)

[Koprowski, 2009b](#)). Additionally, our results broadly corroborate findings regarding red squirrel response to mountain pine beetle outbreaks in lodgepole pine systems, where red squirrel occupancy is also negatively related to beetle outbreaks and their severity ([Drever and Martin, 2007; Johnson et al., 2015; Saab et al., 2014](#)).

In contrast to snowshoe hares, the near immediate, negative response of red squirrels to bark beetle outbreaks is not unlike their response to wildfire or clearcutting. Across boreal Canada from British Columbia ([Kelly and Hodges, 2020](#)) to Ontario ([Thompson et al., 1989](#)) to Quebec ([Allard-Duchêne et al., 2014](#)), red squirrel density is acutely and negatively impacted by wildfire and/or clearcutting due to loss of nesting cover, escape cover, and food resources (i.e. cone crops) associated with the canopy layer of mature forests ([Fisher and Wilkinson, 2005](#)). We assume that loss of large trees and overstory canopy due to bark beetle outbreaks operates similarly on red squirrel ecology.

Our results add to the already substantial evidence that red squirrel abundance declines precipitously after bark beetle outbreaks, and furthermore is negatively related to the severity of the outbreak. Perhaps the main outstanding question is the timeframe required for red squirrel populations to regain their pre-outbreak status on a broad scale. We hypothesized that this may partly depend on the extent of non-host species (e.g., subalpine fir in our system) left in a given stand to provide food and cover for squirrels. However, we did not find evidence for any “rescue effect” of large live fir trees relative to squirrels. Density was not related to the basal area of live fir trees in a stand, only to the basal area of dead spruce, or dead trees in general.

If spruce trees are indeed requisite for meaningful recovery of red squirrels, realization of pre-beetle densities may take decades. Sapling and pole-sized trees remaining after an outbreak may produce seeds, but seed production from regenerating trees is unlikely to be significant for a half century or more (Alexander and Shepperd, 1984). Thompson et al. (1989) noted that it took 20–30 years post-harvest before squirrel indices in clearcut stands in Ontario began to approach those of uncut stands. In Quebec, red squirrel indices peaked 40 and 60 years post-cutting and post-fire, respectively (Allard-Duchêne et al., 2014). Kelly and Hodges (2020) observed post-disturbance indices of squirrel abundance re-aligned with that of mature stands as early as a decade post-fire in British Columbia, but our findings in drier forests of the Southern Rockies have already exceeded that time frame.

Snowshoe hares are the primary prey of Canada lynx throughout lynx range (Aubry et al., 2000; Koehler and Aubry, 1994; Mowat et al., 2000); red squirrels are the main alternative prey, and can comprise a significant portion of lynx diet when snowshoe hare abundance is depressed (Brand et al., 1976; Ivan and Shenk, 2016; O’Donoghue et al., 1998a, 1998b). Survival is generally not impacted by the switch from hares to squirrels, but reproduction ceases (Mowat et al., 1996; O’Donoghue et al., 2001; Poole, 1994; Slough and Mowat, 1996). Thus, bark beetle outbreaks have the potential to impact Canada lynx via cascading effects on vegetation that in turn mediate prey abundance. Understanding and predicting such relationships is especially important at the southern extent of lynx range where the species is naturally rare and federally threatened (U.S. Fish and Wildlife Service, 2000). The widespread, severe spruce beetle outbreak in the Southern Rockies has not, as yet, had discernible impacts to either snowshoe hare occupancy (Ivan et al. 2018) or density. Similarly, it does not appear to have significantly impacted Canada lynx on a broad scale as lynx distribution in the area remained constant before and after the outbreak (Squires et al., 2022), and lynx continue to “actively use and select forests impacted by spruce beetles” (Squires et al., 2020). These findings bode well for the continued existence of Canada lynx at the extreme southern edge of their range. However, snowshoe hare abundance fluctuates through time (e.g., Ivan et al., 2014), and may be weakly cyclic in the southern portion of lynx-hare range (Hodges, 2000a). Whether enough red squirrels remain on the landscape to sustain lynx when hare numbers decline is an open conservation question, at least in the near term.

5. Conclusions

In the first decade post-outbreak, snowshoe hare density was unrelated to years elapsed since spruce beetle outbreak or severity of the outbreak. Instead, hare density during this period appears more strongly associated with horizontal cover, especially cover due to stem density of small diameter and understory subalpine fir as opposed to spruce. Hare density was negatively associated with dense ground cover, which potentially offset the benefit to hares from improved horizontal cover, resulting in the overall lack of relationship to beetle outbreaks. Conversely, red squirrel density was strongly, negatively related to years elapsed since outbreak and outbreak severity. Basal area of remaining large live fir trees was not related to squirrel density indicating that regeneration of spruce and associated cone crops may be necessary for recovery of red squirrels, which may take several decades. Given that

snowshoe hares are the primary prey of Canada lynx in the Southern Rockies and elsewhere, these findings are encouraging with respect to lynx conservation in beetle impacted areas. Whether enough red squirrels persist to sustain lynx when snowshoe hare numbers naturally fluctuate remains unknown.

CRediT authorship contribution statement

Jacob S. Ivan: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Eric S. Newkirk:** Conceptualization, Methodology, Software, Investigation, Data curation, Writing – review & editing. **Brian D. Gerber:** Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Links to all data files and code are provided in the manuscript.

Acknowledgments

Funding: This work was supported by Colorado’s Species Conservation Trust Fund. Tim Hanks, Erin Sawa, Laurel Reisman, Anna Machowicz, Mark Ratchford, Adam Fuest, Emily Latta, Mary Grant, Trevor Besosa, Cara Thompson, Taelor Mullins, Grete Wilson-Henjum, Alex Dyson, and Melissa Butinski conducted the difficult work of collecting snowshoe hare, red squirrel, and vegetation data. Quresh Latif provided analytical advice for the red squirrel analysis. USFS Rio Grande National Forest provided housing and logistical support. Development of Bayesian models presented here was aided by participation in a workshop (“Bayesian Models for Ecological Data”) hosted by Colorado State University and funded by NSF Award DEB 0003437455.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121147>.

References

- Agee, J.K., 1993. Subalpine ecosystems. In: *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, D. C., pp. 250–279.
- Alexander, R.R., Shepperd, W.D., 1984. *Silvical characteristics of Engelmann spruce*. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Allard-Duchêne, A., Pothier, D., Dupuch, A., Fortin, D., 2014. Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession. *For. Ecol. Manage.* 313, 17–25. <https://doi.org/10.1016/j.foreco.2013.10.046>.
- Armstrong, D.M., Fitzgerald, J.P., Carron, A.M., 2011. *Mammals of Colorado*, 2nd ed. University Press of Colorado, Boulder, Colorado, USA.
- Aubry, K.B., Koehler, G.M., Squires, J.R., 2000. Ecology of Canada lynx in southern boreal forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C. J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and Conservation of Lynx in the United States*. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA, pp. 373–396.
- Baker, W.L., Veblen, T.T., 1990. Spruce beetles and fires in the nineteenth-century subalpine forests of western Colorado, USA. *Arct. Alp. Res.* 22, 65–80.
- Bentz, B.J., Logan, J.A., Macmahon, J.A., Allen, C.D., Ayres, M.P., Berg, E., Carroll, A., Hansen, M., Hicke, J., Joyce, L., Macfarlane, W., Munson, S., Negron, J., Paine, T., Powell, J., Raffa, K., Regniere, J., Reid, M., Romme, B., Seybold, S.J., Six, D., Tomback, D., Vandygriff, J., Veblen, T., White, M., Witcosky, J., Wood, D., 2009. Bark beetle outbreaks in western North America: causes and consequences. *Bark Beetle Symposium, Snowbird, Utah*. University of Utah Press, Salt Lake City, Utah, USA.

- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60, 602–613. <https://doi.org/10.1525/bio.2010.60.8.6>.
- Borchers, D.L., Efford, M.G., 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64, 377–385.
- Brand, C.J., Keith, L.B., Fischer, C.A., 1976. Lynx responses to changing snowshoe hare densities in central Alberta. *J. Wildl. Manage.* 40, 416–428.
- Campbell, E.M., Antos, J.A., vanAkker, L., 2019. Resilience of southern Yukon boreal forests to spruce beetle outbreaks. *For. Ecol. Manage.* 433, 52–63. <https://doi.org/10.1016/j.foreco.2018.10.037>.
- Chandler, R.B., Royle, J.A., King, D.I., 2011. Inference about density and temporary emigration in unmarked populations. *Ecology* 92 (7), 1429–1435.
- Cheng, E., Hodges, K.E., Scott Mills, L., 2015. Impacts of fire on snowshoe hares in Glacier National park, Montana, USA. *Fire Ecol.* 11, 119–136. <https://doi.org/10.4996/fireecology.1102119>.
- Colorado State Forest Service, 2018. 2018 Report on the health of Colorado's forests. Colorado State University, Fort Collins, CO, USA.
- Colorado State Forest Service, 2021. 2021 Report on the health of Colorado's forests: managing Colorado's forests during drought. Colorado State University, Fort Collins, CO, USA.
- DeRose, R.J., Bentz, B.J., Long, J.N., Shaw, J.D., 2013. Effect of increasing temperatures on the distribution of spruce beetle in Engelmann spruce forests of the Interior West, USA. *For. Ecol. Manage.* 308, 198–206. <https://doi.org/10.1016/j.foreco.2013.07.061>.
- Devineau, O., Shenk, T.M., White, G.C., Doherty, P.F., Lukacs, P.M., Kahn, R.H., 2010. Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. *J. Appl. Ecol.* 47, 524–531. <https://doi.org/10.1111/j.1365-2664.2010.01805.x>.
- Dixon, G.E., 2002. Essential FVS: a user's guide to the Forest Vegetation Simulator. USDA Forest Service, Forest Management Service Center, Fort Collins, Colorado, USA.
- Drever, M.C., Martin, K., 2007. Spending time in the forest: responses of cavity-nesters to temporal changes in forest health in interior British Columbia. In: Bissonette, J.A., Storch, I. (Eds.), *Temporal Dimensions of Landscape Ecology: Wildlife Responses to Variable Resources*. Springer, New York, New York, USA, pp. 236–251.
- Ellis, M.M., Ivan, J.S., Schwartz, M.K., 2014. Spatially explicit power analyses for occupancy-based monitoring of wolverine in the U.S. Rocky Mountains. *Conserv. Biol.* 28, 52–62. <https://doi.org/10.1111/cobi.12139>.
- Ferron, J., Potvin, F., Dussault, C., 1998. Short-term effects of logging on snowshoe hares in the boreal forest. *Can. J. For. Res.* 28, 1335–1343.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *For. Ecol. Manage.* 238, 24–53. <https://doi.org/10.1016/j.foreco.2006.10.011>.
- Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mamm. Rev.* 35, 51–81. <https://doi.org/10.1111/j.1365-2907.2005.00053.x>.
- Fiske, I.J., Chandler, R.B., 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23. <https://doi.org/10.18637/jss.v043.i10>.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. *Science* 80-.), 349, 819–822. <https://doi.org/10.1126/science.aaa9092>.
- Gelman, A., Hill, J., 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, New York, New York, USA.
- Graham, R.T., Jain, T.B., 1998. Silviculture's role in managing boreal forests. *Conserv. Ecol.* 2. <http://www.consecol.org/vol2/iss2/art8/>. <https://doi.org/10.5751/es-00053-020208>.
- Griffin, P.C., Mills, L.S., 2007. Precommercial thinning reduces snowshoe hare abundance in the short term. *J. Wildl. Manage.* 71, 559–564. <https://doi.org/10.2193/2004-007>.
- Hansen, E.M., Bentz, B.J., 2003. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). *Can. Entomol.* 135, 697–712.
- Hart, S.J., Veblen, T.T., Schneider, D., Molotch, N.P., 2017. Summer and winter drought drive the initiation and spread of spruce beetle outbreak. *Ecology* 98, 2698–2707. <https://doi.org/10.1002/ecy.1963>.
- Hodges, K.E., 2000a. Ecology of snowshoe hares in southern boreal and montane forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA, pp. 163–206.
- Hodges, K.E., 2000b. The ecology of snowshoe hares in northern boreal forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA, pp. 117–161.
- Hodges, K.E., Mills, L.S., Murphy, K.M., 2009. Distribution and abundance of snowshoe hares in Yellowstone National Park. *J. Mammal.* 90 (4), 870–878.
- Hodson, J., Fortin, D., Bélanger, L., 2011. Changes in relative abundance of snowshoe hares (*Lepus americanus*) across a 265-year gradient of boreal forest succession. *Can. J. Zool.* 89, 908–920. <https://doi.org/10.1139/z11-079>.
- Holbrook, J.D., Squires, J.R., Olson, L.E., Lawrence, R.L., Savage, S.L., 2016. Multiscale habitat relationships of snowshoe hares (*Lepus americanus*) in the mixed conifer landscape of the Northern Rockies, USA: Cross-scale effects of horizontal cover with implications for forest management. *Ecol. Evol.* <https://doi.org/10.1002/ece3.2651>.
- Holloway, G.L., Malcolm, J.R., 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. *J. Wildl. Manage.* 70, 1735–1745. [https://doi.org/10.2193/0022-541x\(2006\)70\[1735:shrfim\]2.0.co;2](https://doi.org/10.2193/0022-541x(2006)70[1735:shrfim]2.0.co;2).
- Ivan, J.S., Seglund, A.E., Truex, R.L., Newkirk, E.S., 2018. Mammalian responses to changed forest conditions resulting from bark beetle outbreaks in the southern Rocky Mountains. *Ecosphere* 9, e02369. <https://doi.org/10.1002/ecs2.2369>.
- Ivan, J.S., Shenk, T.M., 2016. Winter diet and hunting success of Canada lynx in Colorado. *J. Wildl. Manage.* 80, 1049–1058. <https://doi.org/10.1002/jwmg.21101>.
- Ivan, J.S., White, G.C., Shenk, T.M., 2013a. Using auxiliary telemetry information to estimate animal density from capture-recapture data. *Ecology* 94 (4), 809–816.
- Ivan, J.S., White, G.C., Shenk, T.M., 2013b. Using simulation to compare methods for estimating density from capture-recapture data. *Ecology* 94 (4), 817–826.
- Ivan, J.S., White, G.C., Shenk, T.M., 2014. Density and demography of snowshoe hares in central Colorado. *J. Wildl. Manage.* 78, 580–594. <https://doi.org/10.1002/jwmg.695>.
- Johnson, T.N., Buskirk, S.W., Hayward, G.D., Raphael, M.G., 2015. Timber harvest interacts with broad-scale forest mortality to affect site occupancy dynamics of a vertebrate seed predator. *For. Ecol. Manage.* 340, 95–102. <https://doi.org/10.1016/j.foreco.2014.12.030>.
- Kellner, K.F., Meredith, M., 2022. Package “jagsUI”.
- Kelly, A.J., Hodges, K.E., 2020. Post-fire salvage logging reduces snowshoe hare and red squirrel densities in early seral stages. *For. Ecol. Manage.* 473, 118272. <https://doi.org/10.1016/j.foreco.2020.118272>.
- Kemp, G.A., Keith, L.B., 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. *Ecology* 51, 763–779.
- Kery, M., Royle, J.A., 2016a. Advanced hierarchical distance sampling. In: *Applied Hierarchical Modeling in Ecology*. Elsevier, New York, New York, USA, pp. 463–550.
- Kery, M., Royle, J.A., 2016b. Modeling abundance using hierarchical distance sampling. In: *Applied Hierarchical Modeling in Ecology*. Elsevier, New York, New York, USA, pp. 393–461.
- Koehler, G.M., 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Can. J. Zool.* 68 (5), 845–851.
- Koehler, G.M., Aubry, K.B., 1994. Lynx. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J. (Eds.), *The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx, and Wolverine in the Western United States*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA, pp. 74–98.
- Koprowski, J.L., Alanen, M.L., Lynch, A.M., 2005. Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Conserv.* 126, 491–498. <https://doi.org/10.1016/j.biocon.2005.06.028>.
- Koprowski, J.L., 2005. Pine squirrel (*Tamiasciurus hudsonicus*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. <http://www.fs.fed.us/r2/projects/scp/assessments/pinesquirrel.pdf> Accessed July 25, 2018.
- Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *For. Ecosyst.* 5, 1–15. <https://doi.org/10.1186/s40663-018-0142-2>.
- Latif, Q.S., Ivan, J.S., Seglund, A.E., Pavlacky, D.L., Truex, R.L., 2020. Avian relationships with bark beetle outbreaks and underlying mechanisms in lodgepole pine and spruce-fir forests of Colorado. *For. Ecol. Manage.* 464, 118043. <https://doi.org/10.1016/j.foreco.2020.118043>.
- Linden, D.W., Fuller, A.K., Royle, J.A., Hare, M.P., Frair, J., 2017. Examining the occupancy-density relationship for a low density carnivore. *J. Appl. Ecol.* 54 (6), 2043–2052. <https://doi.org/10.1111/1365-2664.12883>.
- Mowat, G., Slough, B.G., Boutin, S., 1996. Lynx recruitment during a snowshoe hare population peak and decline in Southwest Yukon. *J. Wildl. Manage.* 60, 441–452.
- Mowat, G., Poole, K.G., O'Donoghue, M., 2000. Ecology of lynx in northern Canada and Alaska. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), *Ecology and Conservation of Lynx in the United States*. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA, pp. 265–306.
- National Oceanic and Atmospheric Administration, 2020. Climate Data Online. National Centers for Environmental Information, <https://www.ncdc.noaa.gov/cdo-web/accessed/3/6/20>.
- Newbury, T.L., Simon, N.P.P., 2005. The Effects of clearcutting on snowshoe hare (*Lepus americanus*) relative abundance in central Labrador. *For. Ecol. Manage.* 210 (1-3), 131–142.
- Nudds, T.D., 1977. Quantifying the vegetative structure of wildlife cover. *Wildl. Soc. Bull.* 5, 113–117.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Murray, D.L., Hofer, E.J., 1998a. Behavioural responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 82, 169–183.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., Hofer, E.J., 1998b. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79 (4), 1193–1208.
- O'Donoghue, M., Boutin, S., Murray, D.L., Krebs, C.J., Hofer, E.J., Breitenmoser, U., Breitenmoser-Würsten, C., Zuleta, G., Doyle, C., Nams, V.O., 2001. Coyotes and lynx. In: Krebs, C.J., Boutin, S., Boonstra, R. (Eds.), *Ecosystem Dynamics of the Boreal Forest*. Oxford University Press, New York, New York, USA, pp. 275–323.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), *Systems Analysis of the Global Boreal Forest*. Cambridge University Press, New York, New York, USA, pp. 144–169.
- Plummer, M., 2017. JAGS: Just Another Gibbs Sampler.
- Poole, K.G., 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. *J. Wildl. Manage.* 58, 608–618.
- Potvin, F., Courtois, R., Bélanger, L., 1999. Short-term response of wildlife to clear-cutting in Quebec boreal forest: multiscale effects and management implications. *Can. J. For. Res.* 29, 1120–1127. <https://doi.org/10.1139/x99-040>.

- Potvin, F., Breton, L., Courtois, R., 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: A reassessment 10 years after cut. *Can. J. For. Res.* 35, 151–160. <https://doi.org/10.1139/x04-151>.
- R Development Core Team, 2022. R: a language and environment for statistical computing.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58, 501–517. <https://doi.org/10.1641/b580607>.
- Rocca, M.E., Brown, P.M., MacDonald, L.H., Carrico, C.M., 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. *For. Ecol. Manage.* 327, 290–305. <https://doi.org/10.1016/j.foreco.2014.04.005>.
- Rodman, K.C., Andrus, R.A., Carlson, A.R., Carter, T.A., Chapman, T.B., Coop, J.D., Fornwalt, P., Gill, N.S., Harvey, B.J., Hoffman, A.E., Kelsey, K.C., Kulakowski, D., Laughlin, D.C., Morris, J.E., Negron, J., Nigro, K.M., Pappas, G.S., Redmond, M.D., Rhoades, C.C., Rocca, M.E., Schapira, Z.H., Sibold, J.S., Stevens-Rumann, C., Veblen, T.T., Wang, J., Zhang, X., Hart, S.J., 2022. Rocky Mountain forests are poised to recover following bark beetle outbreaks, but with altered composition. *J. Ecol.* XX 1–54.
- Royle, J.A., Converse, S.J., Freckleton, R., 2014. Hierarchical spatial capture-recapture models: modelling population density in stratified populations. *Methods Ecol. Evol.* 5 (1), 37–43.
- Royle, J.A., Young, K.V., 2008. A hierarchical model for spatial capture-recapture data. *Ecology* 89 (8), 2281–2289.
- Royle, J.A., Dawson, D.K., Bates, S., 2004. Modeling abundance effects in distance sampling. *Ecology* 85, 1591–1597. <https://doi.org/10.1890/03-3127>.
- Rusch, D.A., Reeder, W.G., 1978. Population ecology of Alberta red squirrels. *Ecology* 59, 400–420.
- Russell, R.E., Lehmkuhl, J.F., Buckland, S.T., Saab, V.A., 2010. Short-term responses of red squirrels to prescribed burning in the Interior Pacific Northwest. *USA. J. Wildl. Manage.* 74, 12–17. <https://doi.org/10.2193/2008-342>.
- Saab, V.A., Latif, Q.S., Rowland, M.M., Johnson, T.N., Chalfoun, A.D., Buskirk, S.W., Heyward, J.E., Dresser, M.A., 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in Western North American forests. *For. Sci.* 60, 539–559. <https://doi.org/10.5849/forsci.13-022>.
- Savilaakso, S., Johansson, A., Häkkinä, M., Uusitalo, A., Sandgren, T., Mönkkönen, M., Puttonen, P., 2021. What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. *Environ. Evid.* 10, 1–38. <https://doi.org/10.1186/s13750-020-00215-7>.
- Schapira, Z., Stevens-Rumann, C., Shorrock, D., Hoffman, C., Chambers, A., 2021. Beetlemania: Is the bark worse than the bite? Rocky Mountain subalpine forests recover differently after spruce beetle outbreaks and wildfires. *For. Ecol. Manage.* 482, 118879. <https://doi.org/10.1016/j.foreco.2020.118879>.
- Schebeck, M., Hansen, E.M., Schopf, A., Ragland, G.J., Stauffer, C., Bentz, B.J., 2017. Diapause and overwintering of two spruce bark beetle species. *Physiol. Entomol.* 42, 200–210. <https://doi.org/10.1111/phen.12200>.
- Slough, B.G., Mowat, G., 1996. Lynx population dynamics in an untrapped refugium. *J. Wildl. Manage.* 60, 946–961.
- Smith, F.W., 2000. Forestry practices and forest fragmentation in the Southern Rocky Mountains. In: Knight, R., Smith, F., Buskirk, S., Romme, W.H., Baker, W.L. (Eds.), *Forest Fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, Colorado, USA, pp. 123–134.
- Squires, J.R., Holbrook, J.D., Olson, L.E., Ivan, J.S., Ghormley, R.W., Lawrence, R.L., 2020. A specialized forest carnivore navigates landscape-level disturbance: Canada lynx in spruce-beetle impacted forests. *For. Ecol. Manage.* 475, 118400. <https://doi.org/10.1016/j.foreco.2020.118400>.
- Squires, J.R., Ivan, J.S., Paolini, K.E., Olson, L.E., Jones, G.M., Holbrook, J.D., 2022. Keystone structures maintain forest function for Canada lynx after large-scale spruce beetle outbreak. *Environ. Res.: Ecology* 2 (1), 011001.
- St-Laurent, M.-H., Cusson, M., Ferron, J., Caron, A., 2008. Use of Residual Forest by Snowshoe Hare in a Clear-cut Boreal Landscape. *Northeast. Nat.* 15 (4), 497–514.
- Temperli, C., Veblen, T.T., Hart, S.J., Kulakowski, D., Tepley, A.J., 2015. Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model. *Ecosphere* 6 (11), art231. <https://doi.org/10.1890/es15-00394.1>.
- Thomas, J.P., Reid, M.L., Barclay, R.M.R., Jung, T.S., 2019. Salvage logging after an insect outbreak reduces occupancy by snowshoe hares (*Lepus americanus*) and their primary predators. *Glob. Ecol. Conserv.* 17, e00562.
- Thompson, I.D., Curran, W.J., 1995. Habitat suitability for marten of second-growth balsam fir forests in Newfoundland. *Can. J. Zool.* 73, 2059–2064. <https://doi.org/10.1139/z95-242>.
- Thompson, I.D., Davidson, I.J., O'Donnell, S., Brazeau, F., 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Can. J. Zool.* 67 (7), 1816–1823.
- Thornton, D.H., Wirsing, A.J., Roth, James, D., Murray, D.L., 2012. Complex effects of site preparation and harvest on snowshoe hare abundance across a patchy forest landscape. *For. Ecol. Manage.* 280, 132–139. <https://doi.org/10.1016/j.foreco.2012.06.011>.
- U.S. Fish and Wildlife Service, 2000. Endangered and threatened wildlife and plants: determination of threatened status for the contiguous U. S. distinct population segment of the Canada lynx and related rule, final rule. *Fed. Regist.* 65, 16052–16086.
- Veblen, T.V., 2000. Disturbance patterns in southern Rocky Mountain forests. In: Knight, R.L., Smith, F.W., Buskirk, S.W., Romme, W.H., Baker, W.L. (Eds.), *Forest Fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, Colorado, USA, pp. 31–54.
- Veblen, T.T., Hadley, K.S., Reid, M.S., Rebertus, A.J., 1991. The Response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72, 213–231.
- White, G.C., Cooch, E.G., 2017. Population abundance estimation with heterogeneous encounter probabilities using numerical integration. *The Journal of Wildlife Management* 81, 322–336.
- Whitman, E., Parisien, M.A., Thompson, D.K., Flannigan, M.D., 2019. Short-interval wildfire and drought overwhelm boreal forest resilience. *Sci. Rep.* 9, 1–12. <https://doi.org/10.1038/s41598-019-55036-7>.
- Yahner, R.H., 2003. Pine squirrels. In: Feldhamer, G., Thompson, B., Chapman, J. (Eds.), *Wild Mammals of North America*. The Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 268–275.
- Zugmeyer, C.A., Koprowski, J.L., 2009a. Habitat selection is unaltered after severe insect infestation: concerns for forest-dependent species. *J. Mammal.* 90, 175–182. <https://doi.org/10.1644/07-mamm-a-399.1>.
- Zugmeyer, C.A., Koprowski, J.L., 2009b. Severely insect-damaged forest: A temporary trap for red squirrels? *For. Ecol. Manage.* 257, 464–470. <https://doi.org/10.1016/j.foreco.2008.09.020>.

Further reading

- Royle, J.A., Dorazio, R.M., 2012. Parameter-expanded data augmentation for Bayesian analysis of capture-recapture models. *J. Ornithol.* 152, 521–537. <https://doi.org/10.1007/s10336-010-0619-4>.