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Keystone structures maintain forest function for Canada lynx after large-scale spruce beetle outbreak

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E-mail: John.Squires@usda.gov**Keywords:** Bhattacharyya's affinity overlap, distribution, forest disturbance, horizontal cover, keystone structures, natural experiment

Abstract

Central to species conservation in an era of increased disturbance from climate change is understanding the primary mechanisms that facilitate how forest-dependent species respond to changes in forest structure and composition. Here, we leveraged a natural experiment to investigate how changed forest structure and function pre-spruce-beetle (*Dendroctonus rufipennis*) and post-beetle disturbance influenced the regional distribution of Canada lynx (*Lynx canadensis*) at their southern range periphery. We compared the distribution of Canada lynx that were reintroduced into Colorado, USA from 1999–2006 to the current (2015–2017) distribution following a spatial large-scale spruce beetle outbreak from 2007 to 2016. Canada lynx did not substantially alter their distribution following the wide-spread alteration of forest structure and composition following the insect outbreak. We used the Bhattacharyya's affinity metric to document that core (50% isopleth) and overall population ranges (95% isopleth) overlapped significantly at 50% and 77% respectively. In addition, areas of low and high relative use remained similar after the bark beetle outbreak and mapped onto one another in nearly a 1:1 fashion (Spearman rank correlation = 0.92, $p < 0.01$). The low impact of forest change on distribution was due to the keystone habitat elements (high horizontal forest cover, snowshoe hares) that remained functional. Thus, our results highlight that conservation scientists should increase their focus to understand the underlying mechanisms that impact wildlife distributions as climate-related disturbances becomes ever more amplified.

1. Introduction

As megadisturbances such as wildfire and insect damage rapidly transform forests globally (Millar and Stephenson 2015), what are the implications for wildlife? One approach to better understand the mechanisms underlying the effects of spatial large-scale disturbances on wildlife is to examine responses by taxa that we predict will be especially sensitive to structural and functional forest changes. Forest carnivores exhibit sensitivity to increased natural disturbance (Vanbianchi *et al* 2017, Squires *et al* 2020), increases in forest fragmentation by humans (Olson *et al* 2014, Holbrook *et al* 2018), climate gradients (Zielinski *et al* 2017), and an expanded human footprint through urbanization and outdoor recreation (Stewart *et al* 2016, Slauson *et al* 2017, Olson *et al* 2018, Heinemeyer *et al* 2019, Squires *et al* 2019). Canada lynx (*Lynx canadensis*; hereafter interchangeably as 'lynx') is a forest carnivore that may be particularly sensitive to environmental change due to their highly specialized adaptations for hunting snowshoe hares (*Lepus americanus*) during winter in boreal and subalpine forests (Aubry *et al* 2000, Mowat *et al* 2000). Indeed, lynx exhibit spatial, behavioral, and demographic responses to changes in the structural and functional elements

of forests (Squires *et al* 2013, Holbrook *et al* 2017, 2019, Kosterman *et al* 2018). However, the observational nature of most field studies leaves us uncertain about the response of lynx, and other forest carnivores, to structural and functional changes associated with spatial large-scale disturbances that are increasing with climate change (Stephens *et al* 2018, Davis *et al* 2019, Fetting *et al* 2019).

Natural experiments are perhaps one of the most powerful approaches in ecology and conservation science to increase understanding of spatial large-scale disturbance events. In this study, we leveraged a natural experiment by considering how changed landscape structure and function pre-disturbance and post-disturbance would influence the regional distribution of Canada lynx at their southern range periphery. From 1999 to 2006, Colorado Parks and Wildlife (CPW) released 218 wild-caught lynx from Canada and Alaska into Colorado, USA in an effort to establish a viable population of lynx at the species' southern-most periphery (Devineau *et al* 2010). Approximately 85% were released on the Rio Grande National Forest in the San Juan Mountain Range of southern Colorado. Following the release, a spruce beetle (*Dendroctonus rufipennis*) outbreak impacted over half the forests across the San Juan Mountains from 2007 to 2016 (U.S. Forest Service Forest Health Protection 2017). Surveys conducted from 2013 to 2014 confirm that lynx remain present in the region (Ivan *et al* 2018) with anecdotal field observations of females with litters.

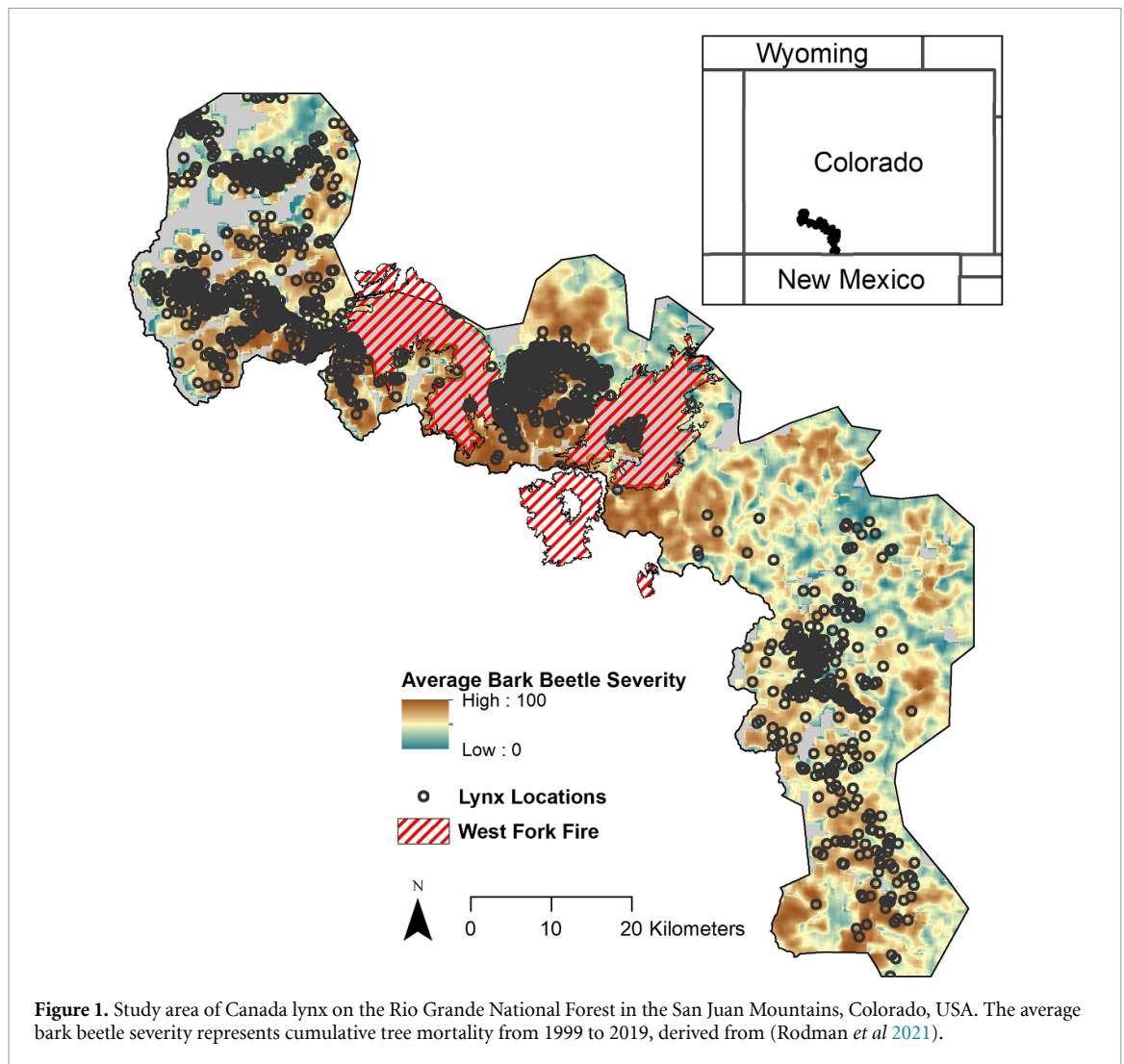
Our research group previously (2015–2017) studied the resource-use patterns of resident Canada lynx that were at least second-generation transplants in the same forests where most individuals were originally released (Squires *et al* 2020). We discovered at a landscape scale that Canada lynx selected forests with a higher proportion of beetle-killed trees, whereas within home ranges during winter they exhibited strong selection for forests with live canopy of Engelmann spruce (*Picea engelmannii*) and higher densities of subalpine fir (*Abies lasiocarpa*). Despite their consistent selection patterns, it remained unclear at a broad spatial scale if the spatial distribution of lynx across the region had shifted due to the changed environmental template from bark-beetle impacts. One potential outcome, assuming behavioral flexibility, would be a changed distribution if beetle-related disturbance altered the function of subalpine forests for Canada lynx. Alternatively, we predicted that Canada lynx would maintain their pre-beetle space-use and distribution, primarily because of the preservation of horizontal vegetation cover for hares in beetle-impacted forests (Ivan *et al* 2018, Squires *et al* 2020). This contrasts with wildfire-based disturbance that we would expect to remove most horizontal cover, causing negative cascading effects on snowshoe hares and Canada lynx. Testing this prediction not only advances the science of lynx conservation in disturbed landscapes, but also contributes to the larger discussion of how disturbance processes impact species space-use and distribution in environments that are most vulnerable to climate impacts.

2. Methods

2.1. Study area

Our study area (3466 km²) included the eastern San Juan Mountains of southern Colorado, USA (location centroid 37.554 Lat, −106.868 Lon; figure 1), which was administered as public land by the US Forest Service, Rio Grande National Forest. Topography of the San Juan Mountains was characterized by steep mountain valleys punctuated with high peaks across an elevation range of approximately 2000–4300 m asl. The high topographic relief provided a mosaic of spruce-fir forests interspersed with meadows and avalanche paths extending up to alpine tundra. The subalpine boreal forests that supported Canada lynx (elevation 2500–3500 m asl) were dominated by Engelmann spruce and subalpine fir. Winters extended from November through May (low elevations) and some snow cover persisted into June. Annual snow water equivalent (1991–2020) for our study area was approximately 510 mm (SD 169), and winter (December–February) temperatures averaged approximately −7.4 °C (SD 0.6) with summer temperatures (June–August) approximately 10.5 °C (SD 1.3) (Wang *et al* 2016, AdaptWest Project 2022).

Prior to 2002, the unmanaged subalpine boreal forests on our study area included mature spruce trees approximately 200–350 years in age; some trees on the Rio Grande National Forest exceeded 600 years (Whipple and Dix 1979, Ryerson *et al* 2003). In 2004, spruce beetles began causing mortality to primarily older Engelmann spruce trees. The beetle outbreak then intensified such that 10% of the study area was impacted by 2007, 20% by 2010, 30% by 2012, 40% by 2014, after which insect activity began to plateau at nearly 50% impact by 2016 (U.S. Forest Service Forest Health Protection 2017). Mortality for individual stands comprised largely of spruce approached 90% in many cases. In addition, the study area was impacted by an extensive (200 km²) fire in 2013 (the West Fork Complex; figure 1), but we did not investigate lynx use of this fire as a part of our research, and thus removed lynx locations within the fire boundary.



2.2. Canada lynx distribution—pre-disturbance and post-disturbance

We used telemetry (very high frequency (VHF), Argos, global positioning system (GPS)) to evaluate if Canada lynx altered their regional distribution in response to disturbance from a spruce beetle outbreak. CPW fitted each lynx with a VHF transmitter as they reintroduced the species to southwestern Colorado (Devineau *et al* 2010). Monitoring lynx movements using VHF technology in remote mountain terrain required low-elevation aircraft. Beginning in April 2000, CPW also then added Argos satellite transmitters to VHF collars. From 2000 to 2009, CPW replaced collars on lynx each winter when possible and they collared new individuals including kittens that were captured. Argos transmitters were programed to transmit 1 d per week and often recorded multiple locations per transmission day. The location error associated with aircraft locations was approximately ± 400 m and approximately < 250 m for the most accurate Argos locations (class 3; www.argos-system.org). For this study, we only included high-quality (VHF locations, class 3 Argos) winter locations collected between 1999 and 2007 and that were obtained at least one year from an animal's initial release date. Prior to 2007, Canada lynx were handled under the guidance of CPW Animal Care and Use Permit # 04-2000 and 03-2005.

In 2015–2017, following the spruce beetle outbreak, we captured adult (> 3 year old) Canada lynx (6 males and 4 females) in box traps (Kolbe *et al* 2003) that we set on lynx tracks from December to March (Squires *et al* 2020). We believe our lynx sample included most individuals present on the study area based on our field observations. We fitted Canada lynx with store-on-board GPS collars (210–230 g; Telemetry Solutions, Concord, California, USA) that took hourly locations, seven days a week. Collars included a drop-off mechanism that automatically activated in early August following summer sampling period. All capture and handling procedures from 2015 to 2017 were conducted under Animal Care and Use Permit # CPW 01-2015.

2.3. Overlap analysis

We analyzed lynx distribution within the study area to assess whether lynx altered their space use patterns after bark-beetle disturbance. We standardized our datasets of pre-disturbance and post-disturbance to only include locations collected during winter months (January–April). This resulted in 849 lynx relocations to document the distribution of lynx in the study area prior to bark beetle outbreaks (53 individuals; $\bar{x} = 7$ locations per individual per year; range = 1–28 locations per individual per year, from 1999 to 2007). We then fit a kernel density utilization distribution across all individuals in this sample. Kernel density estimates can be strongly influenced by sample size (Fieberg 2007, Keating and Cherry 2009), therefore we balanced the pre-disturbance and post-disturbance datasets by randomly selecting 85 locations from the 10 individual lynx live-trapped in 2015–2017 ($n = 850$ GPS locations). We estimated utilization distributions across a range of isopleths (0.40%–95% at 5% intervals) with the *amt* package in R (R Version 4.1.0) and calculated Bhattacharyya's affinity (BA) to obtain overlap estimates across isopleths (Bhattacharyya 1943). BA overlap is commonly implemented for measuring space-use similarity between probability distributions, where values range from 0 (no overlap) to 1 (complete spatial overlap; (Bhattacharyya 1943, Fieberg and Kochanny 2005).

2.4. Distribution analysis

To complement the overlap analysis, we evaluated population-level, post-beetle distribution across the density of pre-beetle lynx locations. If bark beetles changed post-beetle lynx distributions, we would expect post-beetle lynx locations to shift relative to pre-beetle disturbances. To evaluate this question, we created a point density of pre-beetle lynx locations at the full extent of our study area, and binned the frequency of use (i.e. number of locations/1 km²) into deciles (i.e. 10 bins of equal area). We overlaid the post-beetle lynx locations onto the pre-beetle distribution and extracted the bin number (1–10) to our post-beetle data. We then calculated the percentage of post-beetle lynx locations within each bin, which allowed us to assess the degree to which lynx maintained high and low use within the same areas following the beetle outbreak. We estimated a Spearman rank correlation coefficient with the percentage of post-beetle lynx locations as the y -axis and bin number as the x -axis. A positive correlation would indicate that post-beetle lynx locations generally followed the expected distribution if bark beetles had little effect on the distribution of lynx. A random allocation of post-beetle lynx locations would result in 10% of lynx locations contained within each (1–10) of the pre-beetle bins. To further our understanding of the effect of bark beetle disturbance on lynx over time, we assessed the amount of disturbance within lynx distributions. Rodman *et al* (2021) quantified the cumulative severity of bark beetle tree mortality in the Southern Rocky Mountains from 1999 to 2019. We reclassified the severity raster to match our spatial extent and averaged bark beetle tree mortality. We overlaid bark beetle severity onto the pre-beetle lynx distribution. We then estimated the amount of cumulative tree mortality within each bin number (1–10). If beetle disturbance impacted lynx movements, a higher cumulative severity, particularly in high use bins (e.g. 9–10), would indicate that post-beetle distributions would shift away from those areas with high tree mortality.

3. Results

Canada lynx in southern Colorado did not substantially alter their distribution following the wide-spread alteration of forest structure and composition following a spruce bark-beetle outbreak (figure 2). Both the core (50% isopleth) and overall population ranges (90% isopleth) overlapped significantly at 50% and 77%, respectively. Thus, at the larger population-level distribution, BA overlap remained relatively stable and started to asymptote indicating that lynx persisted within the same areas despite substantial changes to the forest overstory following a spruce beetle outbreak (figure 3). The lower overlap at the core-distribution level was mostly a function of subsequent fire in the beetle-impacted landscape (figure 2).

Similarly, a reshuffle analysis that evaluated the density of post-beetle point data relative to the pre-beetle distribution demonstrated the distribution of lynx within the study area remained spatially consistent. Areas with low relative use (low point density) and high relative use remained similar after the bark beetle outbreak (figure 4) and mapped onto one another in nearly a 1:1 fashion (Spearman rank correlation = 0.92, $p < 0.01$). Thus, Canada lynx were not randomly distributed across the landscape following the outbreak, which would have been indicated by 10% of the post-beetle locations falling within each decile of the pre-beetle bins (dashed line, figure 4), or a Spearman rank correlation near zero. Moreover, our cumulative severity analyses also illustrated that forest mortality from bark beetles occurred relatively homogeneously across the pre-beetle space use (i.e. low and high use areas; figure 5). Taken together, these results show that despite substantial bark beetle outbreaks across the eastern San Juan Mountains, lynx did not significantly alter population-level space use patterns.

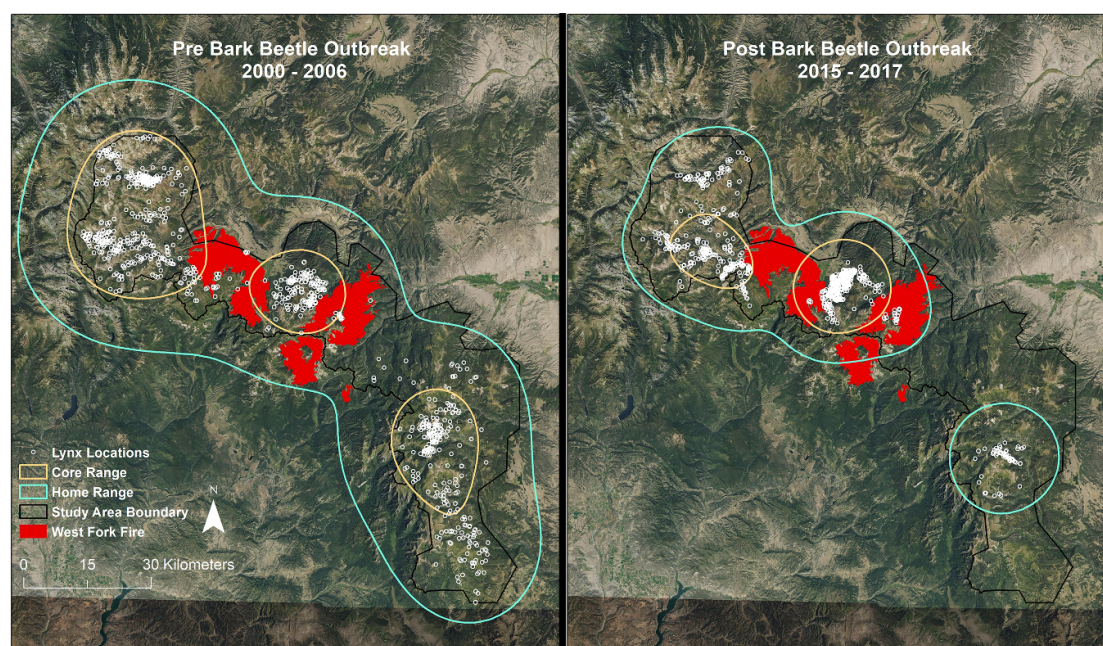


Figure 2. Population-level kernel density estimates for Canada lynx at the core range and entire range, 50% and 95% respectively, for pre-beetle and post-beetle data.

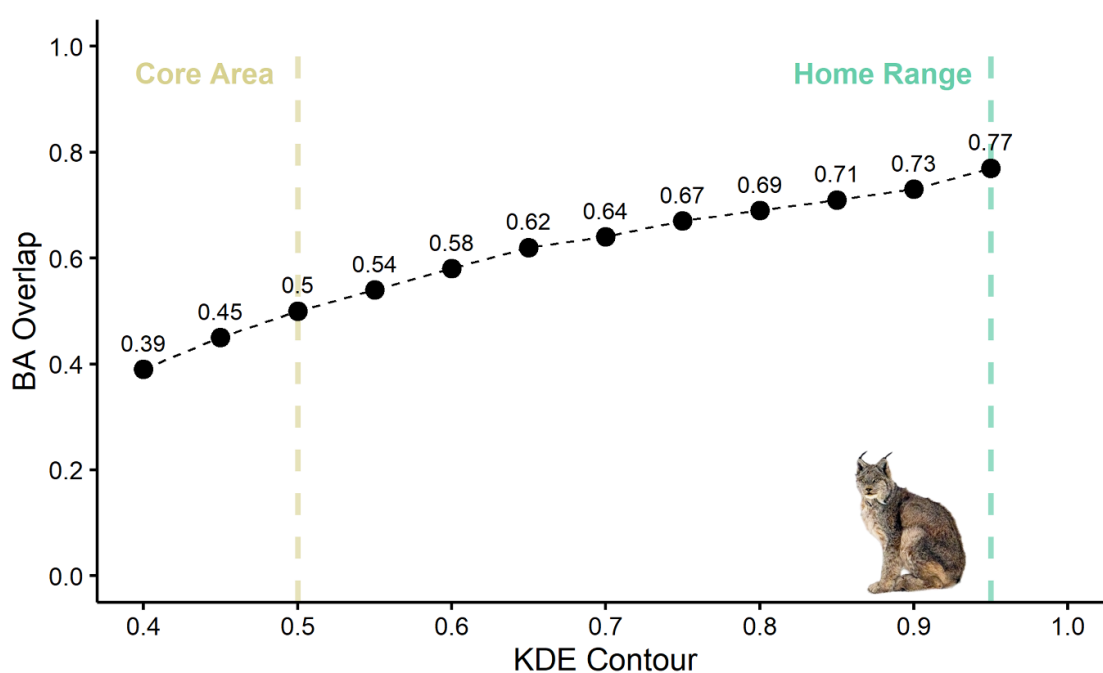


Figure 3. Bhattacharyya's affinity (BA) index for pre-beetle and post-beetle data for population-level kernel density estimates (KDE) of Canada lynx in the San Juan Mountains, Colorado, USA.

4. Discussion

We demonstrated through a unique natural experiment that Canada lynx retained their pre-disturbance spatial distribution despite significant changes to the structure and composition of subalpine forests from beetle-related disturbance. This result is with the caveat that we only assessed changes to distribution up to a decade following beetle impacts. Understanding and testing how species respond to structural and functional changes in environmental heterogeneity is fundamental to developing effective conservation strategies (Sparrow 1999, Stein *et al* 2014, Trevail *et al* 2019, Jones *et al* 2020). We know that changes in the structure

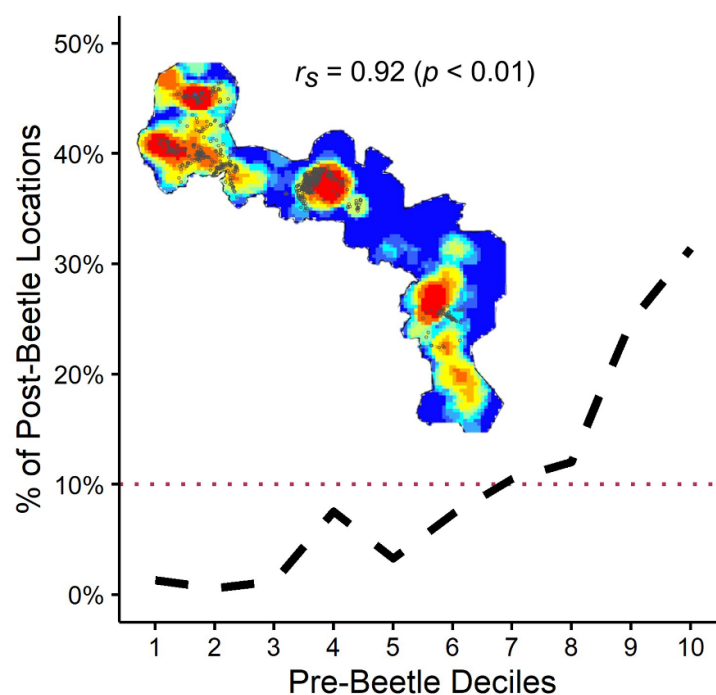


Figure 4. The distribution of Canada lynx locations post-beetle disturbance across the density of pre-beetle relocations (i.e. 10 bins of equal area) as evaluated using a Spearman rank correlation. The red dotted line represents if lynx were to randomly distribute across the landscape following the bark beetle outbreak. The map represents the kernel density estimate from the pre-beetle lynx distribution that we reclassified into 10 equal-area bins, where blue depicts low use (i.e. bin 1) and red depicts areas of high pre-beetle use (i.e. bin 10); gray dots represent the post-beetle relocations relative to the pre-beetle kernel density estimate across our study area.

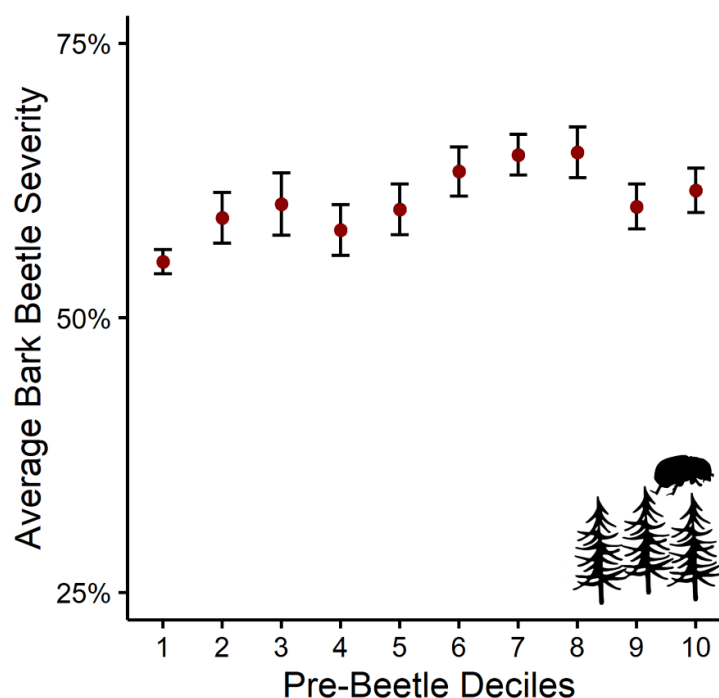


Figure 5. The average cumulative severity of bark beetle tree mortality from 1999 to 2019 (Rodman *et al* 2021) across the density of pre-beetle relocations (i.e. 10 bins of equal area).

and function of vegetation are central drivers of species richness in communities (Tews *et al* 2004, Stein *et al* 2014), but they also alter animal behavior, such as foraging efficiency, with potential impacts to fitness (Trevail *et al* 2019). We also recognize that changes to environmental heterogeneity may impact groupings of

species that may be linked by ‘keystone structures;’ understanding these structures is central to conservation science (Tews *et al* 2004).

Insect outbreaks generally release shade tolerant understory trees that were already established when the outbreak occurred (Hawkins *et al* 2012, Rhoades *et al* 2017, Carlson *et al* 2020). Seedling establishment can occur as well, which can contribute a multitude of new stems to severely impacted areas, but this generally takes decades and does not contribute to additional understory cover immediately post-outbreak (Veblen *et al* 1991). Thus, areas with relatively high density of conifer seedlings and saplings (and thus high horizontal cover) pre-beetles were likely to have relatively high densities of these size classes (and high horizontal cover) post-beetles. Ivan *et al* (2018) found that snowshoe hare occupancy changed little up to a decade after bark beetle outbreaks in Colorado, likely reflecting minimal changes in understory vegetation. Therefore, we suggest that despite significant changes to forest structure (loss of canopy cover and large stems) and composition (dominance of live stems shifted toward subalpine fir) from spruce beetle impacts, the distribution of horizontal cover and snowshoe hares remained largely in place, as did lynx exploitation of these keystone elements. However, Canada lynx in the Southern Rockies may exhibit increased population vulnerability due to reductions in alternative prey, such as red squirrels (*Tamiasciurus hudsonicus*) from beetle impacts (Ivan *et al* 2018), and to fire disturbance that alters these keystone elements (Vanbianchi *et al* 2017, Squires *et al* 2020).

‘Megadisturbances’ that result from human-caused climate change continue to threaten forested ecosystems worldwide (Millar and Stephenson 2015). Disturbance may especially impact the persistence of boreal and subalpine forests (Sherriff *et al* 2011, Price *et al* 2013, Gauthier *et al* 2015, Millar and Stephenson 2015) that lynx require, even though vegetation succession in this ecosystem was structured by spatially large-scale disturbances for millennia (Price and Apps 1995, Agee 2000, Eisenhart and Veblen 2011). Yet our results highlight the need for improved understanding of functional relationships between wildlife and their habitat if we want to be able to predict impacts of changing disturbance regimes and climate. For example, we originally predicted that both Canada lynx and snowshoe hares would strongly avoid beetle-killed forests—a prediction that was not supported by the data in previous work (Ivan *et al* 2018, Squires *et al* 2020). Our current results that indicated changes to structure in subalpine forests following a bark beetle outbreak also had little effect on the broad-scale lynx distribution given that key functional elements (e.g. prey abundance and distribution) in these forests supporting lynx were conserved. Predicting effects to lynx or to other wildlife following future bark-beetle outbreaks (e.g. those that are more extensive or severe), wildfire, and other disturbances (e.g. thinning or logging) may therefore hinge on our ability to understand associated changes in forest function (Tingley *et al* 2020). As climate-related disturbances become more amplified, conservation scientists must shift their focus to understand mechanisms that underly wildlife-habitat relationships.

Our insights also reinforce the importance of long-term research in science and conservation. A major challenge to understanding how spatial large-scale disturbance influences animal populations is a disconnect between duration of research and the timeline of change (Clutton-Brock and Sheldon 2010). Often, research and monitoring is limited in temporal scope (Hayes and Schradin 2017), which directly impacts derived inference (Pauly 1995). By investing in monitoring and research of Canada lynx in the Southern Rockies before and after a bark-beetle epidemic, we were able to leverage a natural experiment and evaluate how bark-beetles impact the distribution of a federally threatened carnivore that depends on forests. Although we observed little change in distribution, additional pressures, such as expanding wildfires are increasingly impacting subalpine and boreal forest ecosystems (Gauthier *et al* 2015, Millar and Stephenson 2015), and thus additional long-term research is needed to discern across individuals, populations, and communities the consequence of such disturbances, especially within the context of increased climate change.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Ethical statement

The authors declare that they have no known competing financial interests or personal relationships that influenced the research reported in this paper. Institutional or national ethic review was not required in terms of data collection or fieldwork. No clinical trials were required that involved human subjects. Prior to 2007, Canada lynx were handled under the guidance of Colorado Parks and Wildlife Animal Care and Use Permit # 04-2000 and 03-2005. From 2015 to 2017, lynx capture and handling were directed under Colorado Parks and Wildlife, Animal Care and Use Permit # CPW 01-2015.

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