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Forest structure mediates occupancy and extinction of vertebrate prey species on the trailing edge of the boreal forest

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ABSTRACT

Climate change is expected to shift the distributions of global biomes. High latitude biomes, such as the boreal forest, are among the most vulnerable and serve as a bellwether for the effects of climate change on other ecosystems. We examined patterns of occupancy, local extinction, and abundance in a guild of forest-associated vertebrate prey species on the southern margin of the boreal forest in Minnesota (USA). We used multi-season, multi-state, and multi-species occupancy modeling approaches to determine the effects of land cover, forest structural characteristics, and climatic variation on two boreal-associated species, spruce grouse (Canachites canadensis) and snowshoe hare (Lepus americanus), and a forest generalist, ruffed grouse (Bonasa umbellus). Occupancy, abundance, and extinction of spruce grouse was strongly associated with landscape-scale characteristics. In particular, deciduous forest cover may govern their southern range limit. Broadly, forest understory structure played a significant role in occupancy, extinction, and abundance patterns of all three species, with ruffed and spruce grouse generally associated with vegetation density in the lower and mid-canopy layer (5.00-15.00 m) and snowshoe hare associated with density in the shrub layer (1.37-5.00 m) in winter. Cooccurrence varied annually but was greatest in mixed forests during an uncharacteristically warm and snowsparse year. Climatic variables (winter temperature and snowfall) were associated with extinction probabilities for all three species, but the effect was generally weaker than that of forest structure. Our results suggest that forest management practices that promote dense understory structure may help provide climate refugia for vertebrate prey species in boreal forest ecosystems.

1. Introduction

The center-periphery hypothesis of extinction predicts that peripheral populations are more vulnerable to extinction than central populations due to suboptimal habitat conditions, lower population densities, and greater stochasticity (Lawton, 1993). Despite greater extinction risk and generally lower genetic diversity, peripheral populations can have significant conservation value due to potential adaptation to marginal environmental conditions (Hardie and Hutchings, 2010). Deciding whether to prioritize peripheral populations for conservation has been a central focus of climate change adaptation (Lesica and Allendorf, 1995).

Climate change is causing warmer winter conditions and reduced snowfall in many regions. Therefore, habitats and wildlife species are broadly expected to shift northward and upward in elevation in the northern hemisphere (Hickling et al., 2006). Accordingly, populations at the southern margin of species' distributions are expected to contract over the next several decades. In particular, boreal forests are expected to experience one of the most rapid shifts in distribution among the Earth's major biomes (Loarie et al., 2009). Those spatial and temporal shifts suggest conserving "trailing edge" populations (i.e., those at the low-latitude limit of a species' distribution) will be particularly challenging under changing climate conditions (Hampe and Petit, 2005). Understanding habitat and climatic requirements of boreal forest species at their southern range limits can inform climate adaptation strategies for conserving climate-sensitive wildlife species.

Climate change and land-use change are two of the strongest drivers of biodiversity loss globally (Travis, 2003; Maxwell et al., 2016). These processes can be interactive, and anthropogenic land use has the potential to harm (Jetz et al., 2007) or support (Morelli et al., 2012)

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climate-sensitive populations. Forest management can interact with climate change to either ameliorate or accelerate the negative effects of climate change on boreal forest wildlife (Virkkala, 2016). Prioritizing forest management practices that provide refugial habitat for climatesensitive species could mitigate the effects of climate change. Despite this, most wildlife adaptation strategies have focused on large scale reserve-design planning initiatives, while local, management-relevant adaptation strategies have been largely ignored (LeDee et al., 2020).

One ecological community that appears particularly at odds with current climate mitigation priorities is early and mid-successional forest vertebrates. Climate adaptation strategies often prioritize maximizing carbon storage in managed forests, which may exacerbate the effects of climate change on wildlife dependent on early and mid-successional forest (Littlefield and D'Amato, 2022). Management strategies can improve overall adaptive capacity of forest ecosystems by acknowledging trade-offs between forest carbon storage and the need for climate refugia for early and mid-successional forest specialists.

In this study, we examined occupancy patterns of three early and mid-successional forest vertebrate prev species: spruce grouse (Canachites canadensis), ruffed grouse (Bonasa umbellus) and snowshoe hares (Lepus americanus) at the southern margin of the boreal forest in northern Minnesota, USA. These three species overlap spatially in the winter, share predators, and exhibit approximately 10-year population cycles at northern latitudes (Williams et al., 2004, https://www.adfg.ala ska.gov/static/education/wns/grouse.pdf, Pomara and Zuckerberg, 2017, although it is not yet known if trailing edge populations of spruce grouse cycle, Roy and Giudice, 2023). Population cycles have been hypothesized to be due to predator-prey interactions and delayed density dependence at northern latitudes (Williams et al., 2004), with raptors switching to ruffed grouse as snowshoe hare populations decline (Keith and Rusch, 1989). More recently, studies have found support for climate variability driving variability in demographic rates that produce population cycles at northern latitudes (Zimmerman et al., 2008, Yan et al., 2013, Pomara and Zuckerberg, 2017).

Spruce grouse ecology and distribution are closely associated with the boreal forest in North America (Schroeder et al., 2018). Although populations appear to be declining at their southern range margin (Ross et al., 2016), their ecology and status are not as well documented as many North American game birds. Furthermore, research has been focused primarily in the range of the *franklinii* subspecies, which occur within and west of the Rocky Mountains, with even less known about the canadensis subspecies that occurs throughout the eastern boreal forest of North America. The studies on the *franklinii* subspecies suggests spruce grouse prefer dense stands of spruce and fir trees, typically of short to intermediate height (Boag and Schroeder, 1987; Huggard, 2003). These forest characteristics may improve the survival and recruitment of young, which are important factors in population regulation (Boag et al., 1979). Recent work from the range of the canadensis subspecies has also documented an association with younger forests. In the Adirondack Mountains of New York, a decline in spruce grouse occupancy over thirty years was attributed to forest maturation (Ross et al., 2016). In Quebec, at the southern margin of the boreal forest, spruce grouse occupancy was associated with coniferous tree cover and deciduous shrub cover, and deciduous tree cover limited spruce grouse occupancy (Casabona et al., 2022). Because spruce grouse is likely to be affected by warming temperatures (Murray et al., 2017), we considered its niche/ habitat for evaluation in the northern boreal forests of Minnesota.

The two other study species also rely on early to mid-successional forest but are more widespread and widely studied than spruce grouse. The ruffed grouse is the most widely distributed game bird in North America and uses coniferous, deciduous, and mixed coniferous/ deciduous forests throughout its range (Rusch et al., 2000). Ruffed grouse require deciduous forest for forage (Svoboda and Guillon, 1972) and tend to use a mix of young and old stands due to the low cover provided by young trees and the substantial forage provided by older trees (Jones et al., 2008). Last, snowshoe hares are distributed

throughout northern North America and have several adaptations for survival in snow-covered landscapes (Wilson and Reeder, 1993). They have enlarged hind feet and stiff hairs that act like snowshoes in deep snow conditions, and they have seasonal camouflage, molting between brown (summer) and white (winter) coats to blend in with the surrounding landscape. Their reliance on seasonal camouflage for survival makes them particularly vulnerable to climate change, as temporal mismatches between seasonal molting and winter-white conditions can significantly increase predation rates (Zimova et al., 2016).

Our study area in northern Minnesota, USA (Fig. 1) encompassed two Ecoregions as defined by the Minnesota Department of Natural Resources Ecological Land Classification System: The Northern Minnesota and Ontario Peatlands and the Northern Superior Uplands. The study area occurred within the boreal-deciduous ecotone (Goldblum and Rigg, 2010), where the southern limit of the boreal forest meets the northern limit of hardwood-dominated forest. Common stand types in the study area included balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), tamarack (*Larix laricina*), white spruce (*Picea glauca*), and northern white cedar (*Thuja occidentalis*). Overall, the study area was comprised of ~73 % forested land cover including ~49 % coniferous forest (evergreen forest and wooded wetland cover types), ~15 % mixed coniferous/deciduous forest, and ~9 % deciduous forest land cover (Supplemental Table S1).

The objectives of our study were to determine the effects of land cover, climate, and forest structure characteristics on the occupancy, co-



Fig. 1. Map of the study area in northern Minnesota, USA. The study area included the Northern Minnesota and Ontario Peatlands and Northern Superior Uplands Ecoregions defined by the Minnesota Department of Natural Resources Ecological Land Classification System. In the inset map, yellow triangles indicate locations of pellet survey sites for spruce grouse, ruffed grouse, and snowshoe hares (2019–2022). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

occurrence, and local extinction patterns of these three species. We were particularly interested in how peripheral populations of spruce grouse and snowshoe hare were impacted by the combined effects of climate and forest structure in comparison to the widespread ruffed grouse. We expected spruce grouse occupancy to be associated with coniferous forest at a landscape scale, black spruce and jack pine at the stand scale, and younger stands with complex forest structure in the lower- to midcanopy (Robinson, 1969; Pietz and Tester, 1982). Additionally, we expected climate to play a significant role in local extinction of both spruce grouse and snowshoe hare, but not ruffed grouse. Although we hypothesized that ruffed grouse would exhibit weaker occupancy patterns due to more generalist habits, we expected mixed coniferous/deciduous forest to be favored because of their reliance on these forest types in winter (Pietz and Tester, 1982). Finally, given spruce grouse and snowshoe hare associations with boreal forest and ruffed grouse associations with deciduous forest, we expected co-occurrence to be greatest in areas of mixed deciduous/coniferous forest and stands of mixed tree species.

2. Materials and methods

2.1. Fecal pellet surveys

We surveyed for spruce grouse, ruffed grouse, and snowshoe hares using fecal pellet surveys as part of an annual survey coordinated by the Minnesota Department of Natural Resources (MNDNR; Roy et al., 2020). Surveys were conducted by 3 types of observers; 1) seasonal survey technicians hired specifically for this survey, 2) cooperating wildlife biologists, and 3) trained citizen volunteers. Surveys occurred throughout the northern boreal forest of Minnesota as the snowpack was dissipating each spring, usually during the months of March-May from 2019 to 2022. Surveys were organized hierarchically, such that sampling was comprised of 37 routes each with up to five transects (155 transects total). All transects were visited at least once in each of the four years. At least 1 transect per route had \geq 30 % black spruce or jack pine, and all transects were located in stands with >30 % conifer component. We aimed for three repeat visits at each survey location, but personnel availability, particularly during the beginning of the COVID-19 pandemic in 2020, sometimes precluded completion of all three visits. Furthermore, all 2022 sites were visited a single time as the annual survey transitioned from pilot-phase examining detection covariates to a permanent format (Roy and Giudice, 2023). Following the methods outlined by Roy et al. (2020), each pellet survey was conducted along a circular transect by walking the circumference of a complete circle maintaining 100 m distance from a central road-based point. Surveyors searched 1 m on either side of the transect and recorded the number of individual fecal pellets or groups of pellets for each species. A distinct group of pellets was defined as those occurring within a 30 cm diameter circle, as this was the typical size of pellet groups formed by treeroosting grouse and provided a repeatable metric. Spruce grouse pellets were differentiated from ruffed grouse pellets based on length, thickness, uric acid wash, and color (Roy et al., 2020). At each survey transect, we recorded survey conditions on a scale from 0 to 10 (with 0 indicating recent snow covered all pellets and 10 indicating a dissipating snowpack is exposing pellets), snow extent (complete, partial, or none), and whether the pellet was observed on snow or bare ground as possible factors influencing detection of pellets. For the vast majority of surveys, fecal pellets were on top of the snow indicating deposition during the current season. However, the possibility that pellets persisted from a previous year existed during a small number of late-spring surveys (i.e., May) when snow cover was generally lower. We handled this possibility by including snow cover and Julian date as detection parameters in our models, discussed in detail below.

2.2. Forest characteristics

Forest characteristics were derived from several sources, including forest data collected during fecal pellet surveys, stand characteristics including stand age and cover type collected during forest inventory monitoring by MNDNR, U.S. Forest Service, county forestry cooperators, remote sources including geospatial (e.g., National Land Cover Data (NLCD), MN Department of Transportation roads layers), and highresolution aerial LiDAR data (>20 returns m^{-2}) (https://lida rhub-minnesota.hub.arcgis.com). We characterized landscape scale land cover variables as the proportion of NLCD-defined land cover types within a 5-km buffer of the site. Briefly, NLCD defines forest as areas with most trees >5 m tall and more than 20 % of vegetation cover; deciduous forest has >75 % of tree species that shed foliage seasonally; evergreen forest has >75 % of tree species that maintain foliage year round; mixed forest has neither deciduous nor evergreen forest as >75 % of total tree cover; and wooded wetland has >20 % forest or shrub cover with periodically saturated soil or substrate. We recorded three land cover categories: deciduous, mixed deciduous/coniferous, and coniferous (defined as the combination of the NLCD evergreen and wooded wetland [i.e., peatlands]) cover types. Similarly, we recorded road densities at a landscape scale as the linear extent of roads (primary, secondary, and tertiary roads, including dirt forest roads) within a 5-km buffer of the site. During fecal pellet surveys, surveyors recorded the stand type(s) (e.g., jack pine, red pine, black spruce, white cedar, balsam fir, tamarack) defined as any tree species comprising \geq 30 % of the transect length. If no single species accounted for \geq 30 % of the transect, it was recorded as a mixed conifer stand. We used these categorizations as stand scale forest-type predictors. Tree density (i.e., the number of trees) was measured in two circular plots of 3.6 m radius along each pellet transect. One plot was located on each side of the road, at the farthest distance from the road along the transect. We used land cover data from public sources (https://gisdata.mn.gov/) while recently acquired LiDAR-derived grid metrics characterizing vertical forest structure and canopy cover were obtained from MNDNR Forestry Program. In particular, canopy density (based on the proportion of LiDAR returns) in five contiguous vertical strata (0-1.37 m, 1.37-5.00 m, 5.00-10.00 m, 10.00-15.00 m, and >15.00 m) were selected considering their importance in other studies (e.g., Deo et al., 2017). Forest characteristics are summarized in Supplemental Table S2.

2.3. Multi-season occupancy modeling – detection, occupancy, and extinction

We used multi-season occupancy models to assess drivers of occupancy and local extinction (MacKenzie et al., 2003) for each species. We used survey route as a random intercept effect to account for the hierarchical sampling design. We first assessed the effects of several variables on detection probabilities - the probability of detecting a species given it is present. Next, we assessed the effects of several variables on initial occupancy probabilities (i.e., the probability a given site is occupied) while accounting for detectability by using the top detection model obtained in the previous step. Finally, we assessed the effects of several variables on extinction probabilities (i.e., the probability that an occupied site becomes unoccupied in the following year) while accounting for detectability and initial occupancy by using the top detection and occupancy models. For each of these parameters, we used a positive stepwise approach to model construction. We first assessed whether a random intercept effect for each survey route improved model performance due to the hierarchical spatial sampling design. We assessed model performance based on the Leave-One-Out Information Criterion (LOOIC), an analog of Akaike's Information Criterion (Burnham and Anderson 2002) for mixed-effects models. After determining whether the random intercept should be included, we then constructed models with a single (fixed-effect) predictor and assessed their performance based on the statistical significance of their coefficient value (see

Supplemental Table S2 for a list of predictors examined) and LOOIC. We used both 95 % confidence intervals (CI) of predictors and LOOIC as criteria for model selection because LOOIC alone is overly permissive of uninformative variables (Arnold, 2010). We discarded any candidate variables with non-significant coefficient values (i.e., 95 % CI overlapped zero) and considered the top single predictor the one with a significant coefficient and the lowest LOOIC. Next, we constructed models with two predictors; the top single predictor was included in each of these models, in addition to each predictor that had a statistically significant coefficient value. We determined the top two-predictor model based on the same criteria as above. If no two-predictor models outperformed the top single-predictor model, we accepted the singlepredictor model as the top model. Finally, we constructed threepredictor models following the same process. We limited each parameter to three predictors to avoid overfitting. We modeled colonization as a constant to limit the number of predictors in models and because predictors of occupancy and extinction were our top priorities. All models were constructed in the R package 'ubms' using the stan colext function (Kellner et al., 2021). Prior to fitting models, we used a model selection function in the "rfUtilities" package in R to remove any combinations of variables exhibiting multicollinearity (Evans and Murphy, 2019).

2.4. Multi-state occupancy modeling-relative abundance and population growth

To determine whether covariates affecting abundance dynamics differed from those affecting occupancy dynamics, we used a multi-state occupancy modeling approach (MacKenzie et al., 2009). Whereas traditional occupancy modeling approaches only consider two possible occupancy states (i.e., occupied or unoccupied), multi-state occupancy modeling considers multiple types of occupancy states. For example, multi-state occupancy modeling can be used when it is important to distinguish sites with reproductive activity from those that are occupied but show no signs of breeding (McGrady et al., 2017). We selected this approach because snowshoe hare pellet counts were collected using a binned approach (e.g., 0, 1-39, or 40+ pellets) due to logistical constraints in the field. A multi-state approach allowed us to discriminate between sites with relatively fewer (1–39) and relatively greater (40+) pellet piles, as a proxy for abundance. Although continuous values of abundance may be ideal, the large number of snowshoe hare pellets at many sites posed challenges due to excessive time requirements to obtain exact counts and therefore the binned approach was adopted. To maintain consistency among species, we binned the pellet counts of spruce grouse and ruffed grouse to facilitate multi-state occupancy modeling for these species. We calculated the median pellet count values for spruce grouse and ruffed grouse and used these as the cutoffs for pellet abundance bins.

Our objective was to determine environmental predictors of variation in abundance; therefore, we used three occupancy states: 0 = unoccupied, 1 = occupied with relatively low pellet counts, and 2 =occupied with relatively high pellet counts. We focused multi-state occupancy models on predictors of state 2 (i.e., Rho, or "abundance"). We followed the same approach to model construction as in our multiseason occupancy modeling. We first determined predictors associated with the probability of detecting "abundance" (i.e., the probability of observing State 2 given that pellets are abundant at the site, or p[22]). Next, we determined the predictors associated with the probability of initial abundance. Finally, we determined predictors associated with transitions between the two positive occupancy states (i.e., Phi[12] = probability of observing State 2 at a site that was previously in State 1 and Phi[21] = probability of observing State 1 at a site that was previously in State 2, analogous to positive and negative population growth, respectively). We followed the same positive stepwise approach to model construction as described above and limited each parameter to a maximum of three predictors. All multi-state occupancy models were constructed in the R package 'unmarked' using the occuMS function (Fiske and Chandler, 2011).

2.5. Multi-species occupancy modeling-species co-occurrence along environmental gradients

Finally, we constructed multi-species occupancy models to test several hypotheses of species occurrence and co-occurrence along environmental gradients. Each model compared occupancy of one of the boreal-specialist species (spruce grouse or snowshoe hare) with that of the ruffed grouse, a forest generalist. We constructed several models relating the boreal species to a boreal forest type, ruffed grouse to a deciduous forest type, and co-occurrence with an intermediate or mixed forest type. For example, at the landscape scale we constructed cooccurrence models in which spruce grouse were associated with coniferous forest land cover, ruffed grouse with deciduous forest land cover, and hypothesized that co-occurrence was associated with mixed forest land cover. Similarly, at a local scale, we hypothesized that spruce grouse would be associated with black spruce or jack pine stands, ruffed grouse with deciduous stands, and co-occurrence with mixed species composition (i.e., no single species comprising >30 % of the transect) or balsam fir stands (which often co-occurred with aspen). We used the top detection model (determined previously) for each species in each model and assessed models based on AICc compared to a model with no occupancy predictors and the statistical significance of coefficient values. Each model included detection predictors from each respective species' top detection model. We constructed these models using the occuMulti function in 'unmarked'. We constructed models for each of 2019, 2020, and 2021, because these years had repeat survey data, and assessed consistency of multi-species occupancy predictors across years.

3. Results

3.1. Detection probability

The top performing detection models for all species included the effect of observer type (Fig. 2; Fig. 3; Supplemental Table S3). For spruce grouse, snow extent and survey condition were also included in the top model, while survey condition and date were included in the top model for ruffed grouse. The top snowshoe hare detection model did not include additional variables. Overall detection probabilities were 0.62 (0.58–0.67) for spruce grouse, 0.69 (0.66–0.72) for ruffed grouse, and 0.96 (0.95–0.97) for snowshoe hare.

3.2. Occupancy probability

Spruce grouse occupancy was most strongly associated with land cover and forest structure. The top initial occupancy model included the effects of deciduous land cover at a landscape (5-km) scale (negative effect on occupancy) and the density of LiDAR returns at the 5.00-10.00 m (+) and 10.00-15.00 m (+) height strata (Fig. 2; Fig. 4). Additionally, coniferous land cover (+), jack pine stands (+), stand age (-), and density of LiDAR returns at >15.00 m height (-) all outperformed a null model (Supplemental Table S4).

Landscape-scale variables were not strongly associated with ruffed grouse nor snowshoe hare occupancy. Rather, local-scale variables related to forest structure and stand type were among the top predictors. The top initial occupancy model for ruffed grouse included red pine stands (–) as the only predictor (Fig. 2). Other predictors that outperformed a model with no initial occupancy predictors included deciduous forest stands (+) and LiDAR return density at the 5.00–10.00 m stratum (+; Supplemental Table S4). Tree density (+) was the only predictor that outperformed a model without initial occupancy predictors for snowshoe hare, and thus the top model included only the effect of tree density (Fig. 2).



Fig. 2. Coefficients (±95% confidence intervals) of detection, occupancy, and extinction predictors in top-scoring multi-season occupancy models for spruce grouse, ruffed grouse, and snowshoe hare based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Models were constructed using a positive stepwise approach with each parameter limited to a maximum of three predictors (note: some detection predictors are multi-level factors that were considered a single predictor). Full definitions of predictors are defined in Supplemental Table S2.

3.3. Extinction probability

Similar to initial occupancy results, the predictors most strongly associated with spruce grouse extinction occurred at the landscape scale. The top extinction model included the effects of deciduous forest cover (+) and road density (+) at the 5-km scale (Fig. 2; Fig. 4). In single-variable models, tree density (-), structure at the 5.00–10.00 m

stratum (–), winter snowfall (–), and winter temperature (+) also outperformed a model without extinction predictors (Supplemental Table S5).

A variety of variables influenced ruffed grouse extinction probability. The top model included the effects of mixed coniferous/deciduous forest at a landscape scale (–), red pine stands (+), and tree density (+; Fig. 2). In addition, stand age (–), LiDAR density at the 1.37–5.00 m



Fig. 3. Marginal effects of detection predictors in top detection models for spruce grouse, ruffed grouse, and snowshoe hares based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. For categorical variables (observer role, snow extent), error bars represent 95 % confidence intervals (CIs). For continuous variables (survey condition, Julian date), gray shaded areas represent 95 % CIs.

stratum (–), LiDAR density at the >15.00 m stratum (+), jack pine stands (+), balsam fir stands (–), deciduous stands (–), and winter snowfall (–) all outperformed a model without extinction predictors (Supplemental Table S5).

Predictors related to climate and stand-scale forest characteristics were among the top extinction predictors for snowshoe hare. The top extinction model included the effects of LiDAR density at the 1.37–5.00 m stratum (–) and winter snowfall (-; Fig. 2; Fig. 5). In addition, LiDAR density at the 5.00–10.00 m (–) and >15.00 m (+) strata, tree density (–), stands of balsam fir (–), black spruce (–), and red pine (+), and winter temperature (+) outperformed a model with no extinction predictors (Supplemental Table S5).

3.4. Multi-State occupancy probability

Multi-state occupancy models suggested that environmental drivers of occupancy and abundance (i.e., Rho) were similar for spruce grouse, but differed for both ruffed grouse and snowshoe hare. For spruce grouse, the top model for initial abundance and the top model for transitions between high and low pellet counts (e.g., Phi) included the same predictors as models for initial occupancy and extinction probability, respectively (Fig. 6). Stand types were the most important predictors of initial abundance for ruffed grouse, and forest structure characteristics were most important for snowshoe hare. The top abundance model for ruffed grouse included the effects of balsam fir (+) and deciduous (+) stands (Fig. 6; Fig. 7). Forest structure at the 1.37–5.00 m stratum (+) and mixed coniferous/deciduous forest at a landscape scale (+) also outperformed a null model (Supplemental Table S6). The top abundance model for snowshoe hare included the effects of forest structure at the 5.00-10.00 m stratum (+; Fig. 6). Stand age (-), structure at the 1.37–5.00 m (+) and >15.00 m (-) strata, tree density (+), and red pine stands (-) all outperformed a model without abundance predictors (Supplemental Table S6).

ruffed grouse and snowshoe hare. Several vertical strata were associated with year-to-year negative growth (i.e., Phi[21]). The top model describing negative growth for ruffed grouse included the effects of forest structure at the 5.00-10.00 m stratum (–), tree density (+), and jack pine stands (+). The top model describing negative growth for snowshoe hare included the effects of structure at the 1.37-5.00 m (–) and >15.00 m (+) strata. In addition, snowshoe hare were the only species in which interspecies interactions appeared to influence population dynamics. The top model for snowshoe hare also included the effect of ruffed grouse abundance on positive growth (i.e., Phi[12]), which was negative (i.e., greater ruffed grouse abundance reduced the probability of positive growth in snowshoe hares; Supplemental Fig. S1; Supplemental Table S7).

Few of our predictions of species co-occurrence across borealhardwood gradients were supported. However, in 2021, co-occurrence of spruce grouse-ruffed grouse and snowshoe hare-ruffed grouse was positively associated with mixed forest at a landscape scale (Supplemental Table S8). However, no co-occurrence predictors were statistically significant at the stand scale in any year or at the landscape scale in 2019 and 2020.

4. Discussion

4.1. Spruce grouse

Our results support recent work implicating deciduous forest cover as a key factor limiting the range of spruce grouse (Casabona et al., 2022). However, our results suggest that forest structure may be a stronger determinant of spruce grouse habitat selection than the particular stand type. Previous work has suggested spruce grouse occupancy is associated with black spruce and jack pine stands (Robinson, 1969; Pietz and Tester, 1982; Anich et al., 2013). Our models supported an association with jack pine, but no stand-type variables were strong enough to be included in top models. Rather, forest structure of the

Forest structure played a significant role in abundance dynamics for



Fig. 4. Marginal effects of occupancy and extinction predictors in the top multi-season occupancy model for spruce grouse based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Gray shaded areas represent 95 % confidence intervals. Percent deciduous cover and road density were calculated within a 5-km radius of the survey site. LiDAR returns from 10 to 15 m in height, which represents the density of the mid-canopy, were calculated within a 150-m radius of the survey site.

lower and mid-canopy was the key local scale determinant of spruce grouse occupancy and persistence. Dense lower and mid-story canopy provides cover from aerial predators and provides thermal protection in winter (Thompson and Fritzell, 1988).

We expected extinction probabilities of spruce grouse to be closely associated with climatic variables given the position of the study area on their southern range margin. Lower temperatures and greater snowfall were associated with lower spruce grouse extinction probabilities, as expected, but the association was not as strong as landscape-scale land cover and road densities. Snowfall and temperature are important to maintaining a deep snowpack for subnivean roosting in winter, but spruce grouse may mitigate suboptimal snow roosting conditions by roosting in trees within a dense forest structure. Indeed, spruce grouse in Maine were observed moving into denser stands and primarily occupying trees in winter (Allan, 1985). Spruce grouse respond to inadequate snow roosting conditions by tree roosting instead, thereby moderating the effects of climate and temperature in our models. Indeed, as climate conditions are predicted to broadly shift the distribution of forest land cover types northward in our study area (Taylor et al., 2017), the effects of climate on spruce grouse occupancy and extinction may be primarily

indirect. Our results underscore the importance of managing forests for dense lower- and mid-canopy to provide climate refugia for spruce grouse at their trailing edge.

Road densities had a substantial effect on spruce grouse extinction probability. Road construction in working forests can change the predator landscape and alter community dynamics (Sirén et al., 2017). Road densities may be associated with greater densities of predators; thereby, roads can indirectly cause a decrease in the occurrence of prey species (Boan et al., 2014). In the western United States, avoidance of roads and reduced nesting success near roads was considered a potential result of fear or auditory disturbance (Pruett et al., 2009). Additionally, road density may be correlated with greater hunter and/or timber accessibility, thus, local extinction probabilities may be driven by more intense harvest. Although the link is unclear, our study suggests that road-sparse areas may promote spruce grouse persistence.

Occupancy modeling is inherently a presence/absence estimator and may not capture variation in density among occupied sites (Nielsen et al., 2005; Tôrres et al., 2012). Therefore, we hypothesized that models accounting for abundance may be more sensitive to associations with particular stand types. Our results suggested that the same variables



Fig. 5. Predicted extinction probability for snowshoe hares based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Gray shaded areas represent 95% confidence intervals. LiDAR returns from 1.37 to 5.00 m in height, representing the density of the shrub understory, were calculated within a 150-m radius. Snowfall was calculated at the center of the survey site using the National Gridded Snowfall Analysis from the National Oceanic and Atmospheric Administration.

governing spruce grouse occupancy – deciduous forest and vertical forest structure – were the most important predictors of relative abundance. We note that our modeling approach, multi-state occupancy modeling – may still be less sensitive to abundance patterns than a modeling approach that uses precise counts such as N-mixture modeling (Royle, 2004). Therefore, we may have had difficulty identifying some potentially important predictors (i.e., stand types). In addition, our models used an indirect estimator of abundance – the number of fecal pellet groups along a transect. Although the number of pellet groups is likely correlated with abundance (Krebs et al., 2001; Evans et al., 2007; Hanser et al., 2011), this metric could be influenced by other parameters such as use intensity and diet, which could cause variation in fecal deposition rates, and make resolution of statistical patterns more difficult.

4.2. Ruffed grouse

Ruffed grouse occupancy and extinction tended to have stronger associations with stand-level variables than landscape-scale variables, in contrast to spruce grouse. Ruffed grouse home range sizes vary seasonally and throughout their range. Whereas some estimates from the south of their range in Missouri and Tennessee exceed 35 ha (Thompson and Fritzell, 1988; Epperson, 1988), a study conducted during spring in Minnesota found average home ranges of just 6.7 ha (Archibald, 1975). This may have contributed to the lack of landscape-scale habitat associations detected in this study.

Deciduous forests, and particularly aspen, are important sources of forage for ruffed grouse (Svoboda and Guillon, 1972). However, since deciduous forests do not provide substantial thermal cover in winter when snow roosting conditions are unfavorable, mixed deciduous/ coniferous forest stands may provide some roosting habitat for ruffed grouse in the sheltered base of conifer trees. Our multi-state modeling results suggested greater ruffed grouse abundance in deciduous stands and balsam fir stands (which often co-occur with aspen in our study area), supporting the importance of mixed coniferous/deciduous stands for ruffed grouse in winter and early spring. Furthermore, mixed coniferous/deciduous forest was associated with lower extinction probability in the top extinction model, reinforcing the importance of mixed forests for providing both thermal cover and winter forage for ruffed grouse (Jones et al., 2008).

Ruffed grouse occupancy was most strongly associated with a relatively unexpected predictor. Red pine stands were strongly negatively associated with ruffed grouse occupancy and were associated with greater extinction probability in the top extinction model. One possible explanation for the negative impact of red pine is the abundance of red pine plantations in the study area. Pine plantations provide little winter food and sparse understory cover for predator avoidance (Bender et al., 1997) but can have a dense overstory that provides concealment for raptors and other forest predators (Gullion, 1967, 1970). In that regard, ruffed grouse extinction probabilities may have been associated more with forest management practices than with the red pine stand type, per se. Likewise, higher tree densities also increased the probability of ruffed grouse extinction in winter. Although greater tree densities may provide better cover from predators, higher tree densities occur in younger stands; during the winter and early spring, ruffed grouse were more likely seeking food in mature aspen forests while snow was on the ground. Moreover, ruffed grouse tend to select ground roosts when snow is present, even when snow depth is limited and potentially insufficient (Whitaker and Stauffer, 2003). Stands with greater tree densities may limit snow accumulation underneath trees, creating suboptimal ground roosting conditions. Therefore, openings in the forest may promote ruffed grouse survival by providing better snow roosting conditions. Alternatively, higher tree densities may simply be associated with young stands that lack sufficient food resources to support ruffed grouse populations (Jones et al., 2008).

4.3. Snowshoe hare

Due to their widespread occurrence in our study area, few predictors were associated with initial occupancy and abundance of snowshoe hares. Under these conditions, dynamic occupancy models can be more revealing about the environmental conditions that facilitate demographic patterns from year to year (Yackulic et al., 2015). Accordingly, we found stronger patterns in dynamic models (i.e., extinction probabilities and multi-state transition probabilities) for snowshoe hare.

We expected snowshoe hare occupancy, abundance, and survival to be associated with snowpack and structure at the shrub level (1.37–5.00 m). Understory density has been linked to snowshoe hare overwinter survival and spring population densities (Litvaitis et al., 1985). Our results strongly supported this association, as variables related to shrublevel forest structure were among the top predictors of occupancy, extinction, abundance, and transitions in abundance. Furthermore, our results suggested that greater snowfall was related to lower extinction probabilities. Our results underscore the threat of seasonal camouflage mismatch in a warming climate and highlight the increased



Fig. 6. Coefficients (±95% confidence intervals) of detection, abundance (Rho), and growth (Phi) predictors in multi-state occupancy models for spruce grouse, ruffed grouse and snowshoe hare based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Models were constructed using a positive stepwise approach with each parameter limited to a maximum of three predictors (note: some detection predictors are multi-level factors that were considered a single predictor).

vulnerability of populations on the southern range margin (Zimova et al., 2020).

4.4. Species co-occurrence

Based on earlier studies, we expected that co-occurrence would occur along a boreal-hardwood gradient, with both spruce grouse and snowshoe hare associated with boreal forest and ruffed grouse associated with hardwood forest. Our results were inconsistent across years and across scales, and our hypothesis was only supported at a landscape scale during one of the three years we tested. In 2021, snowfall was exceptionally low and temperatures were abnormally high (data not shown). One potential explanation of our findings is that these abnormal climate conditions forced species to be more selective in their resource



Fig. 7. Marginal effects of abundance (Rho) predictors in the top scoring multistate occupancy model for ruffed grouse based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Error bars represent 95 % confidence intervals. BF/D Mix = stands with \geq 30 % cover of both balsam fir and deciduous forest. Other = all stands with <30 % balsam fir and <30 % deciduous forest.

use, resulting in greater spatial overlap at the boreal-hardwood interface. Species co-occurrence models have previously shown the importance of elevational gradients in partitioning species distributions (Estevo et al., 2017). Similarly, the habitat gradient in our study coincides with a latitudinal transition from northern hardwood forests to northern boreal forests. As the climate warms, this transition zone is expected to shift northward as the leading edge of hardwood forests replace the trailing edge of boreal forests (Taylor et al., 2017). Our results suggest that warmer climate conditions with shallower snowpack may amplify interactions between boreal and sub-boreal species during this transition.

We sought to understand species interactions by examining changes in abundance (i.e., multi-state occupancy) in response to the occupancy state of other focal species in the study. Investigating changes in occupancy states over time can identify when interspecific interactions, such as competition, are integral to the demographic parameters of one or both species (Yackulic et al., 2014). The only significant relationship we discovered was an apparent regulating effect between ruffed grouse and snowshoe hare - (i.e., greater ruffed grouse abundance was associated with a lower probability of snowshoe hare population growth). This result corresponds with the well-documented co-cycling of ruffed grouse and snowshoe hare populations (Keith, 1963). This result may be related to a shared predator base (Hoffman, 1958). As predator populations grow and populations of one prey species shrinks due to predation pressure, predators may switch to targeting the more abundant prey species, resulting in correlated population dynamics. Our study design does not allow direct assessment of predator-prey interactions, but our results are consistent with correlated population dynamics resulting from such processes.

5. Conclusions

We examined occupancy, abundance, and local extinction patterns in a suite of forest-associated vertebrate prey species at the southern margin of the boreal forest. We found similar habitat associations of the two boreal-associated species that occur at their trailing edge in our study area. Interestingly, these species may partition niches vertically; spruce grouse were most closely associated with lower and mid-canopy cover (5.00-15.00 m) and snowshoe hares were most closely associated with shrub-level cover (1.37-5.00 m). Snowshoe hare were the most climate-sensitive species in our study, most likely due to seasonal camouflage requirements, and spruce grouse may mitigate suboptimal climate conditions by selecting tree-roosts when lower and mid-canopy cover is sufficient. We detected a potential boreal-hardwood gradient of species co-occurrence in a year when climate conditions were suboptimal, suggesting future climate change may result in more frequent species interactions as the boreal-hardwood transition zone shifts northward. Overall, the occupancy, extinction, abundance, and population growth of all species were strongly associated with structural density of the shrub and/or lower canopy layer. This work underscores the importance of maintaining dense forest structure for this guild of forest prey species in winter. Harvest strategies that involve thinning forest stands to facilitate timber extraction may be especially harmful. Forest management practices that maintain dense vegetation in the lower canopy, mid-canopy and shrub layer of conifer forests could provide climate change refugia for boreal-associated species at the trailing edge.

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

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121568.

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