SPRUCE GROUSE AS INDICATORS OF BOREAL FOREST CONNECTIVITY

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SUMMARY OF FINDINGS

We completed a 4-year study (2019-2022) to examine spruce grouse (*Canachites canadensis*) occupancy of conifer forest patches, responses to timber harvest, and genetic connectivity in the boreal forest of northern Minnesota. We conducted a pellet survey of forest stands during late winter/early spring and documented the presence/absence of spruce grouse and other forest wildlife species, as it related to various landscape and forest attributes and climate variables. We examined changes in spruce grouse survival and space use in response to timber harvest with radio-marked birds. We also collected feathers from hunters and during capture efforts to examine landscape connectivity for spruce grouse using landscape genetic methods. Our occupancy results indicated that forest management practices that promote dense vegetation structure may benefit spruce grouse, especially a dense mid-canopy layer (5.0 – 15.0 m). The mid-canopy layer was not as important for the other wildlife species we examined. Our telemetry data indicated that spruce grouse have lower survival after timber harvest, but that most harvested conifer stands were avoided prior to harvest, likely due to the sparse midstory vegetation structure in many of these mature stands. We suggest that reduced spruce grouse survival after timber harvest may be due to indirect effects of timber harvest, such as harvest-related changes in predator behavior or predator space use (e.g., edge effects, changes in predator density in nearby stands) rather than habitat loss. Finally, our genetic data indicated that spruce grouse exist as a single interconnected population in Minnesota, with coniferous forest land cover and lower average temperatures during spring dispersal being the best predictors of gene flow. Therefore, climate change could potentially threaten the persistence of the single interconnected population.

OBJECTIVES

1. We determined whether occupancy of forest stands by spruce grouse and other wildlife species (i.e. ruffed grouse, snowshoe hare) was related to landscape-level, stand-level, and climate variables.
2. We determined spruce grouse responses to timber harvest by radio-marking spruce grouse and examining survival and space use before and after timber harvest.
3. We determined current boreal forest connectivity for spruce grouse using a landscape genetic approach.

METHODS

Occupancy

We used fecal pellet surveys to examine occupancy of conifer stands by spruce grouse, ruffed grouse (*Bonasa umbellus*), and snowshoe hares (*Lepus americanus*) as part of the annual ~~spruce grouse survey during~~ 2019-2022 (Roy et al. 2022). We built single-species multi-season

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occupancy models to examine detection, occupancy and extinction, and multi-species occupancy models to examine co-occurrence of spruce grouse and ruffed grouse.

We used a stepwise approach to construct occupancy models, guided by *a priori* hypotheses for each single fixed-effect predictor. We subsequently built hypothesis-driven multivariate occupancy models using predictors that outperformed a null model (i.e., a model with no fixed-effects predictors). We examined landscape-scale, stand-scale, and climate variables as predictors of occupancy (Table 1). We also examined numerous detection covariates related to observers and survey conditions, including observer type (i.e., citizen volunteer, permanent DNR or cooperator staff, or seasonal DNR technician), the number of observers, survey conditions (0-10, with 10 representing optimal survey conditions), the extent of snow cover (i.e., none, partial, complete), survey date, and whether pellets were detected on snow or bare ground. We used the survey route as a random intercept to account for the sampling design of 67 routes comprised of 4-5 circular transects centered on road-based points (Roy et al. 2022). We constructed all single-species dynamic (i.e., multi-season) occupancy models in R package 'ubms' using the stan_colext function (Kellner et al. 2021).

We also constructed multi-species occupancy models to examine environmental conditions associated with species co-occurrence in late winter/early spring. We focused this analysis on spruce grouse and ruffed grouse. We used the most-supported models for each species from single-species occupancy models, then tested several hypotheses of co-occurrence. We expected co-occurrence to be associated with mixed coniferous/deciduous forest at a landscape scale. We constructed multi-species occupancy models in the R package 'unmarked' using the occuMulti function (Fiske and Chandler 2011) but did not include random intercepts because this program did not support random effects.

Responses to Timber Harvest

Study area

We had 2 focal study areas in northwestern Minnesota—Red Lake Wildlife Management Area (RLWMA) in Lake of the Woods and Roseau Counties, and another near Big Falls in the Littlefork MNDNR Forestry work area in Koochiching County (Fig. 1). We identified stands scheduled for harvest by working with wildlife managers and foresters. Eighteen black spruce stands (*Picea mariana*, 11–145 ac, 4–59 ha) and 17 jack pine (*Pinus banksiana*) stands (9–43 ac, 4–17 ha) were identified for harvest near RLWMA (C. Tucker, pers. comm.). An additional 43 black spruce stands (3–221 ac, 1–89 ha) were identified in the Littlefork Forestry area (B. Feldt and J. Rengo, pers. comm.), along with 87 black spruce stands (0.1–79 ac, 0.04–32 ha) and 10 jack pine stands (1.6–11 ac, 0.6–4.5 ha) identified by Koochiching County Land and Forestry (N. Heibel, pers. comm.). A few additional red pine (*Pinus resinosa*, n = 4) and white spruce (*Picea glauca*; or mixed spruce (n = 13) stands were planned for harvest but given a lower priority than black spruce and jack pine stands in the study. We added spruce top harvests and a birch pole harvest adjacent to jack pine stands during the study based on new permits and conversations with managers and foresters. Some stands were harvested after the study concluded.

Field methods

We captured spruce grouse with noose poles (Zwickel and Bendell 1967) in areas near planned timber harvest. We located birds for capture by broadcasting the female cantus call in spring (Fritz 1979, Boag and McKinnon 1982, Schroeder and Boag 1989, Whitcomb et al. 1996, Lycke et al. 2011), working with volunteers with trained dogs when weather was conducive, locating spruce grouse with other radio-marked birds or while walking in the woods, or when birds came to roads for grit. We fitted spruce grouse with necklace-style VHF transmitters (A-3950) from

Advanced Telemetry Systems® (Roy et al. 2016).

We used homing techniques to obtain GPS coordinates and habitat data for bird locations throughout the year. Birds were tracked 1-2 times weekly to characterize home ranges and survival before and after timber harvest. Locations were obtained throughout the day (excluding night) from within a few meters of the birds.

Additionally, we surveyed transects for spruce grouse pellets during winter and early spring to locate spruce grouse for capture in stands scheduled for harvest and to examine spruce grouse use of these stands. Pellet surveys were conducted >3 days after snowfall, unless harvest was imminent, and a survey had to be completed earlier. Otherwise, we surveyed each stand $\geq$3 times (Huggard 2003). We determined transect lengths based on timber stand area and sampled at a rate of 10 m/ac (25 m/ha). We placed transects systematically through timber harvest areas with a starting point on the harvest boundary. We spaced transects $\geq$150 m apart (Evans et al. 2007). We searched 1 m on either side of the transect for spruce grouse pellets (Evans et al. 2007, Schroeder and Vander Haegen 2014, Roy et al. 2020) and also recorded grouse observed, tracks, and ruffed grouse pellets (Huggard 2003) both on and off transect. Every 100 m along the transect, we measured habitat characteristics in a habitat plot (Huggard 2003), collecting the same data as collected at capture sites and at telemetry locations to characterize habitat in the stand. Specifically, we recorded GPS coordinates, overstory stand type, the center tree species, center tree circumference, distance to the nearest tree, nearest tree species and circumference, and the number of live trees in a 3.6-m radius from the center tree (40.7 m^2 plot), which is similar in size to the 1/100-ac fixed-radius plot that is used in Cooperative Stand Assessment Field Procedures (MNDNR 2001). At 3.6 m from center in the 4 cardinal directions, we collected spherical densiometer readings (Fiala et al. 2006, Paletto and Rosi 2009, Baudry et al. 2014) and measured shrub density in 1-m^2 plots. We selected these habitat measurements based on vegetation attributes that differed between stands where spruce grouse were observed and where they were not observed (Potvin and Courtois 2006), or other attributes that predicted spruce grouse presence or occupancy, including stem density, shrub cover, basal area, and canopy cover (Huggard 2003, Ross et al. 2016).

Analysis

For each individual, we determined whether $\geq$1 location occurred $\leq$500 m from a harvested stand. We used harvest date to categorize locations as pre-harvest or post-harvest. We categorized all locations for an individual as non-harvest if none overlapped a harvested stand.

We calculated 90% minimum convex polygons (MCPs) with R package ‘adehabitatHR’ (Calenge 2015). We chose 90% to be restrictive of outliers because a small number of birds made short-term (i.e., 2-3 weeks) movements to irregular locations that were not seasonal or harvest-related movements. We compared home range size in pre-harvest, post-harvest, and non-harvest treatments. We predicted that pre-harvest home ranges would be larger than post-harvest home ranges due to loss of available habitat.

To assess harvest effects on space use, we calculated the proportion of each MCP that overlapped a harvested stand and the proportion that overlapped a 500-m buffer area surrounding a harvested stand. We predicted more overlap between harvest areas and buffer areas in pre-harvest MCPs than post-harvest MCPs.

We fit Kaplan-Meier curves in the R package ‘survival’ to examine the impact of harvest on survival (Therneau et al. 2015). We estimated the probability of survival for >1 yr for pre-, post-, and non-harvest home ranges. We predicted that survival probability would be higher for pre- or non-harvest treatments than post-harvest.

Landscape Genetics

We collected hunter-submitted feathers from throughout northern Minnesota and feathers from birds captured from the Big Falls study area and RLWMA to obtain genetic samples. This genetic information can be linked to spatial information to examine the connectivity of the landscape for spruce grouse. Areas that share greater connectivity will be similar genetically, whereas areas with restricted connectivity will become more genetically dissimilar over time. We identified 3 putative populations: Superior Uplands, Big Falls study area, and RLWMA (Fig. 2).

We obtained unambiguous genotype data for 7 microsatellite loci from the University of Minnesota Genomics Center (Table 2). Microsatellites are highly variable, neutral (non-coding) genetic loci that are useful for studies of population structure (i.e., differences) and in landscape genetic applications. We used a non-spatial method in program STRUCTURE to assess genetic structure (Pritchard et al. 2000) with the default admixture and correlated allele frequency model (Falush et al. 2003). We summarized the results with StructureHarvester (Earl and von Holdt 2012) and determined best-supported K values with log likelihood scores and also using the ΔK approach (Evanno et al. 2005).

We used a landscape genetics approach based on causal modeling to examine environmental drivers of genetic connectivity for spruce grouse (Cushman et al. 2006). We constructed resistance surfaces for each of our hypothesized landscape predictors (Table 3), such that areas we hypothesized would facilitate gene flow had low resistance, and areas that we hypothesized would impede gene flow had high resistance. We tested two categorical resistance surfaces representing land cover: 1) coniferous forest (combining the wooded wetland and evergreen forest categories from the National Land Cover Dataset [Dewitz and USGS 2021]), and another using 2) spruce grouse preferred stand types based on the literature (i.e., combining jack pine, black spruce, and tamarack [*Larix laricina*] forest) from the GAP Land Cover Dataset (USGS 2011; Robinson 1969; Pietz and Tester 1982; Allan 1985; Anich et al. 2013). We also tested 5 continuous resistance surfaces representing the influence of humans (road density), mean annual snowfall (NOAA 2023), mean spring temperature (PRISM 2023), and two types of stand age resistance. In the first type of stand age resistance we considered, resistance increased with older stand age. In the second, resistance increased with greater deviance from age 40-yr because previous work suggested spruce grouse occupancy declines with forest succession, but that occupied stands were approximately 40-yr-old (Ross et al. 2016). We gave any land categorized as non-forest (i.e., lacking a stand age value) the highest value of resistance (R_{max}).

We used the Maximum Likelihood Population Effect (MLPE) approach to construct landscape genetics models (Clarke et al. 2002). Genetic distance was the response, and resistance distances were predictors to determine which environmental variables were strong predictors of genetic distance. We used the dist_euclidean function in the R package ‘gstudio’ to calculate genetic distance between individuals (Dyer 2012). We used Circuitscape 5 to calculate resistance distance between individuals for each resistance surface (Anantharaman et al. 2020). We included a random intercept effect in each model for each of the 3 regions due to the clustered sampling design. We determined the R_{max} value that resulted in the model with the strongest predictive performance for each variable using the corrected Akaike’s Information Criterion (AIC_c; Burnham and Anderson 2002). We used a “null” model based on a uniform resistance surface where every cell had a value of 1 as a standard with which to compare other candidate models. If more than one R_{max} value outperformed the null model, we used only the most-supported R_{max} value (based on AIC_c) for further modeling. Finally, we built multivariate models by combining all subsets of landscape variables receiving more support than the null model.

We predicted functional connectivity across the study area using the parameters from the most-supported model. We used the Raster Calculator tool in ArcGIS (ESRI 2011) to make a composite resistance surface raster based on the intercept and β coefficients of predictors in the most-supported model. We summed the intercept and the product of each resistance surface and their respective β coefficients in the most-supported model. We then normalized the values in this raster to a 1-100 scale to conduct circuit-based connectivity mapping. We mapped functional connectivity using Circuitscape (Koen et al. 2014; Aylward et al. 2020) and also Omniscape (Landau et al. 2021), which has the potential to produce more biologically realistic scenarios of connectivity but also has different assumptions.

RESULTS

Occupancy

The most-supported detection model for spruce grouse and ruffed grouse included observer type and survey condition, with spruce grouse detection also influenced by snow extent and ruffed grouse detection influenced by survey date (Table 4). Detection probability was greater for partial snow cover than complete or no snow cover, and detection probability was highest for seasonal technicians and lowest for citizen volunteers. For spruce grouse and ruffed grouse, detection probability increased with improving survey condition, but detection probability was consistently high for snowshoe hare and influenced only by observer type. Detection probability was 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.

Spruce grouse occupancy was best explained by land cover and forest structure (Table 4). The most-supported multi-season occupancy model included mid-canopy density (+) (i.e., LiDAR 5-15 m) and deciduous forest land cover (-) (Fig. 3). Models with tree density (+) and stand age (-) also outperformed a null model but were not included in multivariate models due to correlations with mid-canopy density. Spruce grouse extinction probability included the effects of deciduous forest land cover (+) and road density (+). Ruffed grouse occupancy was influenced by red pine (-), which also increased the probability of extinction, along with tree density (+) and mixed forest (-). In contrast, snowshoe hare occupancy was related to tree density (+), with extinction influenced by snowfall (-) and the density of lower canopy (i.e., LiDAR 1.37-5 m) (-).

Multi-species occupancy modeling indicated that co-occurrence of spruce grouse and ruffed grouse was associated with mixed coniferous/deciduous forest (+) (Table 5). Models with stand-scale variables were not more supported than a model without co-occurrence predictors.

Responses to Timber Harvest

We radio-marked 107 spruce grouse to examine responses to timber harvest, with 62 near Big Falls and 45 at RLWMA. Thirteen focal timber stands near Big Falls and 18 stands at RLWMA were harvested during the study. Additionally, 4 spruce top harvests and 1 birch pole harvest were executed in focal stands in the Big Falls area. In Big Falls, we completed pellet surveys and accompanying habitat measurements along transects in 20 stands and detected spruce grouse pellets in 3 stands. At RLWMA, we found spruce grouse pellets in 6 of 18 surveyed stands.

Overlap of MCPs with harvested areas was low in both study areas and was near 0 at RLWMA (Table 6). Near Big Falls, overlap decreased after harvest, but few birds overlapped harvested stands. More individuals overlapped with 500-m buffer zones around harvested stands, facilitating more robust statistical analysis. In both study areas overlap of MCPs with buffer zones decreased post-harvest relative to pre-harvest levels. Survival of individuals with an MCP overlapping a harvested stand was lower post-harvest than pre-harvest and was lower than for individuals in the non-harvest treatment (Table 7).

Landscape Genetics

The model representing a single interconnected spruce grouse population had the greatest log-likelihood. Land cover, stand age, and climate variables were included in $\geq$1 model that was more supported than the null model. However, the most-supported model included coniferous forest land cover and temperature during spring dispersal (Tables 8, 9).

Circuitscape and Omniscape produced similar maps of functional connectivity with high gene flow indicated in the northwestern and northeastern portions of the study area (Fig. 4). Movement corridors were more apparent in Circuitscape than Omniscape, but both analyses emphasized coniferous forest stands as areas of greater gene flow. Omniscape indicated several areas of no flow, corresponding to regions >7 km from source areas. For example, Red Lake and the Mesabi Range had low flow in both Circuitscape and Omniscape maps. Otherwise, the region was characterized by relatively well-connected flow, with higher flow in coniferous forest stands.

DISCUSSION

Occupancy

Our models suggest mid-canopy density was the key stand-scale determinant of spruce grouse occupancy and persistence, which is likely related to cover from predators and thermal protection (Thompson and Fritzell 1988). Forest structure may be a stronger determinant of spruce grouse habitat selection than stand type, which may explain the widely varying descriptions of stand types used by spruce grouse in the literature (Boag and Schroeder 1992, Lycke et al. 2011, Anich et al. 2013). In the Great Lake States, spruce grouse prefer areas of black spruce with some jack pine interspersed, but they have also been reported using balsam fir (*Abies balsamea*), tamarack, eastern hemlock (*Tsuga canadensis*), and northern white cedar (*Thuja occidentalis;* Robinson 1969, Pietz and Tester 1982, Anich et al 2013). In Wisconsin, spruce grouse used closed canopy coniferous uplands near lowland conifer swamps, especially mature black spruce-tamarack swamps and jack pine 16–29 years old (Anich et al. 2013). Similarly in Minnesota, but with a modest sample size, spruce grouse used lowland conifers with black spruce and mixed bogs during the breeding season and used jack pine during winter (Pietz and Tester 1982). Various successional stages are used throughout spruce grouse range, including early-successional (Boag and Schroeder 1992), mid-successional (Ross et al. 2016), and mature forest (Anich et al. 2013). We also found deciduous forest cover to be a key factor limiting the range of spruce grouse (Casabona et al. 2022).

The strongest predictors of both occupancy and local extinction probabilities for spruce grouse were landscape-scale land-cover variables and mid-canopy density (5-15 m). Temperature was a predictor in the most-supported multivariate extinction model but had a small effect relative to land cover, road density, and canopy structure. Road densities were positively related to spruce grouse extinction probability. Road densities may be positively associated with predator density, which can affect prey species occurrence (Boan et al. 2014). Road density may also be correlated with hunter accessibility and localized harvest pressure near roads. Areas with fewer roads may promote spruce grouse persistence.

Spruce grouse and ruffed grouse occurrence aligns with a coniferous-deciduous forest gradient with co-occurrence most probable in the mixed coniferous/deciduous transition zone. The land cover-based gradient coincides with the large-scale latitudinal transition from northern boreal forests to southern deciduous forests. This transition zone is expected to shift northward as climate warms and deciduous forests replace boreal forests (Taylor et al. 2017). Our work suggests that ruffed grouse are likely to replace spruce grouse as a result of changing habitat conditions in the study area.

Responses to Timber Harvest

Timber harvest reduced survival of spruce grouse. Timber harvest has negative demographic effects in several bird species, usually through an increase in predator activity in the edges created by harvest (Yahner and Mahan 1997, Duguay et al. 2000). Importantly, most spruce grouse occurred near harvested stands, but spruce grouse were rarely within harvested stands even before harvest. Therefore, reduced survival near harvested stands might occur indirectly through edge effects or from predator displacement from harvested stands producing greater predator densities in nearby stands used by spruce grouse. However, we did not collect data on predator responses to timber harvest in this study to evaluate such explanations.

We predicted spruce grouse would avoid harvested stands after harvest, due to the loss of cover, but did not anticipate that harvested stands would be avoided before harvest. This avoidance suggests that many harvested stands were not suitable for spruce grouse before harvest. Many stands mature enough to harvest in Minnesota may lack the vegetation structure necessary to support spruce grouse. Spruce grouse declined with forest succession in a New York study (Ross et al. 2016). Timber harvest may increase spruce grouse mortality but may also be necessary at some level to promote regeneration of stands with denser vegetation structure that supports spruce grouse.

At the home-range scale, MCPs initially overlapped harvested stands but exhibited large decreases in overlap post-harvest (from 81 to 56% at the Big Falls study area and 41 to 16% at RLWMA), although 95% CIs overlapped. This reduction in overlap is likely explained by higher predator activity near the edges of harvested stands (Yahner and Mahan 1997). However, in Quebec, spruce grouse remained in residual strips after harvest, seemingly unaffected by edge effects (Potvin and Courtois 2006). Our study area had abundant residual habitat, which might partially explain the differences in spruce grouse responses between this study and the Quebec study.

Landscape Genetics

The spruce grouse population in Minnesota currently exists as a continuous population with no distinct spatial demes. Distinct spatial demes would indicate that gene flow is restricted and that barriers to connectivity and movement exist that fragment the population into separate subpopulations. Gene flow was positively related to spring temperature during dispersal and coniferous forest land cover. Two approaches to connectivity modeling gave complementary perspectives of genetic connectivity, highlighting greater potential for gene flow in the northeast and northwest than central portions of the study area. Omniscape suggested more continuous gene flow than Circuitscape, but both indicated several partial barriers to gene flow, including Red Lake and the Mesabi Range. Forest management to promote gene flow through conifer forest cover may influence the connectivity of this region for spruce grouse with climate change. Our data indicate the central part of the study area may be most vulnerable to climate change impacts to gene flow. The cooler northwestern and northeastern portions of spruce grouse range in Minnesota may provide climate refugia and maintain some spruce grouse gene flow and connectivity (Huntingford and Lowe 2007; Anderson et al. 2020). This research highlights climate change and associated changes in conifer forest cover as important considerations for spruce grouse population connectivity at their southern range periphery.

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Table 1. Variables used in occupancy modeling for spruce grouse, ruffed grouse and snowshoe hare in northern Minnesota during 2019-2022. Data sources included National Land Cover Data (NLCD), unpublished MNDNR data, fecal pellet surveys (Roy et al. 2022), habitat surveys, Light Detection and Ranging (LiDAR) data, National Oceanic and Atmospheric Administration (NOAA) snowfall data, and PRISM Climate Group temperature data (https://prism.oregonstate.edu/).

Category	Name	Description	Source
Land cover	Deciduous forest	Percent deciduous forest land cover ≤5-km buffer	NLCD
Land cover	Mixed forest	Percent mixed conifer/deciduous forest land cover in 5-km buffer	NLCD
Land cover	Coniferous forest	Sum of wooded wetland + conifer forest land cover in 5-km buffer	NLCD
Roads	Road density	Linear road length in 5-km site buffer	MNDNR
Stand type	Balsam fir	Binary variable for balsam fir comprising >30% transect	Pellet surveys
Stand type	Black spruce	Binary variable for black spruce comprising >30% transect	Pellet surveys
Stand type	Jack pine	Binary variable for jack pine comprising >30% transect	Pellet surveys
Stand type	Red pine	Binary variable for red pine comprising >30% transect	Pellet surveys
Stand type	Tamarack	Binary variable for tamarack comprising >30% transect	Pellet surveys
Stand type	Deciduous forest	Binary variable for deciduous spp. comprising >30% transect	Pellet surveys
Stand structure	Stand age	Mean stand age along transect	MNDNR
Stand structure	Tree density	Number of trees ≤3.6 m from habitat plot center	Habitat data
Stand structure	LiDAR 0-1.37 m	Proportion LiDAR returns 0 – 1.37 m	LiDAR
Stand structure	LiDAR 1.37-5 m	Proportion LiDAR returns 1.37 – 5 m	LiDAR
Stand structure	LiDAR 5-10 m	Proportion LiDAR returns 5 – 10 m	LiDAR
Stand structure	LiDAR 10-15 m	Proportion LiDAR returns 10 – 15 m	LiDAR
Stand Structure	LiDAR >15 m	Proportion LiDAR returns >15m	LiDAR
Climate	Snowfall	Cumulative Jan + Feb snowfall	NOAA
Climate	Temperature	Mean daily high temperature in Jan and Feb	PRISM

Table 2: Microsatellite loci analyzed by University of Minnesota Genomics Center for our use in a landscape genetic approach for spruce grouse in northern Minnesota during 2014-2021. We did not retain all 16 loci in the analysis because of difficulties calling alleles when >2 products amplified or alternatively because of possible linkage to coding regions (i.e., $\leq$2 alleles) at some loci.

Locus	Source	Retained in analysis	Reason for exclusion
BG03	Wang et al. 2012	No	Low diversity
BG04	Wang et al. 2012	No	Low diversity
BG15	Wang et al. 2012	Yes	
BG21	Wang et al. 2012	No	Low diversity
BG26	Wang et al. 2012	No	Low diversity
BG29	Wang et al. 2012	No	Low diversity
BG94	Wang et al. 2012	No	Low diversity
CUAAGG37	Gibson et al. 2005	Yes	
LLSD2	Piertney and Dallas 1997	Yes	
LLSD6	Piertney and Dallas 1997	No	Ambiguous alleles
TTD4	Caizergues et al. 2001	No	Ambiguous alleles
TTD6	Caizergues et al. 2001	Yes	
TUD7	Segelbacher et al. 2000	No	Ambiguous alleles
TUT1	Segelbacher et al. 2000	Yes	
TUT3	Segelbacher et al. 2000	Yes	
TUT4	Segelbacher et al. 2000	Yes	

Table 3. We considered categorical and continuous variables in a landscape genetic approach for spruce grouse in northern Minnesota during 2014-2022. We hypothesized that coniferous forest and spruce grouse stand types would have lower resistance for spruce grouse gene flow in northern Minnesota during 2014-2022 than other land cover types, that greater road density would have higher resistance, and that stand age would either have (a) a positive linear relationship resistance or (b) a parabolic relationship with minimal resistance at age 40-yr and increasing resistance with greater deviance from 40 yr. We also hypothesized that areas with more average snowfall or lower average spring temperatures would have lower resistance.

Variable	Description	Source
Coniferous forest	Categorical: Wooded wetland and evergreen forest land cover	NLCD[a]
Spruce grouse stand types	Categorical: Black spruce, jack pine, and tamarack land cover	GAP[b]
Road density	Continuous: Linear length of roads/km^2	MNDNR[c]
Stand age	Continuous: Yr since harvest	MNDNR[c]
Snowfall	Continuous: Mean annual snowfall	NOAA[d]
Temperature	Continuous: 30-yr temperature during Mar-Apr	PRISM[e]

[a] Dewitz J, United States Geological Survey [USGS]. 2021. National Land Cover Database (NLCD). 2019. Products (ver. 2.0, Jun 2021). USGS data release. https://doi.org/10.5066/P9KZCM54

[b] U. S. Geological Survey [USGS]. 2011. Gap Analysis Program, 20160513, GAP/LANDFIRE National Terrestrial Ecosystems. https://doi.org/10.5066/F7ZS2TM0

[c] Minnesota Department of Natural Resources

[d] National Oceanic and Atmospheric Administration [NOAA] 2023. National Gridded Snowfall Analysis. https://www.nohrsc.noaa.gov/snowfall

[e] PRISM Climate Group (PRISM) 30-Yr Normals. 2022. Oregon State University. https://prism.oregonstate.edu

Table 4. Multi-season occupancy model coefficients for detection, occupancy, and extinction in the most-supported models for spruce grouse, ruffed grouse, and snowshoe hare in northern Minnesota during 2019-2022. We used a positive stepwise approach, limiting each model parameter to $\leq$3 predictors.

Parameter or predictor	Coefficient (95% Confidence interval)
Spruce grouse detection	
Survey condition	0.46 (0.30 – 0.63)
(Observer type) technician	0.06 (-0.30 – 0.42)
(Observer type) volunteer	-1.41 (-2.02 – -0.82)
(Snow extent) none	0.25 (-0.18 – 0.68)
(Snow extent) partial	0.79 (0.41 – 1.17)
Spruce grouse occupancy	
Deciduous (5 km)	-0.88 (-1.44 – -0.38)
Light Detection and Ranging (LiDAR; 5-10 m)	1.37 (0.72 – 2.11)
LiDAR (10-15 m)	1.06 (0.49 – 1.69)
Spruce grouse extinction	
Deciduous (5 km)	0.91 (0.33 – 1.53)
Road density (5 km)	1.04 (0.29 – 1.82)
Ruffed grouse detection	
Survey condition	0.46 (0.31 – 0.62)
Date	0.28 (0.12 – 0.43)
(Observer type) technician	0.63 (0.32 – 0.95)
(Observer type) volunteer	-0.22 (-0.69 – 0.23)
Ruffed grouse occupancy	
Red pine	-1.77 (-2.97 – -0.60)
Ruffed grouse extinction	
Mixed forest (5 km)	-1.17 (-2.11 – -0.36)
Red pine	1.86 (0.55 – 3.24)
Tree density	0.87 (0.26 – 1.53)
Snowshoe hare detection	
(Observer type) technician	1.03 (0.21 – 1.90)
(Observer type) volunteer	-1.33 (-2.07 – -0.59)
Snowshoe hare occupancy	
Tree density	1.75 (0.05 – 3.98)
Snowshoe hare extinction	
LiDAR (1.37-5 m)	-2.27 (-3.47 – -1.24)
Snowfall	-0.78 (-1.49 – -0.12)

Table 5. Multi-species occupancy modeling of spruce grouse as related to a coniferous forest type, ruffed grouse occupancy with a deciduous forest type, and co-occurrence with a mixed forest type (mix). Models with a significant co-occurrence predictor are bolded and underlined, non-significant (ns) relationships are indicated, and Akaike's Information Criterion (AIC_c) is provided.

Predictors (Coniferous / co-occur / deciduous)	2019		2020		2021	
	AIC_c	Coefficient	AIC_c	Coefficient	AIC_c	Coefficient
None	1003.6	NA	604.1	NA	1020.5	NA
Landscape-scale						
Coniferous / mix / deciduous	989.5	+ / ns / ns	590.9	+ / ns / ns	**<u>1015.3</u>**	**<u>+ / + / ns</u>**
Stand-scale						
Black spruce / mix / deciduous	1004.6	ns / ns / ns	609.0	ns / ns / ns	1025.1	ns / ns / ns
Jack pine / mix / deciduous	998.6	+ / ns / ns	599.9	+ / ns / ns	1023.4	ns / ns / ns
Black spruce / balsam fir / deciduous	1002.9	ns / ns / ns	608.0	ns / ns / ns	1025.2	ns / ns / ns
Jack pine / balsam fir / deciduous	995.3	+ / ns / ns	600.8	+ / ns / ns	1024.1	ns / ns / ns

Table 6. Percent overlap of spruce grouse minimum convex polygon (MCP) home ranges with harvested timber stands and 500-m stand buffers pre- and post-harvest in northern Minnesota during 2019-2022.

Study Area	Pre-Harvest (95% CI)	Post-Harvest (95% CI)
Big Falls		
% MCP in harvested stand	12 (2 – 22)	7 (4 – 10)
% MCP in harvest buffer	81 (57 – 100)	56 (42 – 70)
Red Lake Wildlife Management Area		
% MCP in harvested stand	0 (0 – 1)	0 (0 – 0)
% MCP in harvest buffer	41 (8 – 74)	16 (0 – 37)

Table 7. Number of spruce grouse home ranges (n) and deaths observed for each harvest category in the survival analysis and the restricted mean estimated survival time and 95% confidence interval (CI) for each category. Mean survival (days) was restricted to $\leq$1 yr (365 days) for harvest home range survival analysis.

Harvest category	n	Deaths	Survival in days (95% CI)
Non-harvest	50	13	307 (278 – 336)
Pre-harvest	23	1	349 (319 – 379)
Post-harvest	53	21	258 (220 – 296)

Table 8. Comparisons of landscape genetics models for spruce grouse in northern Minnesota during 2014-2022 using the change in Akaike's Information Criterion (ΔAIC_c). Variables in models included spruce grouse preferred stand types (black spruce, jack pine, and tamarack; BJT), snowfall, stand age, spring temperature, and coniferous forest and wooded wetland land cover (conifer cover). Models with road density did not perform better than the null model so are not included here.

Model	df[a]	logLikelihood	AIC_c	ΔAIC_c	Weight[b]
Conifer cover + temperature	6	-5767.68	11547.36	0.00	0.73
Conifer cover + snowfall + temperature	7	-5767.72	11549.46	2.10	0.26
Conifer cover + stand age + temperature	7	-5771.25	11556.50	9.14	0.01
Conifer cover + BJT + temperature	7	-5774.17	11562.36	15.00	0.00
Conifer cover + stand age + snowfall	7	-5785.21	11584.43	37.07	0.00
Conifer cover + BJT + snowfall	7	-5787.29	11588.58	41.22	0.00
Conifer cover + snowfall	6	-5788.60	11589.21	41.85	0.00
Conifer cover	5	-5801.39	11612.78	65.42	0.00
Snowfall + temperature	6	-5800.54	11613.08	65.72	0.00
Conifer cover + stand age	6	-5801.42	11614.84	67.48	0.00
Temperature	5	-5803.25	11616.50	69.14	0.00
Conifer cover + BJT + stand age	7	-5803.74	11621.48	74.12	0.00
BJT + temperature	6	-5805.27	11622.55	75.19	0.00
Conifer cover+ BJT	6	-5805.36	11622.73	75.37	0.00
Stand age + temperature	6	-5806.36	11624.73	77.37	0.00
BJT + snowfall	6	-5817.15	11646.30	98.94	0.00
Stand age + snowfall	6	-5824.71	11661.42	114.06	0.00
Snowfall	5	-5831.64	11673.29	125.93	0.00
BJT + stand age	6	-5841.35	11694.70	147.34	0.00
BJT	5	-5846.06	11702.12	154.76	0.00
Stand age	5	-5849.97	11709.94	162.58	0.00
Null model	4	-5851.48	11710.96	163.60	0.00

[a] Degrees of freedom

[b] Model weight from model selection

Table 9. Coefficient values of coniferous forest land cover and spring temperatures from the most-supported landscape genetics model used to parameterize a composite resistance surface for connectivity mapping for spruce grouse in northern Minnesota during 2014-2022.

Variable	R_{max}	Beta (95% Confidence intervals)
Intercept	--	2.509 (2.403 – 2.616)
Coniferous forest land cover	100	0.004 (0.003 – 0.005)
Spring temperature	100	0.005 (0.004 – 0.006)

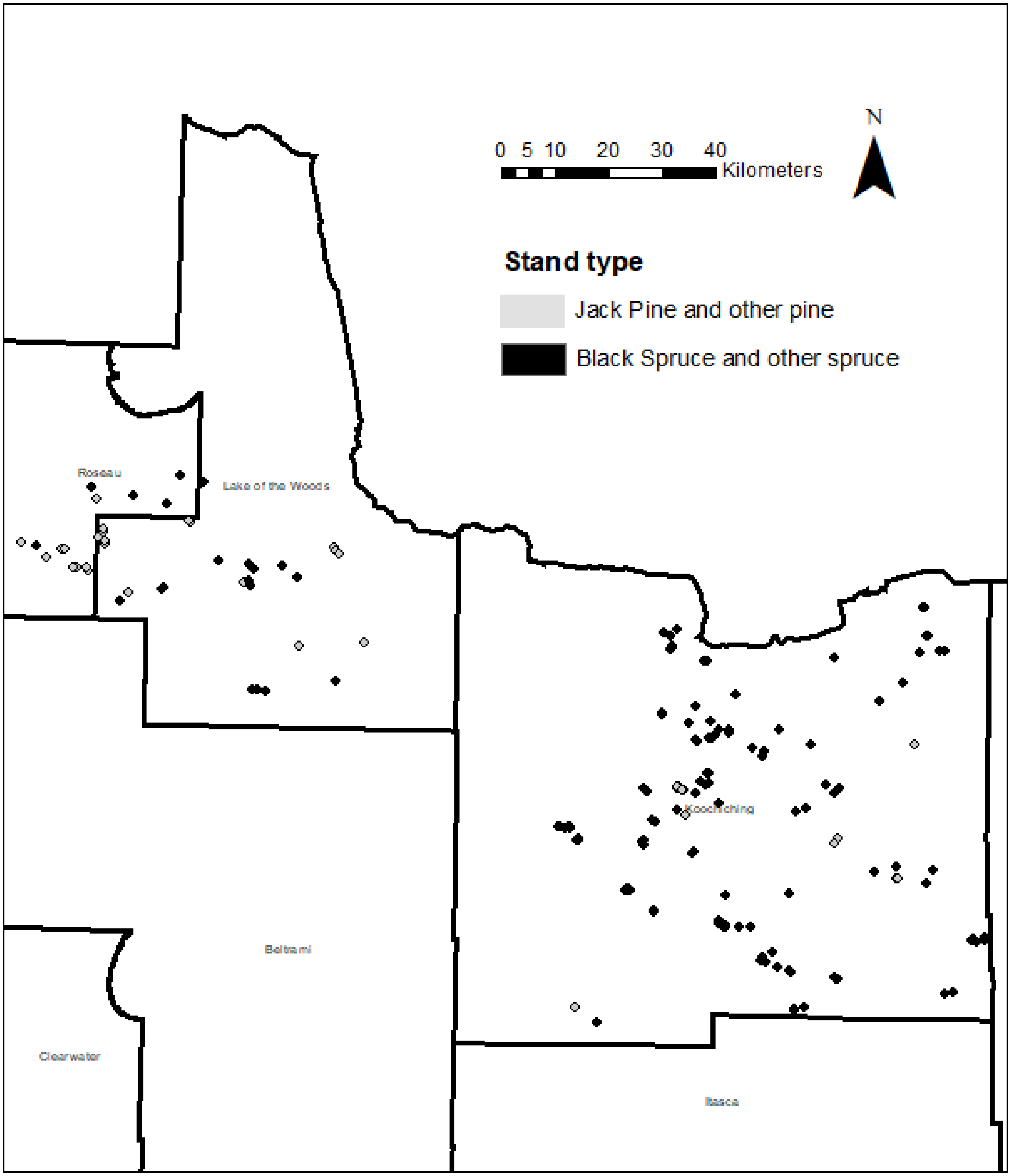

Figure 1. The spruce grouse timber harvest study area in northern Minnesota during 2019-2022 with 2 focal areas, one in Lake of the Woods and adjacent Roseau County with more jack pine than black spruce stands scheduled for harvest and another centered on Big Falls in Koochiching County which had more black spruce than jack pine stands scheduled for harvest.

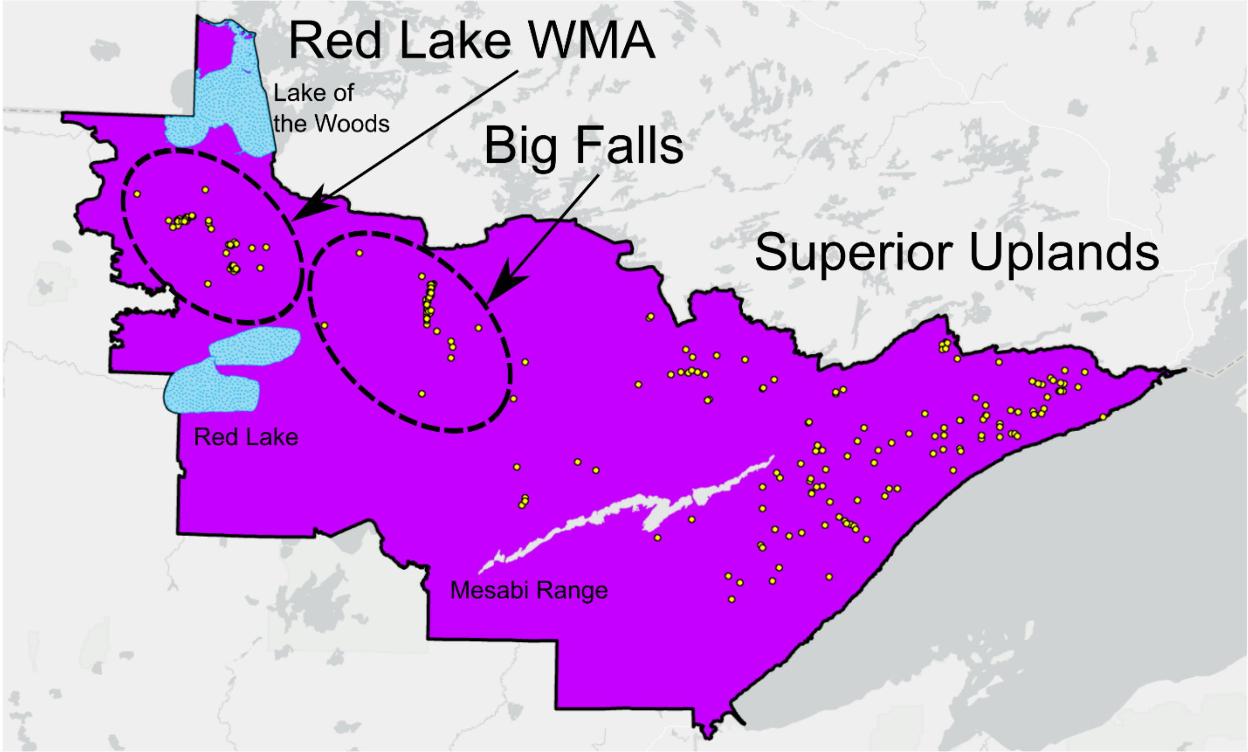

Figure 2. Areas sampled (yellow dots) for spruce grouse feathers to use in genetic analysis within the 2 timber-harvest study areas (Red Lake Wildlife Management Area [WMA] and Big Falls) and also locations that hunters sampled from these areas and the Superior Uplands in northern Minnesota during 2014-2021.

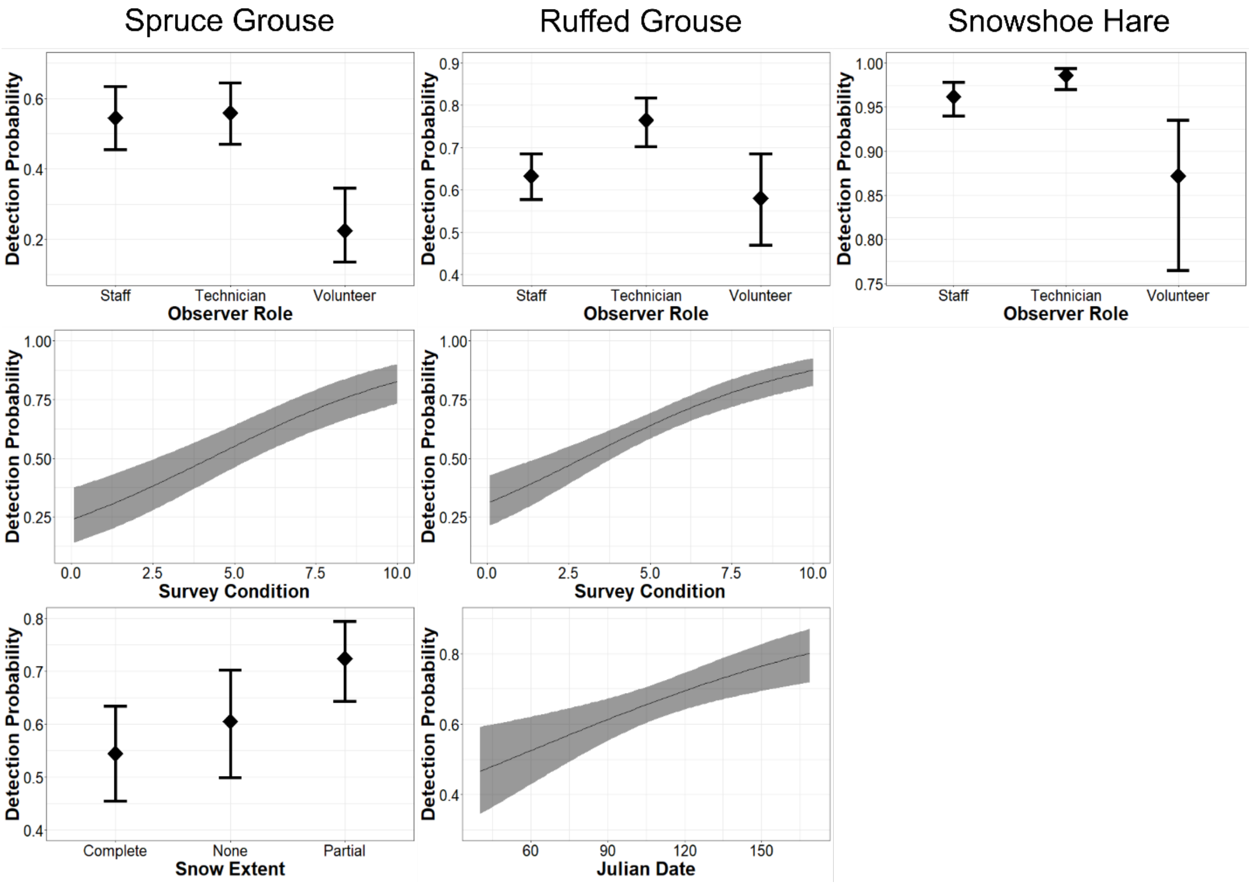

Figure 3. Marginal effects of predictors in most-supported detection models for spruce grouse, ruffed grouse, and snowshoe hares in northern Minnesota during 2019-2022.

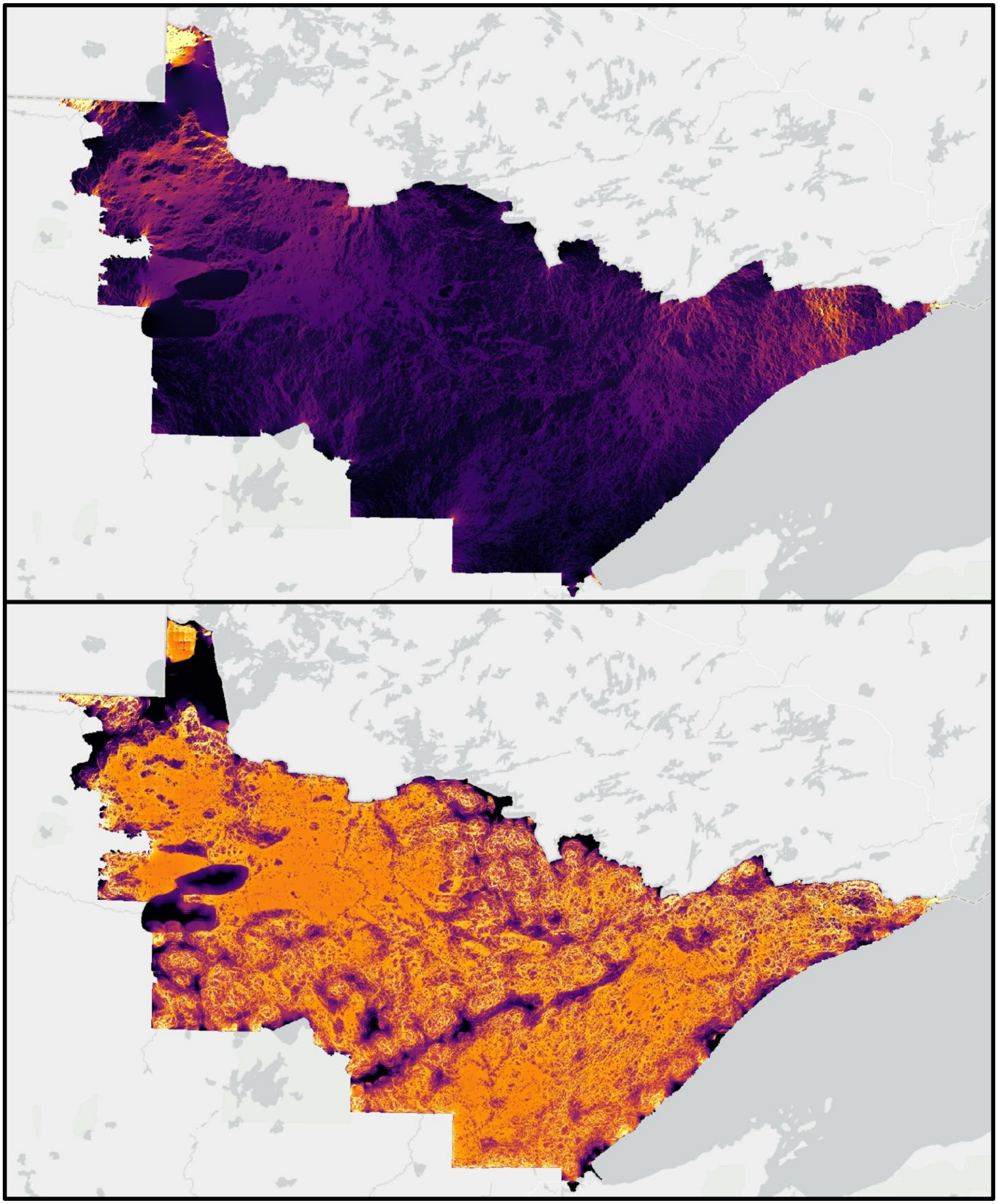

Figure 4. Circuitscape prediction of cumulative gene flow using a resistance surface parameterized from the most-supported landscape genetics model (top). Omniscape prediction of normalized gene flow using the same resistance surface, the proportion of coniferous forest cover within a 5-km radius of a source-strength layer, and a moving window size of 7 km (bottom). In both the top and bottom panels, yellow/orange indicates more gene flow, purple indicates less flow, and black represents no flow.