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Research article

Landscape genetics of spruce grouse at the trailing edge of the boreal forest

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Populations on the periphery of a species range generally occupy marginal or less continuous habitat and can have greater extinction risk than populations in the range-center. For climate-sensitive populations on the trailing edge of a species' distribution (i.e. low latitude or low elevation), the effects of climate change are expected to compound these threats, increasing the vulnerability of these populations. The spruce grouse *Canachites canadensis* is a boreal forest specialist that is expected to experience range contraction at the trailing edge of its range due to climate change. In this study, we investigated the genetic structure, genetic diversity, and connectivity of spruce grouse in Minnesota, along the southeastern range limit in the United States. Clustering algorithms and genetic diversity indices suggested a single continuous population occurred throughout northern Minnesota. We detected no signatures of recent inbreeding or population bottlenecks. We used maximum likelihood population effects modeling and identified coniferous forest land cover and lower average spring temperatures as predictors of gene flow. We used two approaches based on circuit theory to map the potential for gene flow and identified regions of consistently high gene flow in the northwest and northeast of the study area. Omniscape, which incorporated additional parameters representing the likely origins of dispersers and the maximum dispersal distance, suggested a more continuous gene flow landscape than did Circuitscape. Our work highlights the current genetic integrity of one of the largest populations of the eastern subspecies of spruce grouse *C. c. canadensis* in the United States, identifies key landscape attributes for functional connectivity, and demonstrates complementary approaches of Circuitscape and Omniscape for gene flow mapping.

Keywords: boreal forest, *Canachites canadensis*, functional connectivity, genetic structure, landscape genetics, Omniscape



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Introduction

Populations on the margin of a species range are often subject to lower quality habitat and occur in a heterogeneous landscape of suitable habitat and non-suitable matrix (Braunisch et al. 2008). Often, peripheral populations have lower survival, densities, and genetic diversity than those in the core of a species' range (Brussard 1984). Successful dispersal and reproduction are important mechanisms to maintain genetic diversity and provide demographic connectivity (Whiteley et al. 2015, Quinn et al. 2019). Therefore, identifying landscape conditions that improve the probability of successful dispersal through the matrix can aid conservation efforts of peripheral populations (Beier and Noss 1998).

The boreal–hardwood ecotone is the region where the southern edge of the boreal forest meets the northern edge of hardwood forests in the Northern Hemisphere (Goldblum and Rigg 2010). This region represents the southern range limit of many boreal-associated species. Due to climate change, warmer conditions are expected to favor hardwoods in this region in the future, resulting in a northward shift in the ecotone. As a result, boreal-associated species are expected to experience contractions of their southern range limits (Carroll 2007). Remnant boreal forest habitat in this region is likely to become more fragmented as the range contracts; therefore, understanding conditions that facilitate connectivity for boreal-associated species can inform conservation decisions that might improve long-term persistence at southern range limits, such as the identification and protection of key movement habitat (i.e. corridors) that facilitate gene flow.

Landscape genetics provides a powerful toolset for assessing functional connectivity of landscapes by examining associations between landscape conditions and genetic dissimilarity of individuals or populations (Manel et al. 2003). Landscape genetics can provide an empirical basis for identifying gene flow corridors (Spear et al. 2015, Aylward et al. 2020). Whereas corridors are often identified using habitat suitability or occupancy modeling approaches, habitat conditions that facilitate gene flow may differ significantly from conditions required for occupancy (Mateo-Sánchez et al. 2015, Aylward et al. 2020). For example, animals may be able to disperse over suboptimal habitat types that would not support occupancy; therefore, habitat suitability models may overlook potentially important gene flow corridors due to their restrictive parameters (Mateo-Sánchez et al. 2015, Aylward et al. 2020). Landscape genetics can overcome these challenges by inferring dispersal corridors and conditions that facilitate successful dispersal based on measures of genetic connectivity.

The spruce grouse *Canachites canadensis* is a bird species strongly associated with boreal forest habitat (Schroeder et al. 2018). Spruce grouse rely on conifers to provide food; their diet in winter is comprised predominantly of short-needled conifer needles like jack pine and black spruce (MNDNR unpubl.). Conifers also provide protection from predators because spruce grouse plumage is camouflaged amongst the conifer branches. Dense conifers can also limit access by aerial predators like raptors and owls, and provide thermal cover in years where snow conditions are unsuitable for subnivean

roosting, either because the snow is not deep enough and/or it has a thin ice crust that limits diving below the snow surface.

The southern limit of spruce grouse range occurs primarily in the northern United States, including the northern Rocky Mountains in the west *C. c. franklinii*, and northern New England and the northern Great Lakes states in the east and center of their range *C. c. canadensis*. One of the largest populations of spruce grouse in the Great Lakes region occurs in northern Minnesota where minimum temperatures are colder (<https://gisgeography.com/us-temperature-map/>) and the boreal forest is more extensive. In Minnesota, spruce grouse populations are large enough to facilitate regulated harvest. Elsewhere in the region, spruce grouse are listed as threatened in Wisconsin (Wisconsin Department of Natural Resources 2021) and a fully protected Species of Special Concern in Michigan (Michigan Natural Features Inventory 2009). The population in northern Minnesota provides an opportunity to examine spruce grouse genetic diversity and connectivity in one of the most robust populations of *C. c. canadensis* in the United States. The diversity and genetic continuity of this population can be a benchmark to help understand how gene flow in climate-vulnerable systems in early stages of climate-change compare with gene flow in later stages of climate-altered systems. Understanding the genetic diversity and connectivity of spruce grouse may also help understand how climate-induced habitat fragmentation impacts populations as the climate warms and the boreal forest contracts to the north. Previous genetic work on spruce grouse is relatively limited. Genetic data have primarily been used to delimit subspecies in western North America (Barry and Tallmon 2010). Few studies have investigated subpopulation structure, diversity, and connectivity, although recent work has revealed declining mitochondrial genetic diversity at their southern range limit in New York (Kirchman et al. 2020). However, it is unclear if nuclear genetic diversity is declining at their southern range limit, and relationships between landscape variables and gene flow have not been investigated.

Our objective was to characterize the genetic diversity and connectivity of spruce grouse in northern Minnesota. We tested several hypotheses with respect to the relationship between landscape conditions and genetic connectivity. We examined the influence of coniferous forest land cover, particular stand types believed to be preferred by spruce grouse (black spruce, jack pine and tamarack, Robinson 1969, Anich et al. 2013), stand ages, human footprint (road densities), and climate, on spruce grouse genetic connectivity. Then, we used landscape genetics modeling as a basis for constructing a map of hypothesized gene flow using electric circuit theory. Our results provide an empirical basis for wildlife connectivity planning and management of a sentinel boreal forest species at its southern range margin.

Material and methods

Sample collection

We obtained feathers from hunters that harvested birds from throughout the spruce grouse range in Minnesota

(2019–2022), and also from spruce grouse that we captured as part of a pilot telemetry study (2014–2015) at Red Lake Wildlife Management Area (WMA) and during a larger radio telemetry study conducted at Red Lake WMA and a study area located north of Big Falls, MN during 2019–2022. Sampling was relatively even throughout the eastern half of the study area (i.e. the ‘Superior Uplands’), and was more clustered in the central (i.e. ‘Big Falls’) and western (i.e. ‘Red Lake WMA’) parts of the study area. We therefore categorized our samples into three putative populations: Superior Uplands, Big Falls and Red Lake WMA (Fig. 1).

Genetic data

All genetic laboratory work was conducted by the University of Minnesota Genomics Center. DNA extractions were performed using Qiagen DNEasy Blood and Tissue kits following manufacturer’s protocols. We selected microsatellite loci that had been used in spruce grouse (Barry and Tallmon 2010) and other grouse species from the literature (Piertney and Dallas 1997, Caizergues et al. 2001, Piertney and Höglund 2001, Gibson et al. 2005, Wang et al. 2012). Microsatellite PCR used the following thermal profile for all loci: 94°C for 5 min; 45 cycles of 94°C for 20 s, 56°C for 30 s, and 72°C for 60 s; and 72°C for 3 min. Replicate PCRs were conducted for a subset of samples to ensure allelic dropout was not prevalent. Amplicons were visualized on an Agilent Bioanalyzer D1000, D12000 or HS D5000. Microsatellites were then sequenced on an Illumina MiSeq v3 using 300 bp paired-end reads. To check for genotyping consistency, 92% of samples were amplified in duplicate, and two samples were chosen to be amplified four times. Read counts of each possible allele were used to score microsatellite genotypes. If only one allele had a dominant number of reads, we considered the sample homozygous; if a second allele had > 25% of the reads as the dominant allele, we considered the sample heterozygous. If multiple alleles were present in the heterozygous range of read depth, the genotype was considered undetermined. We required a read depth of at least 15 reads to consider an allele valid.

We obtained genotype data for 265 unique individuals at 16 microsatellite loci (Supporting information). Three loci were dropped from analysis due to ambiguity in allele calls and an additional 6 loci were dropped due to lack of diversity potentially associated with linkage to functional genes (Wang et al. 2012). This resulted in a data set of 7 microsatellite loci (BG15 [Wang et al. 2012], CUAAGG37 [Gibson et al. 2005], LLS2 [Piertney and Dallas 1997], TTD6 [Caizergues et al. 2001], and TUT1, TUT3, and TUT4 [Segelbacher et al. 2000]). We tested for Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using Genepop (<http://genepop.curtin.edu.au/>). Additionally, we recorded observed heterozygosity (H_o) and expected heterozygosity (H_e) using GenAEx (Peakall and Smouse 2006), and calculated allelic richness (A_r) using the R package ‘hierfstat’ (Goudet 2005) with rarefaction to the smallest population size ($n = 56$). Finally, we calculated effective population size (N_e) using NeEstimator V2.1 (Do et al. 2014).

To assess genetic structure, we first used a non-spatial method in program STRUCTURE (Pritchard et al. 2000) with the default admixture and correlated allele frequency model (Falush et al. 2003). We ran 500 000 Markov chain Monte Carlo repetitions with a 100 000 repetition burn-in period, with five unique iterations at each putative number of populations (K) ranging from $K = 1–5$. We used ‘StructureHarvester’ (Earl and vonHoldt 2012) to summarize the results and examined best-supported K values both by log likelihood scores and using the ΔK approach (Evanno et al. 2005).

Landscape genetics

To identify potential environmental drivers of genetic connectivity, we used a landscape genetics approach based on causal modeling (Cushman et al. 2006). We constructed resistance surfaces of varying strength for each of our hypothesized landscape predictors (Supporting information). All resistance surfaces were mapped at 1×1 -km spatial resolution. Resistance surfaces characterize the landscape such that

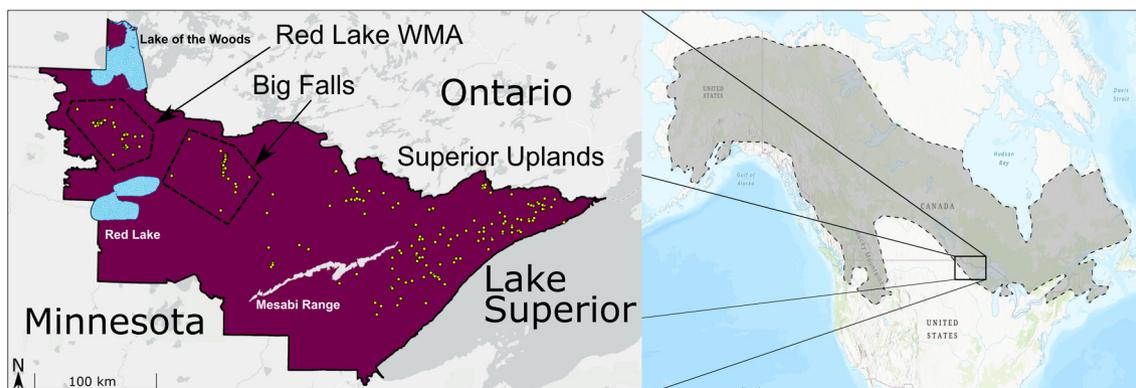


Figure 1. Study area in northern Minnesota showing individual sample locations (yellow dots) and clustered sampling in two locations (dotted lines, Red Lake Wildlife Management Area (WMA) and Big Falls). The remainder of samples were collected from a third area, the Superior Uplands. Three partial barriers to gene flow are also shown: Lake of the Woods and Red Lake (blue polygons) and the Mesabi Iron Range (light gray polygon). Spruce grouse range map (shaded gray) shows the location of the study area within the species’ range.

areas that facilitate gene flow have low resistance and areas that impede gene flow have high resistance.

We tested two categorical resistance surfaces representing land cover: 1) Coniferous forest (combining the Wooded wetland and Evergreen forest categories of the National Land Cover Dataset [Dewitz and USGS 2021]) and 2) Spruce grouse preferred stand types (combining jack pine, black spruce and tamarack forest from the GAP Land Cover Dataset [USGS 2011]; [Robinson 1969, Pietz and Tester 1982, Allan 1985, Anich et al. 2013]). For each categorical resistance surface, the land cover category of interest was set to a resistance of 1 and the rest of the map area was set to a resistance of a higher value (i.e. ' R_{\max} '). We created layers with an R_{\max} of 5, 10, 50, 100 and 500 to test multiple potential hypotheses of landscape resistance.

We tested continuous resistance surfaces representing the influence of human footprint (road density), stand age, and climate variables. Road density was calculated as the linear distance of roads per square km using a Minnesota Department of Natural Resources dataset constructed from national, tribal, state, and county data (Minnesota Information Technology unpubl.). We obtained stand age from the same data set and tested two types of stand age resistance. First, we tested increasing resistance with increasing stand age; second, we tested increasing resistance with increasing deviance from 40 years of age. We selected 40 years as the age with least resistance due to previous work suggesting spruce grouse occupancy declined over time in association with forest succession, but that stands that remained occupied had a mean age of approximately 40 years (Ross et al. 2016). In the stand age data sets, any land categorized as non-forest (i.e. lacking a stand age value) was given the R_{\max} value of resistance. Finally, we created resistance surfaces for mean annual snowfall (NOAA 2023) and mean spring temperature (PRISM 2023). For mean annual snowfall, we obtained cumulative snowfall over the past five years and divided by five to obtain mean annual snowfall for each 1-km² raster cell in the study area. For mean spring temperature, we obtained the mean daily high temperature for March and April over the past 30 years (i.e. the '30-year normal' data set from PRISM) for each 1-km² raster cell in the study area. We selected March and April to coincide with the spring dispersal period prior to mating season (Herzog and Keppie 1980). Each continuous resistance surface was transformed such that the hypothesized optimal value had a resistance of 1 and values further from the optimal value increased in resistance until reaching R_{\max} (Supporting information). Similar to the categorical surfaces, we created continuous resistance surfaces with R_{\max} = 5, 10, 50, 100 and 500 for each variable. To test whether human footprint and warmer climate conditions negatively affected gene flow, we considered resistance positively related to road density and spring temperature and negatively related to snowfall. We considered two stand age resistance schemes, 1) a positive relationship between resistance and stand age, and 2) a positive relationship between resistance and the absolute value of stand age minus 40 (to create a relationship such that 40-year-old stands had the lowest resistance).

We constructed landscape genetics models using the maximum likelihood population effects (MLPE) approach (Clarke et al. 2002). The MLPE approach implements a random intercept effect for each subpopulation to account for the non-independence of samples obtained from the same sampling region. We used this approach to help account for clustered sampling in the Red Lake WMA and Big Falls areas, where inter-sample genetic distance may be lower than in the Superior Uplands simply due to denser sampling. We calculated genetic distance between individuals using the `dist_euclidean` function in the R package 'gstudio' (Dyer 2012). We calculated resistance distance between individuals for each resistance surface using Circuitscape 5 (Anantharaman et al. 2020). We then used MLPE modeling with genetic distance as the response and resistance distances as predictors to determine the environmental variables that were the strongest predictors of genetic distance.

The first step in our modeling approach was determining the best R_{\max} value for each variable. To do this, we constructed a set of models for each variable, with each model using the resistance distance obtained from one of the R_{\max} values as the single predictor of genetic distance. We used the corrected Akaike's information criterion (AICc; Burnham and Anderson 2002) to determine the R_{\max} value that resulted in the model with the strongest predictive performance for each variable. We used a 'null' model based on a uniform resistance surface where every cell had a value of 1 as a benchmark to compare other candidate models. The null model was a Circuitscape-based equivalent of an isolation-by-distance model. If none of the models for a given variable outperformed the null model, the variable was discarded from further consideration. If multiple R_{\max} values outperformed the null model, only the top-scoring R_{\max} value (based on AICc) was used for further modeling. Finally, we constructed multi-variable models by combining all subsets of landscape variables that outperformed the null model.

To select the top-scoring multi-variable model, we first removed from consideration any model with highly correlated predictors. We calculated the variance inflation factor (VIF) of predictors within each multi-variable model and removed any model with a VIF > 10 (Vittinghoff et al. 2012). Using this approach, we did not need to discard entire predictors, but instead discarded models containing highly correlated variables. Of the remaining models, we selected the model with the lowest AICc as the top-scoring multi-variable model. We then used the parameters from this model to construct a resistance surface for predicting functional connectivity across the study area. Specifically, we used the Raster Calculator tool in ArcGIS (ESRI 2011) to create a composite resistance surface raster based on the intercept and β coefficients of predictors in the top model. We multiplied the resistance surface of each landscape variable in the top model by their respective β coefficients, then summed each of these resistance surfaces and the intercept.

We then rescaled this raster from 1–100 to facilitate circuit-based connectivity mapping.

Connectivity mapping

We mapped functional connectivity using two approaches. First, we used a Circuitscape-based approach (Koen et al. 2014, Aylward et al. 2020). We buffered the study area by 300-km and placed 50 focal nodes evenly along the boundary of the buffer to reduce any biases caused by focal node attraction (Koen et al. 2014). This approach removes dependence of the results on the locations where samples were collected. Next, we assigned resistance values of 50 to each raster cell in the buffer area to allow current to flow freely from the nodes to the outer boundary of the final composite resistance surface. We ran Circuitscape in pairwise mode and clipped the resulting cumulative current map to the original study area boundary to remove the artificial buffer zone.

Our second approach to mapping functional connectivity used Omniscape (Landau et al. 2021), which has the potential to produce more biologically realistic scenarios of connectivity but is reliant on some key assumptions. Omniscape offers two key advantages over Circuitscape. First, current is emitted from a ‘source-strength’ raster layer rather than focal nodes. This allows the amount of current emitted from each raster cell on the landscape to reflect the relative abundance of potential dispersers. Second, Omniscape uses a moving-window analysis which can restrict the maximum distance a pulse of current travels on the landscape. In contrast to the Circuitscape-based approach, which allows current to travel unimpeded, the moving window parameter can be constrained to reflect a species’ maximum dispersal distance, facilitating a more biologically realistic estimate of functional connectivity. Based on the assumption that spruce grouse dispersers were most likely to originate from areas with greater proportions of coniferous forest, we created a source-strength raster from the proportion of coniferous forest cells from the National Land Cover Database data set (Dewitz et al. 2021). Based on dispersal distances observed in a study from another spruce grouse population on the southern margin of their range, in Maine (Whitcomb et al. 1996), we used a moving window size of 7-km. This number was equivalent to the 75th percentile dispersal distance observed in preliminary telemetry data from our study area (Minnesota Department of Natural Resources unpubl.). We inferred functional connectivity from Omniscape using a normalized current flow map, which compares the observed current flow to that of a null resistance surface (resistance = 1 for all cells).

Results

Allelic richness, observed and expected heterozygosity, inbreeding coefficient and effective population sizes were similar among the three sampling areas (Table 1). Expected and observed heterozygosity were between 0.66–0.73 for all populations and for the entire study area. No populations exhibited a statistically significant inbreeding coefficient. Effective population size estimates for all populations and the entire study area included infinity. One private allele was detected in LLSD2 in the Big Falls population (2% frequency) and one in TUT4 in the Superior Uplands population (1% frequency).

Structure

The number of populations (K) with the greatest log likelihood was 1 (Supporting information). Based on ΔK , which cannot be measured for $K=1$, the best supported K was 3. However, under scenarios of $K=2$ and $K=3$, the vast majority of individuals exhibited approximately equal ancestry proportions for the two or three groups and no geographic pattern of ancestry was apparent (Supporting information).

Landscape genetics

Land cover, stand age, and climate variables each had at least one model that outperformed the null model. None of the road density models outperformed the null and road density was excluded from further analysis. The optimal R_{\max} values were 100 for coniferous forest and 500 for spruce grouse stand types. Both characterizations of stand age had models that outperformed the null, so we proceeded with the characterization with the lowest AICc, which was a linear negative relationship between stand age and resistance with an R_{\max} value of 50. Optimal R_{\max} values for climate variables included 100 for temperature and 50 for snowfall (Supporting information). In general, multi-variable models that combined four or more variables were often dropped due to high VIF (Supporting information). After removal of such models, the top-scoring model included the effects of coniferous forest land cover and temperature (Table 2). The effect sizes (β coefficients) were small but statistically significant for both coniferous forest land cover ($\beta=0.004$; 95% CI 0.003–0.005) and temperature ($\beta=0.005$; 95% CI 0.004–0.006). The relationships between genetic distance and landscape resistance due to these predictors were weak ($R^2=0.052$ and 0.043, respectively), but stronger than the relationship

Table 1. Genetic diversity estimates within three sampling areas and across the entire study area. n=sample size, Ar=allelic richness rarefied to 118 allele copies, Ho=observed heterozygosity, He=expected heterozygosity, F_{IS} =inbreeding coefficient.

Population	n	Ar	Ho	He	F_{IS}
Red Lake WMA	71	7.75 (6.26–9.24)	0.66 (0.52–0.80)	0.73 (0.65–0.80)	0.06 (–0.22 to 0.33)
Big Falls	56	7.86 (6.48–9.24)	0.71 (0.58–0.85)	0.73 (0.66–0.81)	–0.01 (–0.30 to 0.28)
Superior Uplands	138	8.04 (6.45–9.63)	0.70 (0.60–0.80)	0.73 (0.66–0.80)	0.01 (–0.22 to 0.24)
Study area	265	8.09 (6.54–9.63)	0.69 (0.62–0.76)	0.73 (0.69–0.77)	0.02 (–0.12 to 0.17)

between genetic distance and landscape resistance due to geographic distance alone ($R^2 = 0.019$; Supporting information).

Connectivity modeling

Circuitscape and Omniscape produced similar maps of functional connectivity with high-intensity current generally occurring in the northwestern and northeastern parts of the study area (Fig. 2A–B). Narrow conduits of high-intensity flow generally corresponding to the concept of movement corridors were more apparent in the Circuitscape map than the Omniscape map. However, both maps emphasized black spruce, jack pine, and tamarack stands as areas of concentrated flow. The Omniscape map exhibited several areas of zero current flow, corresponding to regions that were greater than 7 km from the nearest source of current in the source-strength layer. In particular, Red Lake, a large body of water in the northwestern portion of the study area, and the Mesabi Mountain Range in the southeastern portion of the study area had low current flow in both the Circuitscape and Omniscape maps. Both maps identified particularly strong channels of current in the forest stands to the north of Red Lake. Otherwise, the region was characterized by relatively well-connected current flow, with intensity increasing in the black spruce/jack pine/tamarack stands.

Discussion

Our objectives were to assess the genetic structure and diversity of spruce grouse, determine landscape conditions

Table 2. Model comparisons of landscape genetics models using $\Delta AICc$. BJT = preferred spruce grouse stand types (black spruce, jack pine and tamarack), SNW = snowfall, STA = stand age, TMP = spring temperature, WWC = coniferous forest and wooded wetland land cover. Models with road density did not perform better than the null model so are not included here.

Model	df	logLik	AICc	$\Delta AICc$	Weight
WWC+TMP	6	-5767.68	11547.36	0.00	0.73
WWC+SNW+TMP	7	-5767.72	11549.46	2.10	0.26
WWC+STA+TMP	7	-5771.25	11556.50	9.14	0.01
WWC+BJT+TMP	7	-5774.17	11562.36	15.00	0.00
WWC+STA+SNW	7	-5785.21	11584.43	37.07	0.00
WWC+BJT+SNW	7	-5787.29	11588.58	41.22	0.00
WWC+SNW	6	-5788.60	11589.21	41.85	0.00
WWC	5	-5801.39	11612.78	65.42	0.00
SNW+TMP	6	-5800.54	11613.08	65.72	0.00
WWC+STA	6	-5801.42	11614.84	67.48	0.00
TMP	5	-5803.25	11616.50	69.14	0.00
WWC+BJT+STA	7	-5803.74	11621.48	74.12	0.00
BJT+TMP	6	-5805.27	11622.55	75.19	0.00
WWC+BJT	6	-5805.36	11622.73	75.37	0.00
STA+TMP	6	-5806.36	11624.73	77.37	0.00
BJT+SNW	6	-5817.15	11646.30	98.94	0.00
STA+SNW	6	-5824.71	11661.42	114.06	0.00
SNW	5	-5831.64	11673.29	125.93	0.00
BJT+STA	6	-5841.35	11694.70	147.34	0.00
BJT	5	-5846.06	11702.12	154.76	0.00
STA	5	-5849.97	11709.94	162.58	0.00
Null model	4	-5851.48	11710.96	163.60	0.00

associated with gene flow, and map the potential for gene flow at the trailing edge of their distribution in northern Minnesota. Our results suggest that the spruce grouse population in Minnesota represents a single continuous population with no distinct spatial demes. Gene flow was associated with temperature and coniferous forest land cover. Two approaches to connectivity modeling offered complementary perspectives of genetic connectivity; each highlighted stronger potential for gene flow in the northeastern (i.e. Superior National Forest) and northwestern (i.e. Red Lake WMA) portions of the study area relative to the central study area (e.g., east of the Big Falls area), although Omniscape suggested a more continuous gene flow landscape than Circuitscape.

Spruce grouse gene flow and forest composition

At the southern range margin in Quebec, spruce grouse occupancy was significantly reduced when coniferous forest comprised < 40% of the landscape and when deciduous forest comprised > 20% of the landscape (Casabona i Amat et al. 2022). Similarly, preliminary data suggest spruce grouse occupancy in our study area is limited by higher proportions of deciduous forest at a landscape scale (Aylward et al. 2024). These recent findings suggest that the transition from conifer-dominated landscapes in the north to deciduous-dominated landscapes in the south represents a barrier to spruce grouse occupancy, which likely governs their southern range limit. Our results extend this paradigm to the genetic connectivity of spruce grouse.

We found no support for subpopulation structure in our study area, suggesting the contiguity of the boreal coniferous forest landscape in northern Minnesota is sufficient to support a single, large, interconnected population of spruce grouse. However, the southern edge of the boreal forest is at risk of being replaced by northern hardwood forest due to climate change in the coming decades (Hickling et al. 2006). Just as previous studies imply that these effects could result in lower occupancy rates (Casabona i Amat et al. 2022, Aylward et al. 2024), our data suggest that genetic connectivity could be reduced as well. Monitoring the effects of climate change on forest composition at the boreal–hardwood ecotone (Goldblum and Rigg 2010) could have important implications for the health of spruce grouse populations in Minnesota.

Forest structure plays a significant role in spruce grouse occupancy in Minnesota (Aylward et al. 2024). Occupancy modeling work used high-resolution LiDAR data to assess the role of forest structure, but such data were not available continuously across the study area for assessment using landscape genetics modeling. Therefore, we relied on stand age data as a proxy for forest structure characteristics in this study. Our analysis suggested that stand age was a stronger predictor of gene flow than geographic distance alone but had relatively little importance compared to broad-scale coniferous forest land cover. Because stand age may not be a strong indicator of forest structure (Stevens et al. 2016), the role of

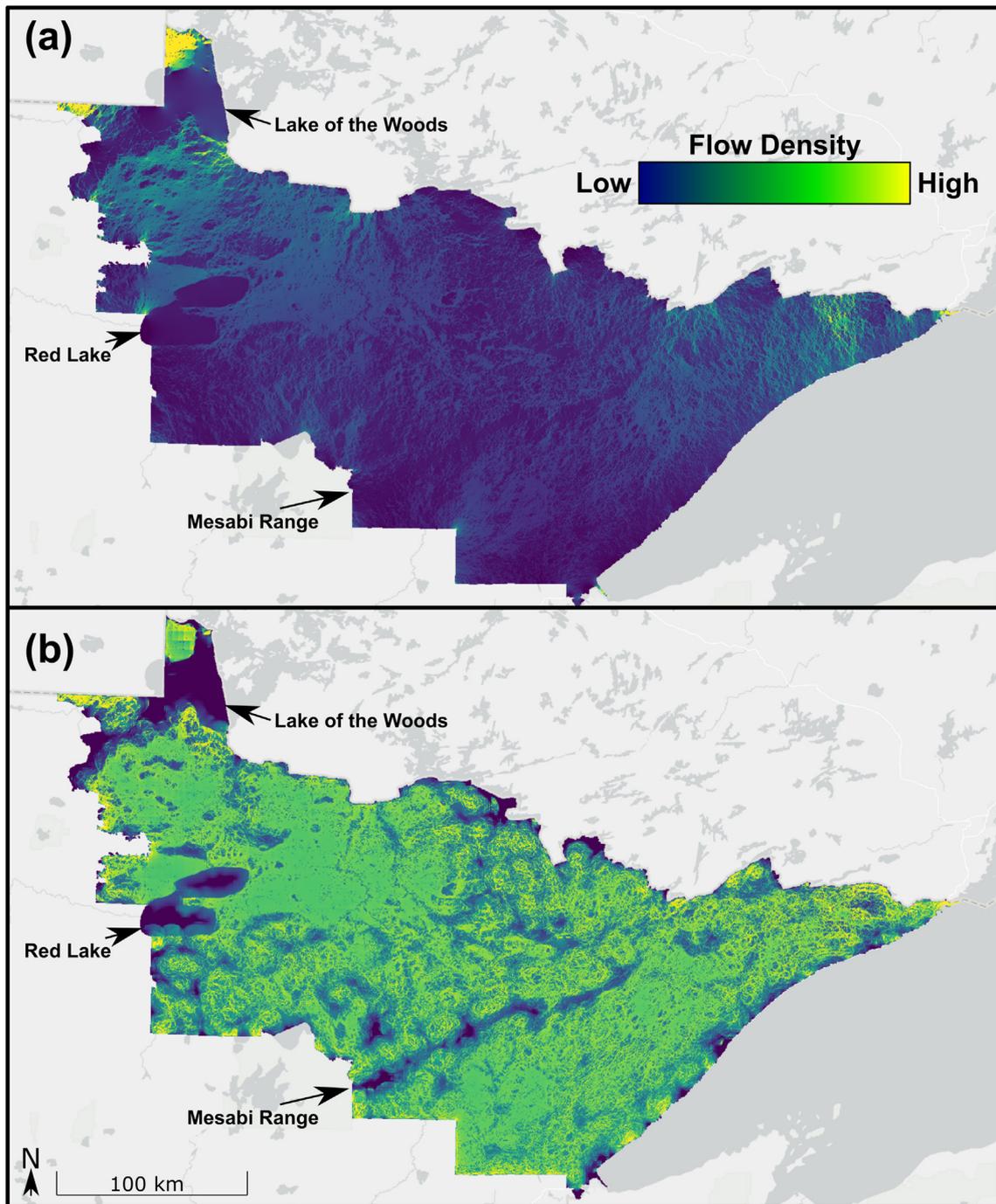


Figure 2. (a) Circuitscape prediction of cumulative current flow using a resistance surface parameterized from the top performing landscape genetics model for spruce grouse in northern Minnesota, USA. (b) Omniscape prediction of normalized current flow using the same resistance surface as (a), the proportion of coniferous forest cover within a 5-km radius as a source-strength layer, and a moving window size of 7 km. In both (a–b), yellow/light green represents greater current flow, light blue represents low current flow, and dark blue represents no current flow.

forest structure in shaping spruce grouse gene flow in our study area may have been underestimated. When continuous LiDAR data become available across the study area, future work could augment our analysis by examining the role of LiDAR-based forest structure characteristics on gene flow in a landscape genetics framework.

Mapping gene flow and connectivity

Maps of cumulative current produced in Circuitscape require nuanced interpretation. Areas of high current flow do not necessarily correlate to high gene flow, rather, they suggest greater facilitation of gene flow relative to their surroundings.

For example, a narrow channel of intermediate resistance – if adjacent to areas of very high resistance – can build up a substantial cumulative current value because all current in the area is strongly avoiding the adjacent cells. Additionally, although areas of low current flow can result from barriers to gene flow, they may alternatively arise from a vast area of uniformly low resistance that precludes current build-up in any singular location (Anderson et al. 2012, McRae et al. 2016). Interpretation of the Circuitscape-based map without considering this nuance could lead to the incorrect conclusion that the center of the study area represents a significant barrier to gene flow. Conversely, the Omniscape-based map more closely reflected genetic structure analysis suggesting a continuous deme throughout the study area. Although current flow was more heterogeneous in the center of the study area than in the northeast and northwest, no complete barriers to gene flow were evident in the Omniscape-based map.

While the Omniscape-based map suggested continuous gene flow overall, several partial barriers to gene flow were apparent. Partial barriers can attenuate gene flow but are not strong enough to cause genetic structure (Landguth et al. 2010). Partial barriers identified in our analysis did not affect spruce grouse population connectivity but could potentially create population substructure in smaller organisms with similar habitat requirements (Chambers and Garant 2010). Lake of the Woods, in the far northwestern part of the study area, represented a complete barrier to gene flow and resulted in an isolated region of high current north of the lake. However, this pattern was primarily driven by the geopolitical boundary of our study area – had our study area included parts of Canada, current would likely have circumvented Lake of the Woods and prevented the buildup of current in the part of Minnesota north of Lake of the Woods. Additionally, two conspicuous regions of low current were consistent with Red Lake, a large body of water in the northwestern part of the study area, and the Mesabi Range, a linear southwest–northeast iron range in the southern portion of the study area. The Mesabi Range is marked by mining operations and relatively little forest cover. Both features were incomplete barriers – Red Lake representing a ‘perforation’ and the Mesabi Range representing an ‘incision’ according to the framework of Jaeger (2000). Overall, despite the presence of these features, our results imply high levels of gene flow throughout the study area.

The accuracy of our Omniscape model is conditional on some key assumptions underlying our source-strength and moving-window-size parameters. Specifically, our model assumes that dispersers are more likely to originate in areas with greater proportions of coniferous forest land cover and that dispersers travel a maximum of 7 km before establishing a new home range. Indeed, previous landscape genetics work on ruffed grouse *Bonasa umbellus* revealed that expanses of unsuitable habitat beyond their typical dispersal distance (2–4 km) were important drivers of genetic distance (Jensen et al. 2019). Preliminary data from our study area suggest longer seasonal dispersals for radio-collared spruce grouse (mean = 5.1 km, max = 11.0 km; Minnesota

Department of Natural Resources unpubl.). Therefore, capturing uncertainty in model parameters is an important future step for refining spruce grouse gene flow patterns.

Expected effects of a changing climate

Resistance modeling suggested that cooler temperatures positively affected spruce grouse gene flow independent of the effect of coniferous forest land cover. During winter and spring, spruce grouse often roost under the snowpack for warmth (Schroeder et al. 2018). If snow depth is too shallow, poor roosting conditions may decrease survival and reduce the probability of successful reproduction. Similarly, freeze–thaw cycles can result in the hardening of the snowpack, which can trap spruce grouse in their roost and lead to mortality (Ménoni et al. 2010). It is possible that warmer temperatures are associated with reduced gene flow due to lower survival in warmer regions with suboptimal roosting conditions.

Climate change is predicted to increase temperatures in the study area (Taylor et al. 2017), likely resulting in a northward contraction of spruce grouse range at their trailing edge (Hickling et al. 2006). A northward range contraction could likely coincide with increasing spatial heterogeneity of spruce grouse populations in Minnesota (Hampe and Petit 2005). In other words, the ‘core’ spruce grouse habitat in northern Minnesota may become peripheral, patchy, and isolated over the next several decades. Presently, the central part of the study area is marginally warmer (~ 5°C) than the northeast and northwest parts of the study area. Continued warming could potentially create unsuitable climate conditions for spruce grouse gene flow in the center of the study area, which would threaten the persistence of genetic continuity throughout northern Minnesota. Furthermore, the distribution of coniferous forest, which also contributed to spruce grouse gene flow, is temperature dependent (Tchebakova et al. 2009, Scheffer et al. 2012, Berner and Goetz 2022). Therefore, climate change could degrade genetic connectivity of spruce grouse populations at their trailing edge through compounding direct and indirect effects.

Comparisons with other studies

Despite special status designations throughout the southern part of their range, relatively little population genetic information exists for spruce grouse. Genetic work has primarily focused on broader subspecies delineation (Gutiérrez et al. 2000, Barry and Tallmon 2010) and has identified declining mitochondrial genetic diversity in the southeastern margin of their range (Kirchman et al. 2020). Although there are biogeographical similarities between our study area and that of Kirchman et al. (2020) in the Adirondack mountains in New York – both occur in the boreal-hardwood ecotone and represent the southern limit of spruce grouse range – our results contrast in that we did not detect signatures of ongoing population fragmentation or loss of genetic diversity. Spruce grouse in New York are state-endangered ([Page 8 of 11](https://</p></div><div data-bbox=)

dec.ny.gov/nature/animals-fish-plants/spruce-grouse) in contrast to a larger, fairly contiguous, harvestable population in Minnesota that would be more likely to maintain genetic diversity. However, the use of different data types (i.e. microsatellites versus mtDNA) in these studies limits their comparability. Microsatellite analysis of spruce grouse in the core of their range in northwestern North America (Barry and Tallmon 2010) provides some context for population genetic data, although possible comparisons with our study are limited due to the use of different sets of microsatellite loci and that these studies focused on another subspecies. Observed and expected heterozygosity in our study were greater than in northwestern North America (Barry and Tallmon 2010). This result is consistent with a biogeographic history of northwestern population expansion following the retreat of ice sheets throughout the Holocene, which has been hypothesized for numerous boreal forest birds and mammals (Arbogast and Kenagy 2001, Ralston et al. 2021). However, to understand range-wide biogeographic patterns, a unified set of microsatellites should be compared throughout the species' range.

Although many boreal species have lower genetic diversity at their northern range limit as a result of their biogeographic history, several boreal species also exhibit lower genetic diversity and greater interpopulation genetic differentiation at their southern range margin due to more recent demographic instability (Browne and Ferree 2007, Kirchman and Ralston 2016, Aylward et al. 2019, Thompson et al. 2019). For example, forest clearing in the northeastern United States has caused reduced genetic diversity and connectivity in American marten *Martes americana* at their southern range limit (Aylward et al. 2019). Red-backed voles *Myodes gapperi* exhibit lower diversity and greater population structure at the southern margin of their range where they occupy boreal 'sky islands' in the Appalachian Mountains (Browne and Ferree 2007). Similarly, a historical resurvey of alpine chipmunks *Tamias alpinus* in the Sierra Nevada mountain range in California revealed an elevational contraction and associated loss of genetic continuity over the past century (Rubidge et al. 2012). Indeed, spruce grouse in the Adirondack Mountains of New York, which have experienced spatial and demographic declines (Ross et al. 2016), have lower mitochondrial genetic diversity and are genetically differentiated from a 'core' population in nearby Algonquin National Park in Ontario, Canada (Kirchman et al. 2020). In an examination of several North American boreal forest bird species, some exhibited a strong 'periphery effect' while others exhibited similar diversity and differentiation among central and peripheral populations (Ralston et al. 2021). Our results suggest the absence of a 'periphery effect' on spruce grouse population genetics in Minnesota, although expanded continuous sampling further north in Canada could improve our understanding. Between 10 000 and 20 000 spruce grouse are harvested each year without affecting the population, suggesting a very large census population size in the state (Minnesota Department of Natural Resources). Despite the climate-sensitivity of spruce grouse (Ralston and Kirchman 2013) and the location of the study area on the southern periphery of their range, our

genetic data support the persistence of a large and interconnected population that has not experienced a recent loss of genetic diversity.

This work represents the first characterization of spruce grouse nuclear genetic diversity and connectivity at their southern range periphery. Our results imply a genetically diverse and interconnected population throughout northern Minnesota at present, but also identify several warning signs that climate change could negatively impact the genetic integrity of spruce grouse at their trailing edge. Based on our maps of potential gene flow, the central part of the study area may be the most vulnerable to loss of genetic connectivity due to climate change. The cooler northwestern and northeastern portions of the study area may represent robust climate refugia for preserving spruce grouse gene flow and connectivity in climate overshoot scenarios (Huntingford and Lowe 2007, Anderson et al. 2020). Our work highlights climate change and associated changes in the distribution of boreal forest habitat as important considerations for spruce grouse population connectivity at their southern range periphery.

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Author contributions

Conceptualization and funding acquisition (CLR). Study design and methodology (CMA, CLR). Data analysis and initial manuscript writing (CMA). Manuscript revision and final approval (CMA, CLR).

Data availability statement

Genetic data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3n5tb2rp4> Location data of birds was obtained voluntarily from hunters on the condition that such information would be kept confidential, thus we are unable to publish this information.

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Allan, T. A. 1985. Seasonal changes in habitat use by Maine spruce grouse. – *Can. J. Zool.* 63: 2738–2742.
- Anantharaman, R., Hall, K., Shah, V. B. and Edelman, A. 2020. Circuitscape in Julia: high performance connectivity modelling to support conservation decisions. – *Juliacon Proc.* 1: 58.
- Anderson, M. G., Clark, M. and Sheldon, A. O. 2012. Resilient sites for terrestrial conservation in the Northeast and Mid-

- Atlantic Region. The nature conservancy, Eastern conservation science. – The Nature Conservancy.
- Anderson, C. M., Weber, C. L., Fabricius, C., Glew, L., Opperman, J. J., Pacheco, P., Pendleton, L. H., Thau, D., Vermeulen, S. J. and Shaw, M. R. 2020. Planning for change: conservation-related impacts of climate overshoot. – *BioScience* 70: 115–118.
- Anich, N. M., Worland, M. and Martin, K. J. 2013. Habitat use by spruce grouse in northern Wisconsin. – *Wildl. Soc. Bull.* 37: 766–777.
- Arbogast, B. S. and Kenagy, G. J. 2001. Comparative phylogeography as an integrative approach to historical biogeography. – *J. Biogeogr.* 28: 819–825.
- Aylward, C. M., Murdoch, J. D. and Kilpatrick, C. W. 2019. Genetic legacies of translocation and relictual populations of American marten at the southeastern margin of their distribution. – *Conserv. Genet.* 20: 275–286.
- Aylward, C. M., Murdoch, J. D. and Kilpatrick, C. W. 2020. Multiscale landscape genetics of American marten at their southern range periphery. – *Heredity* 124: 550–561.
- Aylward, C. M., Deo, R. K. and Roy, C. L. 2024. Forest structure mediates occupancy and extinction of vertebrate prey species on the trailing edge of the boreal forest. – *For. Ecol. Manage.* 553: 121568.
- Barry, P. D. and Tallmon, D. A. 2010. Genetic differentiation of a subspecies of spruce grouse (*Falcapennis canadensis*) in an endemism hotspot. – *Auk* 127: 617–625.
- Beier, P. and Noss, R. F. 1998. Do habitat corridors provide connectivity? – *Conserv. Biol.* 12: 1241–1252.
- Berner, L. T. and Goetz, S. J. 2022. Satellite observations document trends consistent with a boreal forest biome shift. – *Global Change Biol.* 28: 3275–3292.
- Braunisch, V., Bollmann, K., Graf, R. F. and Hirzel, A. H. 2008. Living on the edge – modelling habitat suitability for species at the edge of their fundamental niche. – *Ecol. Modell.* 214: 153–167.
- Browne, R. A. and Ferree, P. M. 2007. Genetic structure of southern Appalachian “sky island” populations of the southern red-backed vole (*Myodes gapperi*). – *J. Mammal.* 88: 759–768.
- Brussard, P. F. 1984. Geographic patterns and environmental gradients: the central-marginal model in *Drosophila* revisited. – *Annu. Rev. Ecol. Syst.* 15: 25–64.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretical approach, 2nd edn. – Springer.
- Caizergues, A., Dubois, S., Loiseau, A., Mondor, G. and Rasplus, J. Y. 2001. Isolation and characterization of microsatellite loci in black grouse (*Tetrao tetrix*). – *Mol. Ecol. Resour.* 1: 36–38.
- Carroll, C. 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the northern Appalachians. – *Conserv. Biol.* 21: 1092–1104.
- Casabona i Amat, C., Blanchette, P. and Desrochers, A. 2022. Habitat occupancy by spruce grouse (*Canachites canadensis*) in the south of its range in Quebec, Canada. – *Can. J. Zool.* 100: 10–18.
- Chambers, J. L. and Garant, D. 2010. Determinants of population genetic structure in eastern chipmunks (*Tamias striatus*): the role of landscape barriers and sex-biased dispersal. – *J. Hered.* 101: 413–422.
- Clarke, R. T., Rothery, P. and Raybould, A. F. 2002. Confidence limits for regression relationships between distance matrices: estimating gene flow with distance. – *J. Agric. Biol. Environ. Stat.* 7: 361–372.
- Cushman, S. A., McKelvey, K. S., Hayden, J. and Schwartz, M. K. 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. – *Am. Nat.* 168: 486–499.
- Dewitz, J. and USGS [United States Geological Survey]. 2021. National land cover database (NLCD) 2019 products (ver. 2.0, June 2021). – US Geological Survey Data Release.
- Do, C., Waples, R. S., Peel, D., Macbeth, G. M., Tillett, B. J. and Ovenden, J. R. 2014. NeEstimator V2: re-implementation of software for the estimation of contemporary effective population size (N_e) from genetic data. – *Mol. Ecol. Resour.* 14: 209–214.
- Dyer, R. J. 2012. The gstudio package. – Virginia Commonwealth Univ.
- Earl, D. A. and vonHoldt, B. M. 2012. Structure harvester: a website and program for visualizing STRUCTURE output and implementing the Evanno method. – *Conserv. Genet. Resour.* 4: 359–361.
- ESRI 2011. ArcGIS desktop: release 10. – Environmental Systems Research Institute.
- Evanno, G., Regnaut, S. and Goudet, J. 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. – *Mol. Ecol.* 14: 2611–2620.
- Falush, D., Stephens, M. and Pritchard, J. K. 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. – *Genetics* 164: 1567–1587.
- Gibson, R. M., Pires, D., Delaney, K. S. and Wayne, R. K. 2005. Microsatellite DNA analysis shows that greater sage grouse leks are not kin groups. – *Mol. Ecol.* 14: 4453–4459.
- Goldblum, D. and Rigg, L. S. 2010. The deciduous forest – boreal forest ecotone. – *Geogr. Compass* 4: 701–717.
- Goudet, J. 2005. Hierfstat, a package for R to compute and test hierarchical F-statistics. – *Mol. Ecol. Notes* 5: 184–186.
- Gutiérrez, R. J., Barrowclough, G. F. and Growth, J. G. 2000. A classification of the grouse (Aves: Tetraoninae) based on mitochondrial DNA sequences. – *Wildl. Biol.* 6: 205–211.
- Hampe, A. and Petit, R. J. 2005. Conserving biodiversity under climate change: the rear edge matters. – *Ecol. Lett.* 8: 461–467.
- Herzog, P. W. and Keppie, D. M. 1980. Migration in a local population of spruce grouse. – *Condor* 82: 366–372.
- Hickling, R., Roy, D. B., Hill, J. K., Fox, R. and Thomas, C. D. 2006. The distributions of a wide range of taxonomic grouse are expanding polewards. – *Global Change Biol.* 12: 450–455.
- Huntingford, C. and Lowe, J. 2007. “Overshoot” scenarios and climate change. – *Science* 316: 829.
- Jaeger, J. A. G. 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. – *Landscape Ecol.* 15: 115–130.
- Jensen, A. M., O’Neil, N. P., Iwaniuk, A. N. and Burg, T. M. 2019. Landscape effects on the contemporary genetic structure of ruffed grouse (*Bonasa umbellus*) populations. – *Ecol. Evol.* 9: 5572–5592.
- Kirchman, J. J. and Ralston, J. 2016. The adirondack archipelago. – *Adirondack J. Environ. Sci.* 20: 17–27.
- Kirchman, J. J., Ross, A. M. and Johnson, G. 2020. Historical decline of genetic diversity in a range-periphery population of spruce grouse (*Falcapennis canadensis*) inhabiting the Adirondack Mountains. – *Conserv. Genet.* 21: 373–380.
- Koen, E. L., Bowman, J., Sadowski, C. and Walpole, A. A. 2014. Landscape connectivity for wildlife: development and validation of multispecies linkage maps. – *Methods Ecol. Evol.* 5: 626–633.

- Landau, V. A., Shah, V. B., Anantharaman, R. and Hall, K. R. 2021. Omniscape.jl: software to compute omnidirectional landscape connectivity. – *J. Open Source Softw.* 6: 2829.
- Landguth, E. L., Cushman, S. A., Murphy, M. A. and Luikart, G. 2010. Relationships between migration rates and landscape resistance assessed using individual-based simulations. – *Mol. Ecol. Resour.* 10: 854–862.
- Manel, S., Schwartz, M. K., Luikart, G. and Taberlet, P. 2003. Landscape genetics: combining landscape ecology and population genetics. – *Trends Ecol. Evol.* 18: 189–197.
- Mateo-Sánchez, M. C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A. and Saura, S. 2015. Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. – *Ecosphere* 6: 1–16.
- McRae, B., Popper, K., Jones, A., Schindel, M., Buttrick, S., Hall, K., Unnasch, B. and Platt, J. 2016. Conserving nature's stage: mapping omnidirectional connectivity for resilient terrestrial landscapes in the Pacific Northwest. – *The Nature Conservancy*.
- Ménoni, E., Léonard, P., Desmet, J. F. and Nappée, C. 2010. Problems of ice crust formation for grouse or partridges, and the possible relation to climate change. – *Grouse News* 39: 6–10.
- Michigan Natural Features Inventory 2009. Michigan's special animals. – Michigan Natural Features Inventory.
- NOAA [National Oceanic and Atmospheric Administration] 2023. National gridded snowfall analysis. – <https://www.nohrsc.noaa.gov/snowfall>.
- Peakall, R. and Smouse, P. E. 2006. GenAlEx 6: genetic analysis in excel. Population genetic software for teaching and research. – *Mol. Ecol. Notes* 6: 288–295.
- Piertney, S. B. and Dallas, J. F. 1997. Isolation and characterization of hypervariable microsatellites in the red grouse *Lagopus lagopus scoticus*. – *Mol. Ecol.* 6: 93–95.
- Piertney, S. B. and Höglund, J. 2001. Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). – *Mol. Ecol. Notes* 1: 303–304.
- Pietz, P. J. and Tester, J. R. 1982. Habitat selection by sympatric spruce and ruffed grouse in north central Minnesota. – *J. Wildl. Manage.* 46: 391–403.
- PRISM Climate Group 2022. PRISM 30-year normals. – Oregon State Univ., <https://prism.oregonstate.edu>.
- Pritchard, J. K., Stephens, M. and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. – *Genetics* 155: 945–959.
- Quinn, C. B., Alden, P. B. and Sacks, B. N. 2019. Noninvasive sampling reveals short-term genetic rescue in an insular red fox population. – *J. Hered.* 110: 559–576.
- Ralston, J. and Kirchman, J. J. 2013. Predicted range shifts in North American boreal forest birds and the effect of climate change on genetic diversity in blackpoll warblers (*Setophaga striata*). – *Conserv. Genet.* 14: 543–555.
- Ralston, J., Fitzgerald, A. M., Burg, T. M., Starkloff, N. C., Warkentin, I. G. and Kirchman, J. J. 2021. Comparative phylogeographic analysis suggests a shared history among eastern North American boreal forest birds. – *Ornithology* 138: ukab018.
- Robinson, W. L. 1969. Habitat selection by spruce grouse in northern Michigan. – *J. Wildl. Manage.* 33: 113–120.
- Ross, A. M., Johnson, G. and Gibbs, J. P. 2016. Spruce grouse decline in maturing lowland boreal forests of New York. – *For. Ecol. Manage.* 359: 118–125.
- Rubidge, E. M., Patton, J. L., Lim, M., Burton, A. C., Brashares, J. S. and Moritz, C. 2012. Climate-induced range contraction drives genetic erosion in an alpine mammal. – *Nat. Clim. Change* 2: 285–288.
- Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E. H. and Chapin, F. S. 2012. Thresholds for boreal biome transitions. – *Proc. Natl Acad. Sci. USA* 109: 21384–21389.
- Schroeder, M. A., Blomberg, E. J., Boad, D. A., Pyle, P. and Patten, M. A. 2018. Spruce grouse. – In: Rodewald, P. G. (ed.), *The birds of North America*. Cornell Lab of Ornithology.
- Segelbacher, G., Paxton, R. J., Steinbrück, G., Trontelj, P. and Storch, I. 2000. Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). – *Mol. Ecol.* 9: 1934–1935.
- Spear, S. F., Cushman, S. A. and McRae, B. H. 2015. Resistance surface modeling in landscape genetics. – In: Balkenhol, N., Cushman, S. A., Storfer, A. T. and Waits, L. P., (eds), *Landscape genetics: concepts, methods, applications*. John Wiley & Sons, pp. 129–144.
- Stevens, J. T., Safford, H. D., North, M. P., Fried, J. S., Gray, A. N., Brown, P. M., Dolanc, C. R., Dobrowski, S. Z., Falk, D. A., Farris, C. A., Franklin, J. F., Fulé, P. Z., Hagemann, R. K., Knapp, E. E., Miller, J. D., Smith, D. F., Swetnam, T. W. and Taylor, A. H. 2016. Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. – *PLoS One* 11: e0147688.
- Taylor, A. R., Boulanger, Y., Price, D. T., Cyr, D., McGarrigle, E., Rammer, W. and Kershaw, J. A. 2017. Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. – *For. Ecol. Manage.* 405: 284–294.
- Tchebakova, N. M., Parfenova, E. and Soja, A. J. 2009. The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. – *Environ. Res. Lett.* 4: 045013.
- Thompson, L. M., Klütsch, C. F. C., Mansseau, M. and Wilson, P. J. 2019. Spatial differences in genetic diversity and northward migration suggest genetic erosion along the boreal caribou southern range limit and continued range retraction. – *Ecol. Evol.* 9: 7030–7046.
- USGS [United States Geological Survey] 2011. Gap analysis program, 20160513, GAP/LANDFIRE national terrestrial ecosystems.
- Vittinghoff, E., Glidden, D. V., Shiboski, S. C. and McCulloch, C. E. 2012. Regression methods in biostatistics: linear, logistic, survival, and repeated measures models. – Springer.
- Wang, B., Ekblom, R., Castoe, T. A., Jones, E. P., Kozma, R., Bongcam-Rudloff, E., Pollock, D. D. and Höglund, J. 2012. Transcriptome sequencing of black grouse (*Tetrao tetrix*) for immune gene discovery and microsatellite development. – *Open Biol.* 2: 120054.
- Whitcomb, S. D., Servello, F. A. and O'Connell, A. F. 1996. Patch occupancy and dispersal of spruce grouse on the edge of its range in Maine. – *Can. J. Zool.* 74: 1951–1955.
- Whiteley, A. R., Fitzpatrick, S. W., Funk, W. C. and Tallmon, D. A. 2015. Genetic rescue to the rescue. – *Trends Ecol. Evol.* 30: 42–49.
- Wisconsin Department of Natural Resources 2021. Wisconsin endangered and threatened species laws and list. – Wisconsin Department of Natural Resources.