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Critical habitat identification of peripheral Sage Thrashers under climate change

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Abstract

The Sage Thrasher (*Oreoscoptes montanus*) has been assessed as "Endangered" in Canada since 1992. Like other species with a geographic range that barely extends into Canada, Sage Thrashers are rare. Thirty-one percent of Canada's bird species listed for recovery under the Canadian Species at Risk Act (SARA) are at the periphery of their range. A listing of "endangered" under SARA requires identification of critical habitat for the species. With anticipated climate change, recovery of species requires a more proactive intervention than relying on historical occurrence to locate suitable habitat. We synthesized 19 years of Sage Thrasher occurrence and related habitat data across the species' northern range in British Columbia (BC) and Washington (WA) to define critical habitat characteristics. We found Sage Thrashers selected less leaf litter and less grass cover in flat or low-slope regions farther from anthropogenic or natural habitat breaks; habitat sensitive to the expected climate change impacts of fire, changes in precipitation, and invasive species establishment. By augmenting the BC data collected in the species' peripheral range with data from their core distribution in WA, we identified key habitat elements of an otherwise data-poor species that do not breed in sufficient numbers in Canada to reliably characterize their habitat. These methods improve the identification of "critical habitat" for peripheral species like Sage Thrashers in preparation for climate-induced range expansion northward. The framework developed demonstrates a useful template for conservation strategies for data-limited peripheral populations in other regions. Focusing on the landscape-level variables that indicate good habitat, and not the locations of habitat, can identify suitable future areas for conservation.

KEYWORDS
climate change, data rescue, *Oreoscoptes montanus*, range periphery, Sage Thrasher, sagebrush ecosystem

1 | INTRODUCTION

Thirty-one percent of Canada's bird species listed for recovery under the Canadian Species at Risk Act (SARA) are considered "peripheral" (COSEWIC, 2016). The Sage Thrasher (*Oreoscoptes montanus*) is among these and has declined from a maximum of 36 pairs in Canada to 3–12 pairs from 1931 to 2014 (Environment Canada, 2014). Like other peripheral species, Sage Thrashers are rare at the edge of their geographic range and as such, are assessed as "endangered" in Canada, with British Columbia (BC) being the only province where the species breeds regularly (COSEWIC, 2010). A listing of "endangered" under SARA requires identification of critical habitat for the species (SARA, s.41.1[c], 2002). Each year, fewer than 30 Sage Thrashers occur in BC, and fewer still successfully raise young (R. A. Cannings, R. J. Cannings, & S. G. Cannings, 1987). Thus, collecting sufficient data to determine a population trajectory or to identify land for conservation to ensure persistence of the species has been difficult.

In BC, the species' range is limited to two valleys: the southern Similkameen and the South Okanagan Valleys. In adjacent Washington (WA), the Sage Thrasher population is stable, but in sufficiently low numbers to be of conservation concern and a candidate for state listing by the Washington Department of Fish and Wildlife (NABCI, 2014). Sage Thrasher populations are declining significantly across the core of their range (−1.09% per year, NABCI, 2014), and showed a 44% decline between 1970 and 2014 (Alexander et al., 2016), most likely due to habitat loss.

Sage Thrashers are dependent on sagebrush ecosystems dominated by Big Sagebrush, or *Artemisia tridentata* spp. with as much as 50% of the original distribution of *Artemisia* already compromised or lost (Adler et al., 2018), there is an urgent need to reverse this loss of habitat. There is now a general understanding that habitat degradation and loss of shrubsteppe ecosystems are the primary factors in the decline of Sage Thrashers and other sagebrush-dependent species (Buseck, Keinath, & McGee, 2004; Knick et al., 2003; Vander Haegen, 2007; Vander Haegen, Dobler, & Pierce, 2000). Fragmentation and degradation of shrubsteppe systems has accelerated in recent decades, driven by additional and expanding threats including invading annual grasses, encroaching conifers due to fire suppression, energy extraction and changes in vegetation communities associated with climate change, and long-term livestock grazing (Bradley, Wilcove, & Oppenheimer, 2010; Hethcoat & Chalfoun, 2015). It has therefore been recommended to prioritize conservation of existing intact habitat, and to minimize further fragmentation or habitat loss (Wisdom et al., 2000).

There is evidence that climate change will become a growing challenge for this region. For example, the Canadian Earth System Model (CanESM2) model hindcasts for the months of May, June and July that the southern Similkameen temperatures from 1901 to 2018 have increased by 0.76°C (st. err. 0.17°C; climatebc.ca). However, the same CanESM2 climate model predicts that by 2085 expected temperatures will be between 1.70°C and 3.23°C warmer for the same months and region. The Audubon Society's Survival by Degrees models predict a northward shift in Sage Thrasher habitat, most of which lies at the northern periphery of the species range (https://www.audubon.org/field-guide/bird/sage-thrasher).

Our objective was to assess and improve Canada's approach to identification of critical habitat for peripheral populations in the context of climate change. In anticipation of a climate-induced range expansion northward of Big Sagebrush (Still & Richardson, 2015), we characterize the landscape and local microhabitat features selected by Sage Thrashers in an expanded Canada–U.S. data set. These results should also be important for identifying critical habitat for other *Artemisia*-dependent species.

2 | METHODS

2.1 | Study sites

The study region forms the northern limit of the Sage Thrasher distribution and northern extent of sagebrush vegetation. Alternatively called the Pacific Northwest Bunchgrass grassland (Tisdale, 1982) or Sagebrush-grass Region (Tisdale & Hironaka, 1981), this region lies between the Coast and Cascade mountains on the west and the Rocky Mountains on the east, extending from southern BC through WA into central Oregon (Wikeem & Wikeem, 2004), a region widely populated by varying densities of Sage Thrashers (Figure 1).

In BC, spatial records of nesting Sage Thrashers date back to 1910 with opportunistic location records continuing today. In this study, higher effort was spent surveying regions of historic and contemporary observations and the adjacent unoccupied habitat. Sites were selected in the only two valleys where *Artemisia* grows and Sage Thrashers have historically nested (Similkameen and Okanagan valleys of South-Central BC, Figure 1). Similarly, study effort in WA was focused on areas of shrubsteppe dominated by sagebrush including sites in eight counties (Figure 1). We matched location and field collection methods for both bird count and local-scale vegetation survey data between different regions and different field crews, resulting in survey locations across the region.

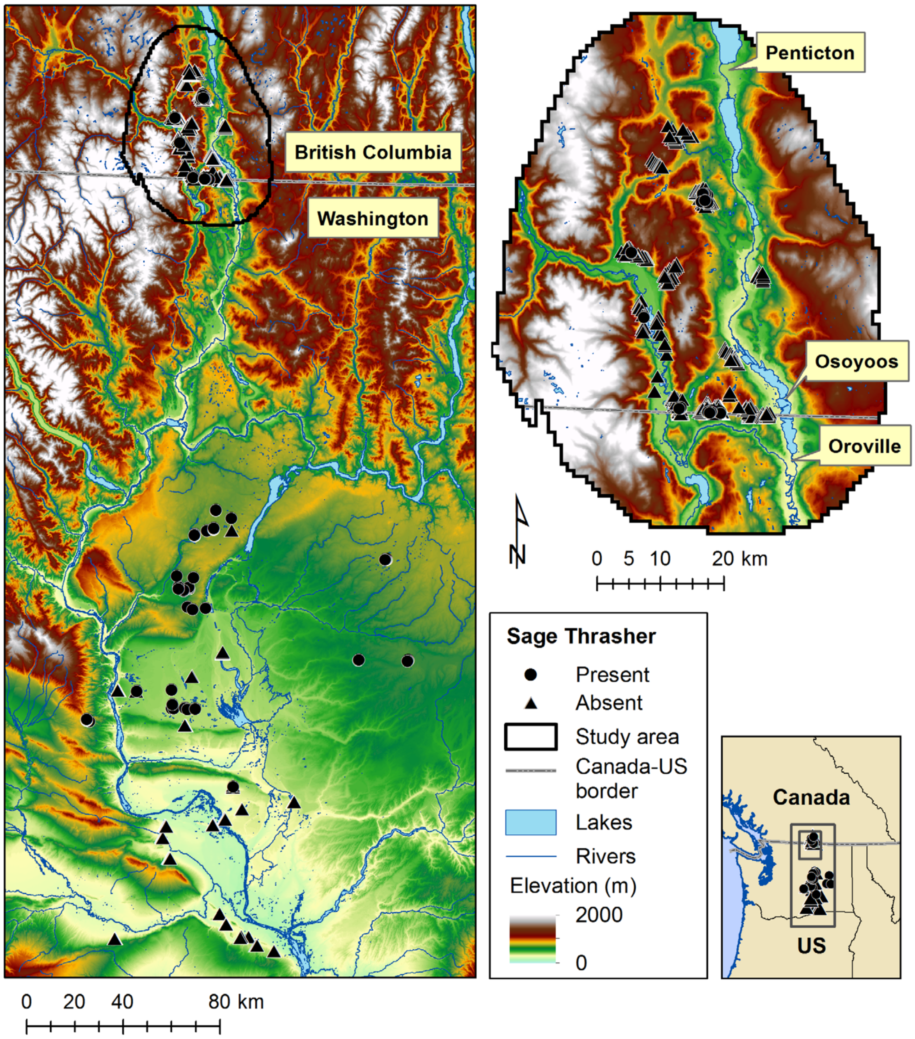

FIGURE 1 Map of point count and vegetation surveys with the oval shaped inset that highlights the more varied topography in British Columbia (BC) with the Similkameen Valley on the left and the Okanagan valley on the right

2.2 | Surveying for sage thrashers

We conducted breeding bird surveys at point count stations spaced 200 m apart along a gradient of historically occupied and unoccupied habitat following systematic point count methodology (Bibby, Burgess, & Hill, 2012; Buckland et al., 2001). Our protocols were designed to maximize detectability at all sites, with surveys conducted during periods of maximum singing activity (May to July; dawn to 09:00 hr) and only in conditions suitable for detection (no rain or high winds). A site was deemed occupied if at least 1 Sage Thrasher was detected by sight or sound within 100 m of the point count during a 5-min survey.

Bird surveys were repeated 1–5 times per point count station per season. Across all years of survey effort, each point count station was surveyed a minimum of two and maximum of nine times. In total, we conducted 1,932-point count surveys at 536 BC locations between 1992 and 2010, and 643 surveys at 125 WA locations between 1993 and 1998 (Table 1), resulting in 2,576 point count surveys at 661 point count stations across the region.

2.3 | Local-scale (field-based) habitat indices

Sage Thrashers are sagebrush obligates and select habitat based on a variety of microhabitat features best measured in the field, as well as landscape (satellite or Geographic Information System [GIS] derived) factors. Vegetation and ground cover measurements were recorded to describe the local habitat at the point count locations. A 20 cm × 50 cm Daubenmire frame (Coulloudon et al., 1999) was used to estimate percent cover for all plant species, and then grouped as perennial grasses, annual grasses (further grouped as "grasses"), native forbs, and introduced forbs. Ground cover within a Daubenmire frame was summarized as percent cover of leaf litter and bare ground. Percent cover was recorded to the exact percent (e.g., 1%), except in 1993 when the mid-

TABLE 1 Sampling effort grouped by years and by field team

British Columbia state				Washington state			
Years of effort	Point counts with SATH	Total number of point counts[a]	Median (range) of # of point counts per station	Years of effort	Point counts with SATH	Total # of point counts	Median (range) of # of point counts per station
1992–1993	68	238	1 (1.6)	1993	4	4	1
1998	3	93	4 (3.9)	1996–1998	56	121	5 (3–9)
2001–2006	13	50	2 (2.4)	–	–	0	–
2010	10	155	7 (1.9)	–	–	0	–
All years	94	536	3 (1.9)	All years	60	125	3 (1.9)

[a]Point counts were repeated 1–5 times within the season to determine occupancy.

points of Daubenmire cover classes (Daubenmire, 1959) were used (e.g., for Cover class 5–26, we used "16") to maintain the fine resolution in an otherwise continuous variable. In BC, cover class was estimated in 20 Daubenmire plots, spaced every 50 m along a line transect, and the data used to characterize habitat at the nearest point count location. In WA, cover class was estimated in 20 Daubenmire plots spaced every 5 m along a 100-m transect.

We used line-intercept transect methods to obtain an estimate for percent sagebrush "cover" in both BC and WA (Canfield, 1941). This method records the sagebrush cover at each point count location as the total start to stop distance of every sagebrush shrub that intercepts the transect centerline, excluding shrubs with <2 cm overlap with the centerline. Other shrub species were rare, but if encountered these were measured using the same line-transect "cover" method. In BC, the percent cover of sagebrush is the sum distance of intersection of each sage bush (start to stop distance of overlap) along a 1,000-m line centered through the point count location. In WA, we used the same method for a 100-m line-intercept transect. These local field-based measures of vegetation and ground cover were conducted once per point count location, although some locations were surveyed for Sage Thrashers multiple times within years, and/or across years. This approach assumes that the collection of local scale variables was not confounded with intra-seasonal changes, and attributes of the local habitat are persistent across our survey period.

2.4 | Landscape-scale GIS-processed variables

We used a GIS to derive landscape-level discriminators of potential Sage Thrasher habitat across the entire study region (Figure 2). Three key GIS process models generated covariate outputs in raster format: (a) a landscape model (elevation, aspect, slope); (b) a landscape-scale cover-class model (Landsat vegetation classification); and (c) a fragmentation model. These models provide cell-based raster values at specific point locations where point count and vegetation plots were conducted, and collectively describe the landscape-scale habitat characteristics that could be linked to Sage Thrashers breeding habitat.

2.4.1 | Landscape model

We used open-access data across the study region for elevation, slope, and aspect, from Shuttle Radar Topography Mission Version 2 enhanced, digital, topographic data (U.S. Geological Survey, 2000). A 30-m raster from this digital elevation model was used to further generate surfaces for elevation, slope, and aspect. We used Landsat 8 scenes from July/August 2014 and 2016 cloud free days to create a mosaic for the entire study region (U.S. Geological Survey, 2017).

2.4.2 | Vegetation cover class model

Using Landsat 8 band combinations, we distinguished between agricultural and native shrubsteppe areas. A false-color vegetation patch analysis was completed using unsupervised classification on Landsat 8 data (bands 7, 5, 3; Wegmann, Leutner, & Dech, 2016) to provide a representation with atmospheric removal to identify contrasts between all vegetation classes for desert regions across the study (Quinn, 2001). Cover of vegetation is then represented by different refractive intensities that can be broken into exclusive categories (U.S. Geological Survey, 2017). We allowed the patch analysis to include five classifications based on a relative comparison of the

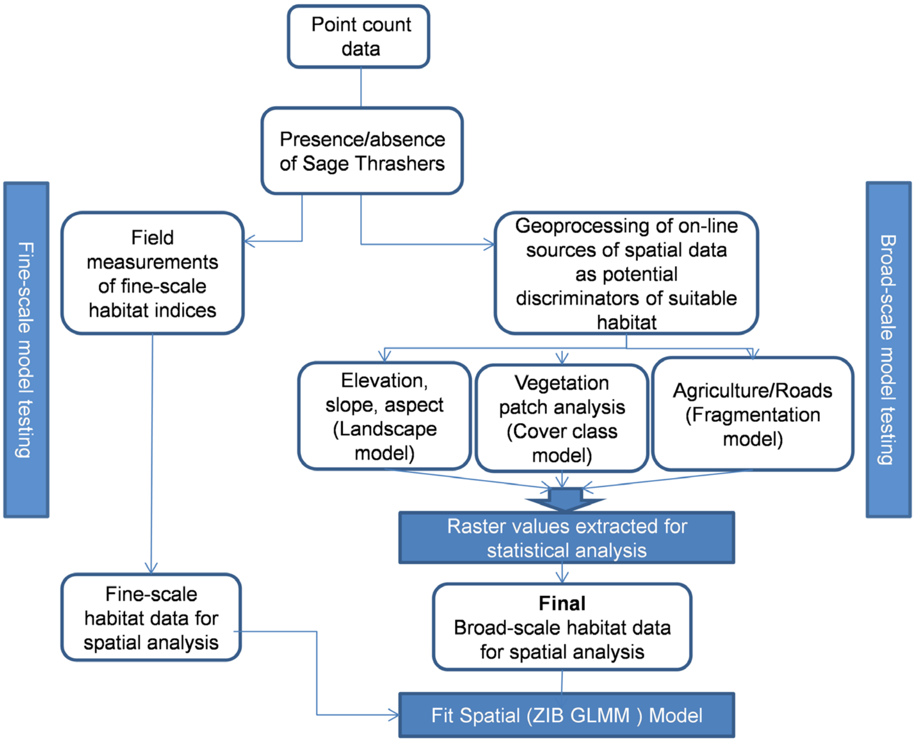

FIGURE 2 Flowchart of the analysis steps taken to derive the multiscale habitat inputs for the spatial regression model fit to predict Sage Thrasher critical habitat in the periphery of their range. Local (fine-scale) data are considered data collected in the field by field biologists, while landscape-level data are broad-scale data derived from satellite or Geographic Information System (GIS) sources

identifiable features on the landscape: open (e.g., barren landscapes), very sparse, sparse, mid-dense, and dense (e.g., forested), and then defined a further reduced set of classifications into two "veg. cover" classes: *open* (open to sparse) versus *dense* (mid-dense, dense). The output was verified visually for alignment of vegetation classes with existing Baseline Thematic Mapping Version 1 land use data (BC Government, 1995), and National Gap Analysis Program Version 2 land cover data (U.S. Geological Survey, 2011). The rasters were masked and clipped to a buffered minimum bounding rectangle of the species data points.

2.4.3 | Fragmentation model

To represent potential habitat fragmentation, a fragmentation model was created from Range Pasture data for BC (BC Government, 2016b), and grazing allotments and pastures data for WA (U.S. Bureau of Land Management, 2016). We added road networks (BC Government, 2016a; Washington State, 2016) and the Canada–U.S. border fence. These datasets were assumed to represent agricultural management units separated by roads, fencing or natural barriers identified through large slope changes. The final fragmentation metric was generated from the least distance to any natural or anthropogenic (road/fence) habitat "edge." Both pasture and grazing layers were visually confirmed to align using GIS tools. For more details on these GIS modeling steps, we refer the reader to Appendix S1.

2.4.4 | GIS-derived habitat metrics for spatial analysis

We produced a set of variables describing the landscape features across the entire study region, representing elevation, slope, and aspect, vegetation cover class, and fragmentation metrics. These GIS products provide a spatially-indexed summary of the landscape-scale habitat features.

2.5 | Spatial analysis

To identify the important environmental features influencing selection of breeding habitat in BC, we linked the occurrence of Sage Thrashers to the local vegetation and sagebrush cover data, and landscape-scale GIS-derived habitat metrics across the study region. Covariates that might have described variability in the detection of Sage Thrashers were not collected, but we restricted survey efforts to good weather and to similar morning hours to reduce the bias of this omission (Mackenzie & Royle, 2005). Ignoring the detection process across multiple site visits, assumes the probability of detection is constant across surveys but avoids the strong assumption that the population is closed, which would be untenable across point counts surveyed both within and across multiple years. Therefore, we estimate the species distribution at any location to be a relative measure but not a true measure of species occupancy (Fithian, Elith, Hastie, & Keith, 2015).

For each 5-min point count survey, a binary indicator summarized Sage Thrashers as either occupied (detected) or absent (undetected) thus providing the data for a standardized index that compares relative occurrence in habitat across the study region. We summed across all point count surveys at each location to calculate the ratio of the number of occupied surveys to the number of point counts conducted. This ratio is the observed probability of detecting a Sage Thrasher conditional on its location and is the binomially distributed response variable in our models.

We used a Bayesian framework to analyze these data within the flexible class of generalized linear mixed models (GLMM), with the canonical logit link function assuming

TABLE 2 Percent cover of annual and perennial grasses in British Columbia (BC) and Washington (WA)

	BC state	WA state
Annual grass cover	1.2% (IQR: 0.4, 12.1)	8.8% (1.3, 19.1)
Perennial grass cover	7.4% (2.0, 21.2)	31.0% (18.4, 45.8)

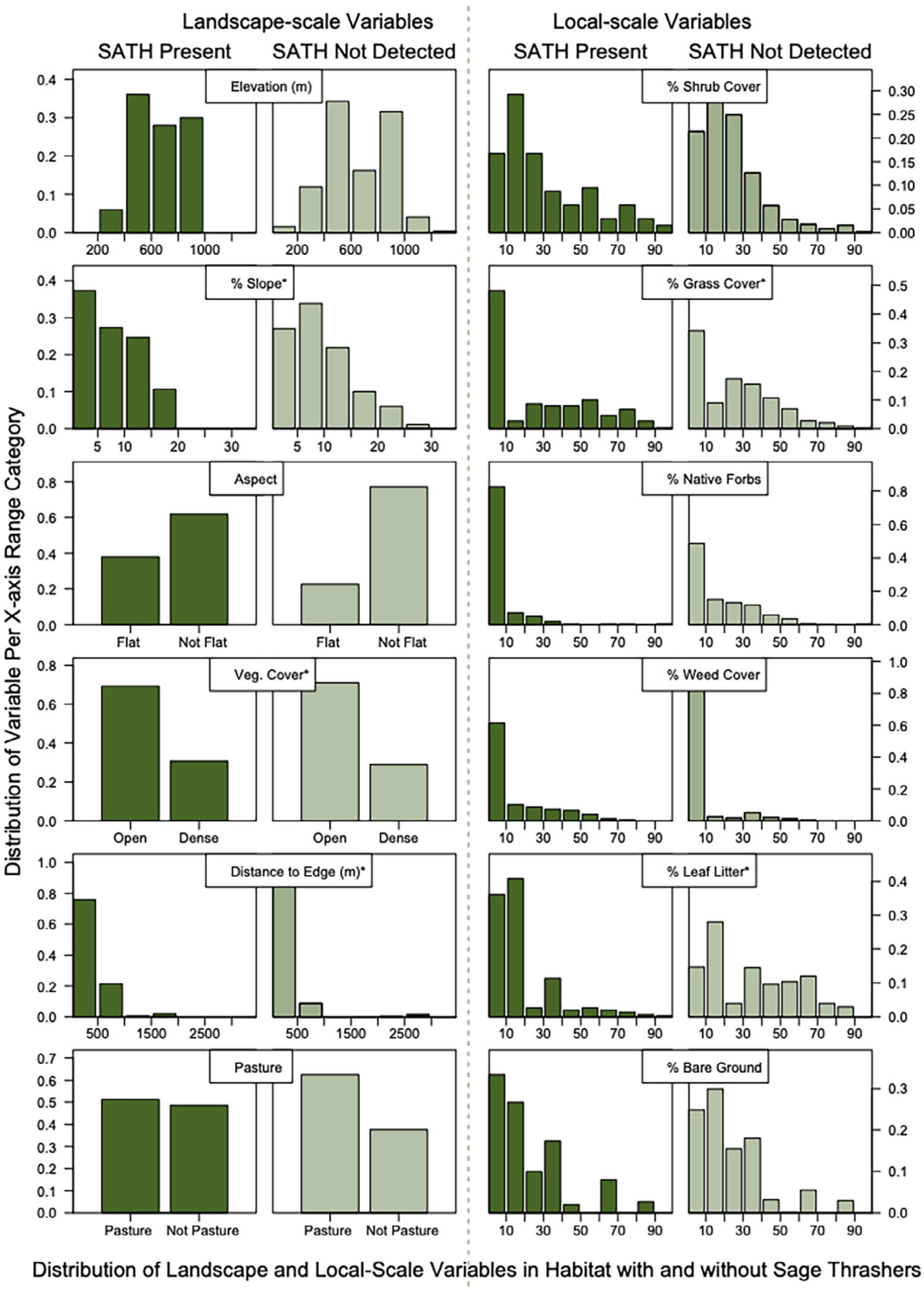

FIGURE 3 Descriptive comparison of all landscape-scale and local-scale habitat variables (as inputs to the spatial model) in regions where Sage Thrashers were present (SATH present; dark bars), and regions where they were undetected (SATH not detected; light bars). The "*" indicates that the variable was significant in one of the landscape-scale or local-scale models (Bayesian *p* value ≤.05). "*X*-axis" label (and units) appears in a box in the upper central position on each panel; the "*Y*-axis" labels represent the proportion of the distribution captured in each bar of the distribution's histogram

binomially distributed errors (Mccullagh & Nelder, 1989). We accounted for overdispersion due to zero-inflation (Sage Thrashers were rare) by fitting the model to a zero-inflated binomial likelihood. We accounted for spatial autocorrelation with a Matérn covariance function using the powerful integrated nested Laplace approximation (INLA) approach proposed by Rue, Martino, and Chopin (2009). For more details on the modeling, we refer the reader to Appendix S2.

We used a multiscale approach to link occurrence of Sage Thrashers to relative habitat suitability and selected two final models for statistical inference. The initial model included both local-scale vegetation data and landscape-scale variables to compare the importance of field-based (local) sampling with larger-scale landscape descriptors of potential habitat. The second model included only landscape-scale variables which permitted spatial predictions of the relative suitability of different regions for Sage Thrashers occurrence.

For each of the local- and landscape-scale models, we solved for the joint posterior distributions of parameter values of interest. From the landscape-scale covariate model, we extracted spatial predictions for the study region. All analyses were carried out in R (R Core Team 2017); for more details on the modeling, we refer the reader to Appendix S2.

3 | RESULTS

Potential habitat areas surveyed in BC were more variable in slope than survey sites in WA with a range of aspects (16% with slopes ≤5%); whereas, survey sites in WA were on the Columbia Plateau and generally flat (85% with slopes ≤5%, Figure 1). All point count locations were dominated by *Artemisia* shrubs, and had low coverage of native and weedy forbs compared to annual and perennial grass cover (Figure 2). On average, point count locations had a similar range of low annual grass cover across the region (WA median 8.8%, interquartile range [IQR] 1.3, 19.1%; BC median = 1.2%, IQR 0.4, 12.1%), with slightly higher perennial grass coverage in WA (median = 31.0%, IQR 18.4, 45.8%) relative to point count locations in BC (median = 7.4%, IQR 2.0, 21.2%; Table 2). When annual and perennial grasses were grouped as "Grass Cover," coverage in WA remained on average higher than that in BC, but with similar broad ranges in coverage across the region.

3.1 | All variable model

We fit several models to describe suitable habitat for Sage Thrashers that included both local-scale (right side of Figure 3) and landscape-scale variables (left panels of Figure 3) across the study region. The best model based on deviance information criterion (DIC) evaluation and cross-validation analysis of the logarithmic score indicated that local-scale variables characterizing both vegetation and ground cover were important in determining Sage Thrasher occurrence (Table 3). Models that included local-scale variables typically improved measures of model fit compared to models with only landscape-scale

TABLE 4 Summary of generalized linear mixed model (GLMM) regression parameters from the best model in Table 3 fit to both local- and landscape-scale covariate data

Regression parameter	Mean (95% credible interval)[a]
% Grasses*	−0.022 (−0.037, −0.008)
% Litter*	−0.050 (−0.066, −0.035)
Veg. cover class*	−0.623 (−1.191, −0.048)
Distance to habitat edge	−0.226 (−0.530, 0.077)
% Slope*	−0.645 (−1.151, −0.147)
Zero-inflation parameter*[b]	0.687 (0.6698, 0.7107)

[a]Posterior estimates of parameter means (and 95% credible intervals).
[b]The zero-inflation parameter is from a binomial Type 1 likelihood (Blangiardo & Cameletti, 2015).
*Significant covariates at $\alpha = .05$.

TABLE 3 Comparison of Bayesian generalized linear mixed model (GLMM) fit using local-scale and landscape-scale variables

Local-scale and landscape-scale models	*p*.eff[a]	DIC	ΔDIC	LS[b]
%Grasses + %litter + veg. cover class[c] + D2Edge[d] + % slope	20.0	913.1	0.0	0.703
%Grasses + %litter + veg. cover class[c] + aspect[e]	22.4	914.7	−1.6	0.710
%Grasses + %litter + veg. cove classr[c] + D2Edge[d] + aspect[e]	20.4	915.9	−2.8	0.708
%Grasses + %litter + D2Edg[d] + aspect[e]	17.6	916.8	−3.7	0.709

Note: We report all models within 4 DIC units of the best model. Distance to habitat edge, D2Edge.
[a]Effective number of parameters (*p*.eff).
[b]Mean logarithmic score (LS).
[c]Vegetation cover class is defined as "open" versus "dense."
[d]Distance to habitat edge (D2Edge)3
[e]Aspect is defined is categorized as "flat" ≤5%, or "not flat" >5.

TABLE 5 Results of Bayesian generalized linear mixed model (GLMM) with only landscape-scale variables

Landscape-scale models	p.eff[a]	DIC	ΔDIC	LS[b]
Veg. cover class[c] + D2Edge[d] + %Slope + aspect[e]	17.4	964.5	0	0.739
Veg. cover classr[c] + aspect[e]	11.4	971.7	−7.2	0.749

Note: We report only the best model and the runner up based on DIC value (Spiegelhalter, Best, Carlin, & Van Der Linde, 2002).
[a]Effective number of parameters (*p*.eff).
[b]Mean logarithmic score (LS).
[c]Vegetation cover class is defined as "open" versus "dense."
[d]Distance to habitat edge (D2Edge).
[e]Aspect is defined is categorized as "flat" ≤5% or "not flat" >5.

variables (Table 5), highlighting the importance of local vegetation (DIC reduced by >50). Sage Thrashers selected habitat in low-slope regions with lower accumulations of leaf litter and grass cover (Table 4), unrelated to percent cover of either forbs or shrubs. Yet landscape-scale measures of open and very sparse habitat classes showed a negative association, indicating a marginal (nonsignificant) preference for more dense vegetation classes (Table 4).

Accounting for the variability in the landscape across the sampled regions, we found Sage Thrashers were selecting similar habitat across the region we sampled (i.e., no significant difference between BC and WA). This implies that the variability within the sampling frame used in Canada and the United States characterizes Sage Thrasher habitat using the existing variables, or at least it is not confounded within some unmeasured covariate linked to country.

3.2 | Landscape-scale variable model

We fit a secondary set of models restricted to include only landscape-scale variables for which cell-based raster values were available for the broader region. As with the all-variable model, we selected the best landscape-scale variable model by DIC evaluation and used the cross-validation analysis of the logarithmic score as a second metric of model performance (Table 5). The best model included slope, distance to natural or anthropogenic habitat "edges," vegetation cover class, and a dichotomous variable discriminating between flat (<5%) and sloped aspects (Table 6). The first three of the four covariates in the model were also identified as important in the all-variable model above. Similarly, this model predicted higher occupancy in regions of low slope, with natural and anthropogenic edges at farther distances, and less open-vegetation classes. Areas with higher likelihood of finding Sage Thrasher habitat corresponded well with the three areas already identified as critical habitat in BC and identified potential new areas currently not under consideration (Figure 4).

4 | DISCUSSION

This is the culmination of 19 years of collaborative work over a broad region of Big Sagebrush shrubsteppe spanning potential Sage Thrasher habitat across the Canada–U.S. border. By combining BC with WA data, this study provided for the first time a spatially explicit characterization of habitat for this species at the northern limit of the species range. Collectively these data provided sufficient statistical power to identify suitable local and landscape scale variables, and areas of potential habitat. Based on occupancy of Sage Thrashers, identification of critical habitat requires both local and landscape variables.

The area modeled is large, beyond individual Sage Thrasher territories, creating a continuum of habitat information from the species' core in WA northward to the current range periphery. This larger area provides a conservation opportunity for identifying adequate space for population expansion as the climate warms. We have modeled a larger area with connectivity to proactively mitigate climate impacts by providing space and capacity for ecosystem function (Harris, Hobbs, Higgs, & Aronson, 2006). As climate change accelerates, identifying land for conservation using only historical references will prove increasingly challenging or fail (Langham, Schuetz, Distler, Soykan, & Wilsey, 2015). Focusing on variables that indicate good habitat rather than the location may identify suitable future areas for conservation. Lags in vegetation response to climatic change are implicit as *Artemisia* can live 100 years and can only make intergenerational range expansion.

The predicted effects of climate change will exacerbate past factors of habitat degradation, fragmentation, and loss (Bradley et al., 2010; Buseck et al., 2004; Hethcoat & Chalfoun, 2015; Knick et al., 2003). Western North America is projected to experience an increase of at least 2.1°C before the end of the century (Christensen et al., 2007). Climate models predict Big Sagebrush growing in the coldest regions to respond positively to warming trends due to a longer frost-free season (Adler

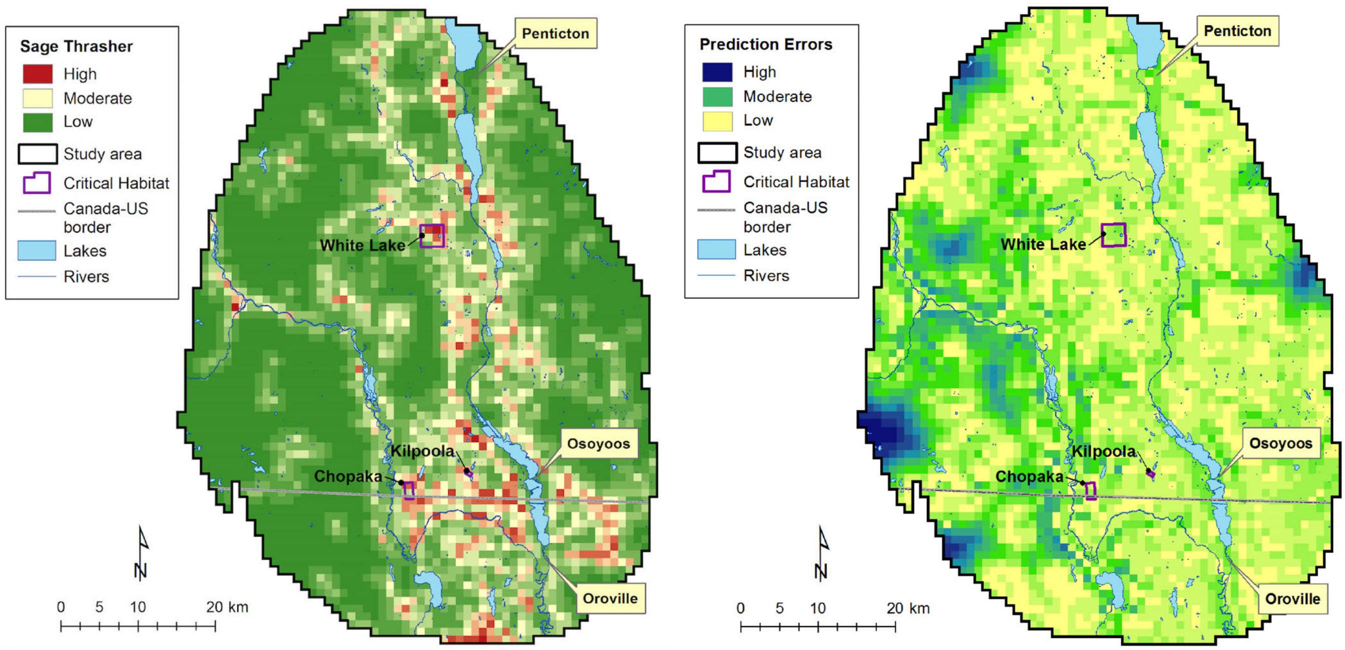

FIGURE 4 Spatial posterior predictions and standard deviations of relative habitat quality based on habitat selection by Sage Thrashers. In the left panel, darker red regions denote regions of higher likelihood of suitable habitat for Sage Thrashers. In the right panel, lighter yellow regions denote regions of more certainty. Three regions of critical habitat previously protected for Sage Thrashers are White Lake, Kilpoola, and Chopaka are outlined. The color scales are selected to show relative likelihood and relative errors but are not expected to translate directly to Sage Thrasher occurrence probabilities

TABLE 6 Summary of generalized linear mixed model (GLMM) regression parameters from the best model in Table 4 fit to landscape-scale variables

Regression parameter	Mean (95% credible interval)[a]
Veg. cover class (open/dense)	−0.541 (−1.075, 0.018)
D2Edge (m)*	−0.334 (−0.599, −0.074)
% slope*	−0.474 (−0.956, −0.008)
Aspect (flat ≤5 or > 5)	−0.295 (−0.974, 0.388)
Zero-inflation parameter*[b]	0.714 (0.702, 0.724)

[a]Posterior estimates of parameter means (and 95% credible intervals).
[b]The zero-inflation parameter is from a binomial Type 1 likelihood (Blangiardo & Cameletti, 2015).
*Significant covariates at $\alpha = 0.05$.

et al., 2018). Climate models anticipate over the next 30 years a 39% loss of suitable climate for one subspecies of *A. tridentata* (Still & Richardson, 2015); all the loss is projected to occur south of the BC border. Sage Thrashers are largely dependent on *Artemisia* for breeding, with a nesting preference for taller *Artemisia* shrubs with more dense foliage (Environment Canada, 2014; Petersen, Best, Rumbaugh, & Johnson, 1991). Therefore, protection and management of suitable habitat, occupied or not, are likely to be more important as climate change accelerates, and potentially the species core habitat moves north into what is currently considered "peripheral". As Sage Thrasher habitat in BC and WA is constrained between mountains on the west and east, the availability of suitable habitat at the northern periphery may provide refuge. As this inter-mountain Big Sagebrush shrubsteppe is particularly sensitive to climate impacts (Washington Department of Fish and Wildlife [WDFW], 2019), understanding the local and landscape characteristics selected by Sage Thrashers will ensure their conservation today while preparing for future climate changes.

4.1 | All variable model

The descriptors of microhabitat that we found Sage Thrashers selected (lower grass cover and low accumulations of leaf litter) are consistent with previous studies in the American West that found Sage Thrashers were associated with less annual and perennial grass cover (Dobler, Eby, Perry, Richardson, & Vander Haegen, 1996; Rotenberry & Wiens, 1980), and more bare ground (Rotenberry & Wiens, 1980). As Sage Thrashers prefer to walk or run along the ground or fly low while foraging (Lukas, 1999; Reynolds, Rich, & Stephens, 2020), these microhabitat features likely make it easier for Sage Thrashers to both move and forage close to the ground and evade predators. Indeed, annual grass cover was low across most of the study region relative to perennial grass cover with the exception in the southernmost areas of WA where annual grasses did, in places, have greater cover than perennial grasses.

The annual grass, *Bromus tectorum*, is an aggressive invader in Idaho, Montana, and Wyoming where Sage Thrashers have declined in abundance (Miller, Bond, Migas, Carlisle, & Kalterneckerk, 2017). This grass species with an average cover of just over 1% at BC sites is not currently listed as a noxious weed in BC (Cranston, Ralph, & Wikeem, 2002; Invasive Species Council of BC, 2018) but was 8% cover at our WA sites, so may yet be limited by climate (Bradley, Curtis, & Chambers, 2016; Ganskopp & Bedell, 1979). Bromus species (Cheatgrass) is expected to spread as native species die due to climate change effects of warming and drought (Bradley et al., 2016). Changes in the timing and amount of precipitation effect growth of cheatgrass, which outcompetes native grasses by its increased capacity to incorporate and hold moisture (Ganskopp & Bedell, 1979). As the progression of climate change accelerates, the relative competitive abilities of native species to invasions of non-native species may become a more significant stressor.

Across the range of Sage Thrashers, the species is dependent on the presence of *Artemisia* for breeding habitat (Braun, Baker, Eng, Gashwiler, & Schroeder, 1976; Dobler et al., 1996). Previous research has shown that they prefer stands with greater cover of *Artemisia* (Dobler et al., 1996) and stands with less grass cover (Dobler et al., 1996; Rotenberry & Wiens, 1980). Using line transect methodology, we did not find local measures of *Artemisia* cover were related to Sage Thrasher presence. However, landscape-scale measures of a denser cover class from Landsat 8 satellite imagery were important in both the local and landscape-scale models. This suggests either Sage Thrashers select their breeding territory based on a broad landscape-scale assessment of *Artemisia* density and quality and not at a local scale; or big sage shrubs that provide the structural cover for ground foraging and nesting are better measured (and modeled) at the landscape scale. This has important implications for identifying potential critical habitat across the species' range, as it suggests that landscape-scale measures of *Artemisia* quality should be included with local-scale attributes of habitat. With climate models predicting a positive response of *Artemisia* in BC to warming trends (Still & Richardson, 2015), climate-related impacts on *Artemisia* at the northern periphery of the Sage Thrasher's range will likely be at both the local and landscape scales.

4.2 | Landscape model

At the landscape scale, we found Sage Thrashers selected flatter areas farther from natural and anthropogenic habitat "edges". "Edges" in our GIS analyses were identified as either changes in the landscape (natural fragmentation) or assumed to occur at roads or other anthropogenic features. Sage Thrashers in Wyoming have been significantly negatively affected at the landscape-scale by increasing road density (Mutter, Pavlacky Jr, Van Lane, & Grenyer, 2015), and in WA, landscape fragmentation greatly reduced the daily survival rate of Sage Thrasher nests and seasonal reproductive output of other sagebrush-dependent birds, (Vander Haegen, 2007). Corvids prey on nests of sagebrush-steppe birds (Howe, Coates, & Delehanly, 2014; Knick et al., 2011; Vander Haegen, Schroeder, & Degraaf, 2002) and may use fence posts as perches for hunting. In this study region, the "distance to habitat edge" indicates several factors associated with fragmentation including road/fence as well as natural landscape features. Large continuous patches of *Artemisia* in BC maintain connectivity corridors between current habitat and future range shifts in *Artemisia* and local and landscape-level shifts in suitable habitat. As arrival dates typically differ between sexes for migratory birds (Allee, Emerson, Park, Park, & Schmidt, 1949), large contiguous patches of *Artemisia* in BC could increase the chances of discovering potential mates, and/or maximize population growth if breeding pairs produce many young that exhibit strong philopatry (Knick & Rotenberry, 2000).

4.3 | Identifying sage thrasher habitat

Previous studies have found grassland shrubsteppe birds select similar habitat features across large spatial regions, including whole mountain ranges (Bulluck et al. 2006), and along elevation gradients (Medin, Welc,h, & Clary, 2000). We treated differences in the vegetation and habitat classification as differences across a north–south continuum affected by local and landscape-scale processes. The landscape-scale model predicted regions of high occurrence for the 3 federal boundaries of critical habitat currently protected for Sage Thrashers in BC (Figure 4, White Lake, Kilpoola, and Chopaka), with suitable habitat adjacent to the existing protected areas. Protecting larger intact regions of Sage Thrasher habitat is therefore possible along the Canada–U.S. border. Additionally, the model identifies regions of higher suitability adjacent to currently protected regions (north-east and south-east of Kilpoola 49.055°N, 119.52°W; Richter Pass; 49.02°N, 119.56°W, respectively; Figure 4). Given expectations of northern range shifts in this species, conservation efforts should include areas to the north likely to change with climate.

The better performance of models that included field measures of vegetation characteristics when compared to landscape-scale models suggests that local-scale variables better describe the key microhabitat features for Sage Thrashers (i.e., lower grass cover and leaf litter). The landscape variables, however, help the model to eliminate unsuitable habitat with incompatible elevation, aspect, and vegetation classes. Taken together, the all-variable and landscape-scale models provide a more complete understanding of Sage Thrasher habitat, and a method to integrate conservation efforts across multiple scales. In a similar way, Alexander et al. (2017) used fine-scale bird occupancy data to guide coarse-scale protected area networks by linking the local habitat data associated with higher bird abundance to ecological processes at the larger scale.

As climate-change related processes will likely operate both at local and landscape scales, identifying the important habitat features is part of a successful long-term management plan for the species. The framework developed here demonstrates a useful template for conservation strategies for data-limited peripheral populations under the specter of climate change. Furthermore, habitat protection and enhancement of sagebrush-steppe habitats for Sage Thrashers will benefit many sagebrush-steppe wildlife species in BC, many of which are also threatened species in the region (COSEWIC, 2010).

4.4 | Study limitations

These data were collected between 1993 and 2010, and no information about the observer detection process remains (i.e., we could not construct a detection function). However, we argue that Sage Thrashers are not vocally cryptic being loud songsters with long melodic songs most often sung from prominent perches in a sagebrush landscape. By further limiting data collection to occur only under optimal conditions, we argue that sufficient diligence in the data collection process reduced variation in detection rate as a source of bias. However, without the detection function, we cannot reconstruct the actual population density for the region. Nevertheless, we do believe that the relative measure of occupancy that we present here lines up well with historic patterns of occupancy in the Okanagan and Similkameen Valleys of BC, providing reassurance that the maps of higher "relative probability of occurrence" predicted from our models are correlated with species' presence, and therefore favorable breeding habitat for Sage Thrashers.

Some study locations within BC and WA were selected preferentially based on known breeding locations of Sage Thrashers and adjacent territory. Sagebrush-dependent species are known to exhibit high site fidelity (Knick & Rotenberry, 2000) reflecting a biological positive bias that is based on philopatry and history of breeding success from previous years, and not merely a function of habitat metrics (see Wiens, Rotenberry, & Van Horne, 1986 field manipulation). To address any effect of nonrandom sampling, spatial predictions (and associated variances) from the species distribution model display only relative occupancy rather than absolute measures.

Future vegetation surveys would benefit from a sampling design that systematically characterized local scale variables at the same time of the year. Synchronizing vegetation surveys to the same time window would rule out potential confounding of site-level vegetation with occupancy, while reducing within-season variability in plant phenology and ground cover.

Further improvements to the model could include higher resolution imagery to reduce any attenuation in effect size estimates (e.g., Graham et al., 2008) as well as advanced imagery methods that estimate height of vegetation, particularly of *Artemisia* (Miller et al., 2017). These data could be further combined with ground-based training data to link local measures of important habitat characteristics to variables at the landscape level (i.e., those of Landsat 8 imagery), although a previous attempt to do so in Southern BC found only weak associations (Paczek, 2002), but see Tuanmu and Jetz (2014).

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

All authors have contributed to designing and/or performing the research and writing the manuscript and have read and approved the manuscript prior to submission.

DATA AVAILABILITY STATEMENT

The data will be archived with Canada Open Data Portal.

ETHICS STATEMENT

No ethics approval was required for this research.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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