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Enhanced shrub growth in the Arctic increases habitat connectivity for browsing herbivores

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Abstract

Habitat connectivity is a key factor influencing species range dynamics. Rapid warming in the Arctic is leading to widespread heterogeneous shrub expansion, but impacts of these habitat changes on range dynamics for large herbivores are not well understood. We use the climate–shrub–moose system of northern Alaska as a case study to examine how shrub habitat will respond to predicted future warming, and how these changes may impact habitat connectivity and the distribution of moose (*Alces alces*). We used a 19 year moose location dataset, a 568 km transect of field shrub sampling, and forecasted warming scenarios with regional downscaling to map current and projected shrub habitat for moose on the North Slope of Alaska. The tall-shrub habitat for moose exhibited a dendritic spatial configuration correlated with river corridor networks and mean July temperature. Warming scenarios predict that moose habitat will more than double by 2099. Forecasted warming is predicted to increase the spatial cohesion of the habitat network that diminishes effects of fragmentation, which improves overall habitat quality and likely expands the range of moose. These findings demonstrate how climate change may increase habitat connectivity and alter the distributions of shrub herbivores in the Arctic, including creation of novel communities and ecosystems.

KEYWORDS

Alaska, Arctic, climate change, habitat connectivity, hares, moose, range shift, shrub expansion, structural connectedness

1 | INTRODUCTION

Globally, many species are shifting their range in response to changes in climate (Parmesan & Yohe, 2003; Root et al., 2003). Climate-driven shrub expansion is one example of a global range shift (Myers-Smith et al., 2011; Naito & Cairns, 2011a) occurring across tundra and alpine ecosystems, including circumarctic regions (Tape, Sturm, & Racine, 2006), European and Australian Alps (Anthelme, Villaret, & Brun, 2007; Cannone, Sgorbati, & Guglielmin, 2007; McDougall, 2003), and the Tibetan Plateau (Brandt, Haynes, Kuemmerle, Waller, & Radeloff, 2013; Zhao, Wu, & Yin, 2011). Experimental studies using increased temperature, shrub dendrochronology, and spatial correlation between summer temperature and shrub growth indicate that summer temperature strongly affects the growth of shrubs in tundra ecosystems (Elmendorf et al., 2012; Forbes, Fauria, & Zetterberg, 2010; Hallinger, Manthey, & Wilmking, 2010; Walker et al., 2006; Wang et al., 2019). The expansion of shrubs may be facilitating range shifts for shrub-dependent species in the Arctic, such as moose (*Alces alces*), snowshoe hares (*Lepus americanus*), and migratory songbirds (Boelman et al., 2015; Tape, Christie, Carroll, & O'Donnell, 2016; Tape, Gustine, Ruess, Adams, & Clark, 2016; Wheeler, Høye, & Svenning, 2018). How shrub expansion will influence patterns and processes of range shift dynamics at the expanding edge in the Arctic is not well understood.

Shrub expansion in the Arctic has broad implications for ecosystem functioning. The presence of shrubs alters surface energy fluxes (Chapin, Eugster, McFadden, Lynch, & Walker, 2000; Chapin et al., 2005; Liston, Mcfadden, Sturm, & Pielke, 2002; Sturm et al., 2001), nutrient and element cycling (Jackson, Banner, Jobbagy, Pockman, & Wall, 2002; Kielland, 2001), surface water and moisture influxes (Liston et al., 2002; Sturm et al., 2001), and biotic interactions and community structure (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Myers-Smith et al., 2011; Post et al., 2009; Walther et al., 2002). Herbivore colonization facilitated by shrub expansion in arctic riparian corridors (Hall Jr., 1973; Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016) could accelerate ecosystem turnover of carbon and nitrogen (Bryant, 1987; Butler & Kielland, 2008; Kielland, Bryant, & Ruess, 1997) and alter shrub structure, productivity, and community composition (Bryant, 1987; Butler, Kielland, Rupp, & Hanley, 2007; Olofsson & Post, 2018; Tape, Lord, Marshall, & Ruess, 2010).

The arrival of new herbivores may also alter biotic interactions and create novel ecosystems in the Arctic. For example, recent colonizers like moose and possibly snowshoe hares may compete with ptarmigan (*Lagopus lagopus*), as well as with each other, for forage on the North Slope of Alaska (hereafter the North Slope) (Zhou, Prugh, Tape, Kofinas, & Kielland, 2017). Through apparent competition (Holt, 1977), moose expansion may also facilitate an increase in shared predators (e.g., wolves: *Canis lupus*, and bears: *Ursus arctos*) with caribou (*Rangifer tarandus*). Habitat alteration has increased moose and deer (*Odocoileus* spp.) populations in southwestern Canada, for instance, which has increased wolf density and threatens woodland caribou (*R. tarandus caribou*) populations through incidental predation (Latham, Latham, McCutchen, & Boutin, 2011; Wittmer, Sinclair, & McLellan, 2005). Thus, shrub expansion and its associated herbivores is predicted to have strong impacts on local community structure and ecosystem functioning (Kielland, Bryant, & Ruess, 2006), though it remains unclear the specific effects of shrub habitat connectivity on large herbivore distribution and population dynamics.

Structural connectedness of habitat patches facilitates movement of organisms within a landscape (Hanski, 1999). Since the development of the niche concept in relation to species distribution (Grinnell, 1917), modern theories of species distribution have recognized dispersal as a key component, together with abiotic habitat conditions (environmental niche) and biotic interactions (Guisan & Thuiller, 2005; Pulliam, 2000; Soberón, 2007). In a patchy landscape, movement via source–sink dynamics among local populations maintains the persistent occupancy of sink habitat patches (Hanski, 1998; Pulliam, 1988), and thus influences range dynamics, where dispersal balances local extinction and colonization rates (Hanski, 1999; Soberón, 2007). By combining the theories of spatial movement (i.e., metapopulation and source–sink dynamics) and the Hutchinsonian niche concept (Hutchinson, 1957), species distributions can be predicted in a given geographic space (Pulliam, 2000; Soberón, 2007). Understanding patterns and dynamics of dispersal barriers, therefore, will improve accuracy and reduce uncertainties in the predictions of distributions under climate change (Araújo & Guisan, 2006). In this paper, we use the climate–shrub–moose system of northern Alaska to examine how shrub habitat will respond to forecasted future warming, including how these changes may impact habitat connectivity and dispersal dynamics of a shrub herbivore at the edge of its range.

Retrospective analyses show that moose colonized the North Slope in early 1900s (Coady, 1980; Hall Jr., 1973; Tape, Gustine, et al., 2016), as shrub expansion created new ecological conditions. It is unknown how moose habitat will change in the future if shrubs expand in the tundra and habitat patches possibly coalesce. Our objectives were to (a) create a detailed, current moose distribution map; (b) predict future trends in tall-shrub habitat for moose under different warming scenarios; (c) describe patterns and spatial structure of future habitat dynamics on the North Slope; and (d) understand how climate-induced habitat expansion could influence habitat connectivity and range shift dynamics. To address our objectives, we developed a species distribution model (Phillips, Anderson, & Schapire, 2006) in conjunction with a simpler temperature-threshold model to estimate moose habitat. Moose habitat was then projected under forecasted warming scenarios to assess potential changes in moose habitat and connectivity in the future. We hypothesize that shrub expansion will increase the structural connectivity of patch networks, which in turn will accelerate moose range extension in the river corridor systems. This research contributes to improved predictions of species responses to climate change.

2 | METHODS

2.1 | Study area

The arctic tundra of northern Alaska covers three major physiographic regions: the Brooks Range, Arctic Foothills, and Arctic Coastal Plain (67.76°–71.37°N, 140.97°–166.22°W). The North Slope in our study area starts from the edge of the Brooks Range mountains in the south and continues onto the open and flat areas of Arctic Coastal Plain. Low arctic vegetation features mainly communities of dwarf shrubs, sporadic tall-shrubs (>1 m), tussocks formed with graminoid and sedge species, and moss tundra (Walker et al., 2005). River and creek drainage systems, where most shrub expansion occurs, host riparian communities of plants dominated by tall-shrubs such as feltleaf willow (*Salix alexensis*) and Siberian alder (*Alnus viridis* ssp. *fruticosa*; Tape, Hallinger, Welker, & Ruess, 2012). Feltleaf willow, a key forage species for moose, is an early successional species that generally occupies active floodplain corridors and tributary creeks. Patches of tall feltleaf willows with herbaceous plants growing between shrub stands serve as critical habitat for herbivores like moose, where they have greater accessibility and mobility during browsing while reducing dangers from predation (Mould, 1977; Zhou et al., 2017).

2.2 | Shrub surveys

We measured riparian habitat characteristics along a 568 km transect crossing three physiographic regions including major environmental gradients, which we accessed via an inflatable boat over a 3 week period in August 2015. We randomly selected 59 sampling sites in riparian areas of three connected rivers: Nigu, Etivluk, and Colville Rivers. At each site, we sampled a 50 m transect perpendicular to the river. Along each 50 m transect, we selected five points (at 10, 20, 30, 40, and 50 m) and at each point, we selected four nearest shrubs within a radius of 5 m. To obtain shrub height and canopy diameter, we measured the height of the tallest live branch of the thicket and averaged the minimum and maximum of canopy diameter of the live shrub stands. Among the 937 individual shrubs we recorded, 406 were feltleaf willows that were analyzed in this paper (further details on field sampling in Zhou et al., 2017).

2.3 | Moose surveys

Spring moose surveys were conducted in our study area in April each year from 1997 to 2015 (n = 19 years). Piper PA-18 and Cessna 182 aircrafts were used to fly survey transects in the management unit, where most of the survey effort was focused on major drainages of the Colville, Anaktuvuk, Chandler, and Killik Rivers. During the surveys, biologists from the Alaska Department of Fish and Game (ADF&G) recorded GPS locations and group size of each moose observed. During April, when the surveys were conducted, the tundra was continuously snow-covered, except for occasional windblown ridges and the riparian shrubs protruding from the snow along rivers and streams. Moose are confined to riparian corridors as their sole source of forage at this time of year (Mould, 1977), and this limiting resource is the focus of our current and future shrub height projections. Moose are highly visible from the air during these surveys, and it is therefore assumed that all moose are counted using this method. This paper used available GPS data from 1997 to 2015 for species distribution modeling.

2.4 | Species distribution modeling

To develop a species distribution model for moose, we used our moose location data and multiple environmental predictor layers at various scales to build a Maxent model (Phillips et al., 2006). Based on the species–environment association, Maxent predicted potential habitat on the North Slope by identifying areas in the landscape that had similar environmental conditions to the locations where moose had been observed (Phillips et al., 2006).

To develop the Maxent model, we randomly split the moose presence data into a training set (2,188 locations, 80% of data) and a testing set (547 locations, 20% of data). We used 14 environmental predictors, including topographic features, land cover types, soil types, river systems, and climatic variables (Table 1). To assess Maxent model performance for predictive accuracy, we used 10-fold cross validation, with area under curve (AUC) of receiver operating characteristics for internal model evaluation (Fawcett, 2006), and the held-out testing data set (20% of presence data) for external model evaluation. We used the jackknife test to assess which variables of environmental predictors are most important in the model (Phillips et al., 2006).

To determine whether a simple model based on temperature and riparian landscape features would adequately predict moose distributions, we examined the association between the growth of tall feltleaf willows and summer temperature to understand how moose habitat will respond to the warming climate in our study area. Moose on the North Slope predominantly inhabit riparian areas with tall-shrubs (Mould, 1977) and their occurrence closely follows tall-shrub distribution in our study area (Zhou et al., 2017).

TABLE 1 Environmental predictors for Maxent model. “Static” predictors are assumed to be spatially static whereas “dynamic” predictors are assumed to change during our modeling period

No.	Categorical names for the environmental predictor	Temporal stability	Data type
1	Aspect	Static	Continuous
2	Slope	Static	Continuous
3	Elevation	Static	Continuous
4	Soil types	Static	Categorical
5	Distance to coastal line	Static	Continuous
6	Distance to major rivers	Static	Continuous
7	Decadal mean July temperature 2000–2009	Dynamic	Continuous
8	Decadal mean January temperature 2000–2009	Dynamic	Continuous
9	Decadal mean annual temperature 2000–2009	Dynamic	Continuous
10	Decadal mean annual precipitation 2000–2009	Dynamic	Continuous
11	Decadal mean summer precipitation 2000–2009	Dynamic	Continuous
12	Decadal mean winter precipitation 2000–2009	Dynamic	Continuous
13	Length of growing season 2000–2009	Dynamic	Continuous
14	Land cover types	Dynamic	Categorical

To explore the relationship between shrub size and summer temperature at each site, we measured the mean shrub height and canopy diameter at each sampling site and calculated shrub canopy volume (volume formula for a cone: $V = \pi r^2 h/3$) as an estimation of shrub size. The mean July air temperature was extracted for each sampling site from a raster map (771 m resolution) of surface air temperature between 1971 and 2000 from Scenarios Network for Alaska and Arctic Planning (SNAP) hosted at the University of Alaska Fairbanks (https://www.snap.uaf.edu/) that used the downscaling method of the PRISM Climate Group (http://prism.oregonstate.edu/). Based on available climatic data, PRISM interpolates a complete climate grid over the region using a peer-reviewed mathematical process that incorporates local physiographic features (Daly et al., 2008). The shrub size was plotted against mean July air temperature, and the threshold for tall-shrub growth was identified with an unsupervised learning method of K-means clustering that separated the observations into two clusters of small and large shrubs.

We used our estimated temperature threshold to identify suitable tall-shrub habitat in the riparian areas. Based on the top predictors in the Maxent model, our temperature-threshold model combined July temperature and river networks to estimate tall-shrub habitat for moose. Areas within 5 km of riparian corridors with mean July temperature above the temperature threshold were classified as potential tall-shrub habitats (i.e., moose habitat). To evaluate the utility of this simple temperature-threshold model for mapping potential shrub habitat for moose, we calculated the proportion of observed moose locations that occurred within identified moose habitat.

2.5 | Climate projection modeling

Projections of future changes in moose habitat were explored with two warming scenarios of the Intergovernmental Panel on Climate Change (IPCC): viz. A2 and B1. These were selected to establish a likely envelope of scenarios; in the A2 warming scenario, surface temperature continues to rise, whereas in the B1 scenario warming peaks at midcentury (IPCC, 2014). For future projections of surface temperature in our study area, we used the modeled decadal means of July temperature in 2010s, 2050s, and 2090s, which was locally fine-tuned to Alaska by SNAP with downscaling processes based on PRIMS climatological dataset from 1971 to 2000. Based on the temperature threshold we identified for shrub growth, we estimated moose habitat for each modeling period under scenarios A2 and B1. All scenarios were run with a five climate-model average, where the model output was from the top five models that best replicated the historical climate of Alaska.

To assess the accuracy of predicted mean July temperatures, we used available weather records from MesoWest (https://mesowest.utah.edu) during 2005–2018. We used Welch two sample *t* test to compare predicted and observed temperatures at three weather stations: Anaktuvuk Pass Airport (11.96°C vs. A2: 11.44°C and B1: 11.66°C) in the Brooks Range, Umiat airfield (12.83°C vs. A2: 12°C and B1: 12.25°C) in the Arctic Foothills, and Nuiqsut Airport (9.08°C vs. A2: 8.06°C and B1: 8.49°C) on the Arctic Coastal Plain.

2.6 | Habitat connectivity metrics

To assess structural connectivity of habitat, we computed three patch metrics using the LecoS python plugin (Jung, 2016) in QGIS (https://qgis.org/en/site/), which is based on the metrics from the FRAGSTATS software hosted at UMass Landscape Ecology Lab (http://www.umass.edu/landeco/research/fragstats/fragstats.html). Metric 1, effective mesh size (Jaeger, 2000), characterizes the fragmentation of a landscape based on the probability of two randomly chosen points in the landscape being connected (i.e., not separated by habitat barriers). The connection probability is given by

$$C = \sum_{i=1}^{n} \left(\frac{A_i}{A_t} \right)^2 ,$$

and the probability is converted to the effective mesh size by multiplying it by the total landscape area:

$$m_{\mathrm{eff}} = A_t C = \frac{1}{A_t} \sum_{i=1}^{n} A_i^2 ,$$

where A_i = area of patch *i*, and A_t = the total area of the landscape. Effective mesh size denotes the size of the continuous patch area that can be accessed from a randomly placed point without leaving the patch. It can be interpreted as the ability of two randomly placed animals to find each other. Increasing effective mesh size causes the habitat patches to become more aggregated, increasing habitat connectivity. Metric 2, area of the largest patch, calculates the area of the largest patch among the patch networks, focusing on the degree of increase in the area of the largest patch with increased landscape connectivity. Metric 3, total core area, measures the total area of the shrub patches after removing the edge-influenced area within 771 m (one cell value in the raster layer recognized by LecoS) from the edge in each shrub patch. Patches of equal area are not necessarily equal in their area exposed to edges. With increased physical connectivity of the landscape, for example, the magnitude of increase in the total core area of elongated and narrow patches with rough edges is smaller than that of round-shaped patches with smooth edges. If patch connectivity and areas of patches increase, both the area of the largest patch and total core area of the patches within the landscape should increase.

3 | RESULTS

Our Maxent model (AUC = 0.884) of moose habitat achieved a 95% accuracy rate based on the 20% withheld dataset of observed moose locations. The jackknife test showed that the most important variable in the Maxent model was distance to major rivers (dist2river), followed by riparian soil types (soil) and mean July temperature (tjul2000_09; Figure S1). Whereas river systems and soil types were assumed to be spatially static during our projection period, mean July temperature was the most important environmental predictor among the dynamic variables.

We identified a temperature threshold for the growth of tall-shrub feltleaf willow in the riparian systems (Figure 1). K-means clustering analysis showed that large willows centered at the estimated mean July temperature of 11.0°C. Canopy volume of feltleaf willow increased abruptly where the estimated mean July temperature exceeded 11.0°C (Figure 1b). Although the threshold was clear, there was an outlier at close to 8°C (dark gray dot in Figure 1b). Using the 11.0°C threshold, we created a map of current moose habitat (Figure 2). Our temperature-threshold model was based on the top three predictors in the Maxent model (Table 1; Figure S1): mean July temperature, distance to rivers (within 5 km of river systems), and riparian soil category (contained within 5 km of river systems). This temperature-threshold model correctly predicted 82% of the observed moose locations recorded during surveys (Figure 2a). Output from the Maxent and temperature-threshold models mimicked the spatial structures of moose habitat (Figure 2). The temperature-threshold model contained 85% of Maxent output in the modeling area, indicating that the far simpler temperature-threshold model performed well in predicting moose habitat.

The mean July temperature averaged across sampling sites showed an upward trend under both A2 and B1 scenarios (Figure 3). During 2005–2018, the predicted mean July temperatures by both A2 and B1 were slightly lower than the observed temperatures at the three remote sites but showed no statistical difference (Table S1), except the A2 prediction at Nuiqsut (observed = 9.08 ± 0.438, A2 = 8.06 ± 0.105, *t* = −2.2593, *df* = 14.499, *p* = .04). Thus, if this period is an indication, warming projections from both scenarios are likely conservative. Under both scenarios, the amount of potential habitat for moose was predicted to increase on the North Slope of Alaska (Figure 4). Moose habitat expansion was predicted to increase

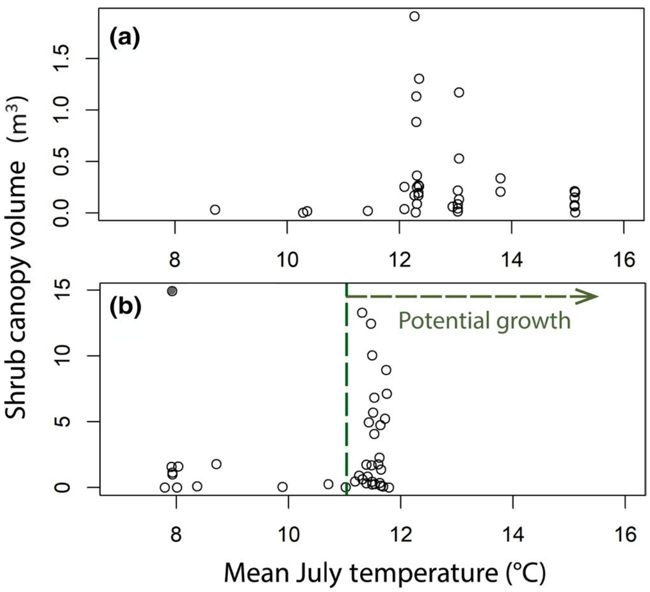

FIGURE 1 Shrub size and mean July temperature by two independent datasets exhibited a similar relationship. (a) Data from Swanson (2015) showed a threshold at mean July temperature of approximately 12°C, and (b) our data showed an estimated threshold of 11.0°C (vertical dashed line)

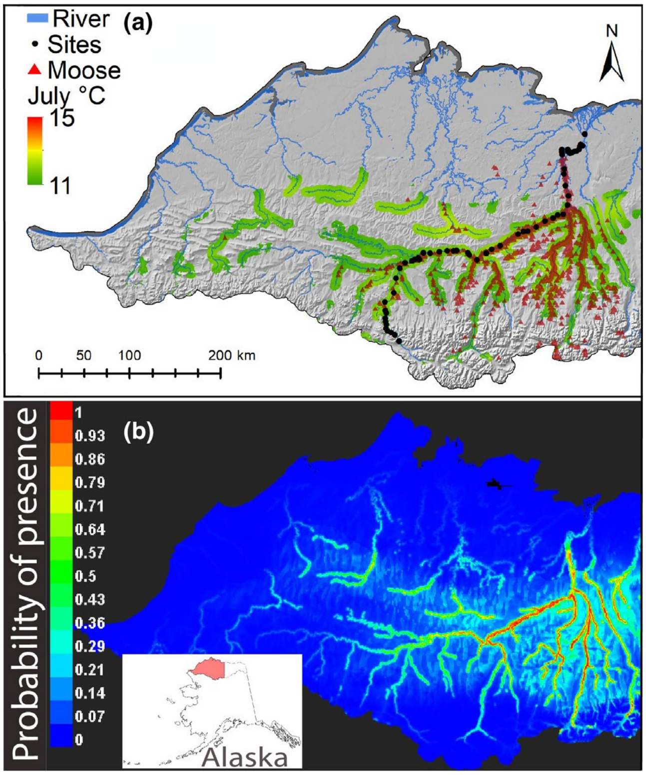

FIGURE 2 Current potential habitat for moose estimated by (a) a temperature-threshold model that refers to the empirical association between summer temperature and tall-shrub growth in the riparian corridors and (b) a Maxent model that is based on 14 environmental predictors processed through the machine-learning algorithm. The habitat estimations (mean July °C) were validated by observed moose locations (red triangles) from 19 years of field survey data. Black dots in (a) show field sites for shrub sampling

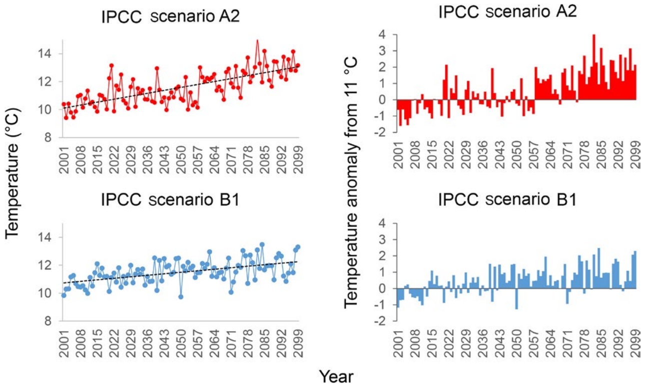

FIGURE 3 Trends in predicted mean July temperature at shrub field sampling sites. Predicted mean July temperature averaged across field sites under IPCC scenario A2 (A1) and B1 (B1), with linear trendlines. Predicted temperature anomalies from 11°C (our estimated threshold) are shown in the right column for A2 (A2) and B1 (B2) scenarios

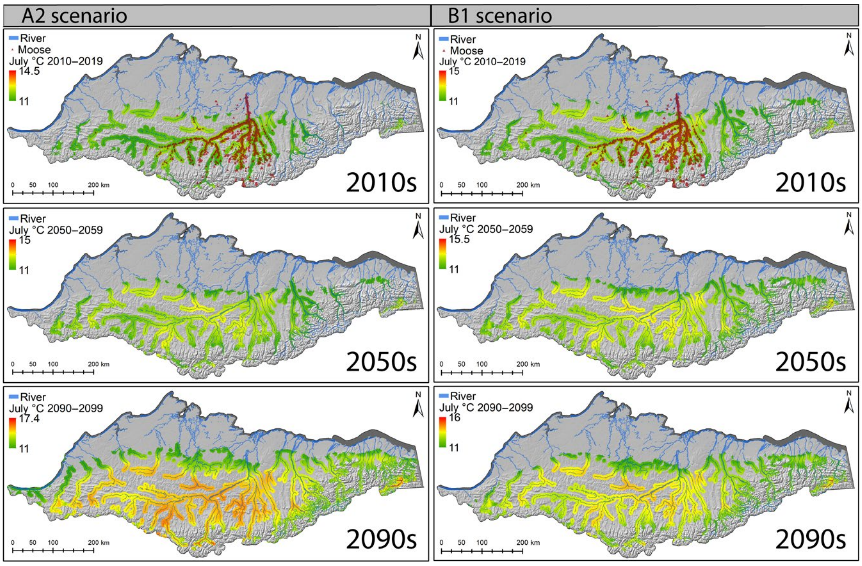

FIGURE 4 Predicted increases in shrub habitat for moose under A2 (left column) and B1 (right column) warming scenarios during (A) 2010s, (B) 2050s, and (C) 2090s. Red triangles represent observed moose locations

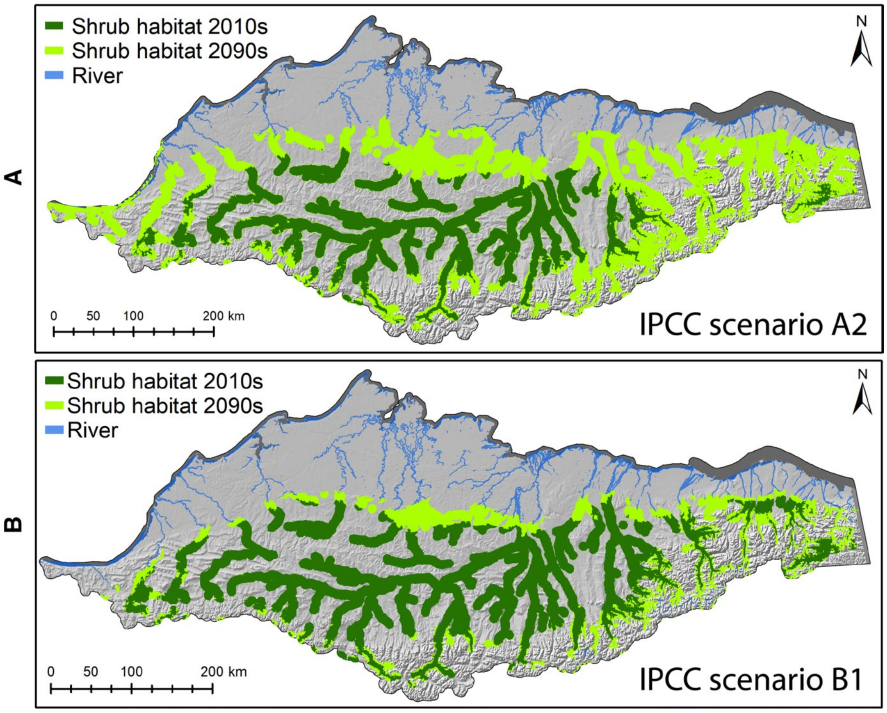

FIGURE 5 Predicted increases in shrub habitat for moose under (A) A2 and (B) B1 warming scenarios between 2010s (dark green) and 2090s (light green)

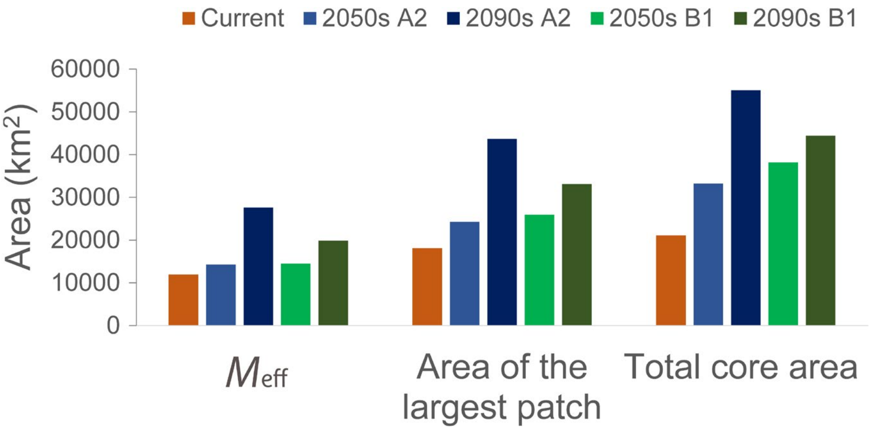

FIGURE 6 Habitat connectivity metrics under warming scenarios A2 and B1. The "M_{eff}" is the effective mesh size, which denotes the continuous patch areas that can be accessed from a random point without leaving the patch. Increasing M_{eff} indicates that the habitat patches are more aggregated and physically connected. "Area of the largest patch" is the area of the patch that has the largest area among all the patches on the landscape. "Total core area" adds all core areas of patches after removing a 771 m buffer to account for edge effects

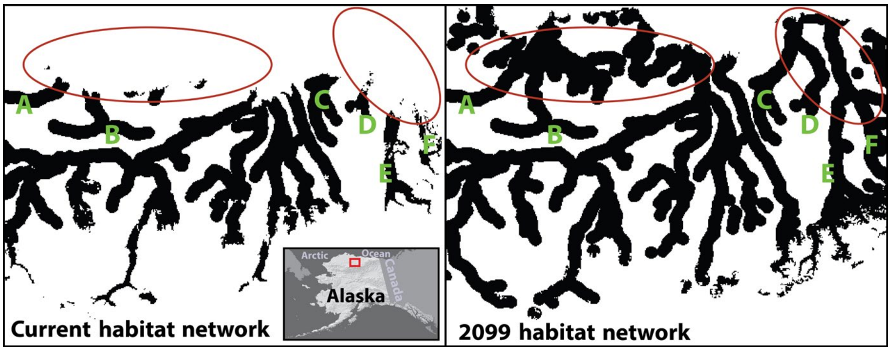

FIGURE 7 Increase in habitat connectivity under A2 warming scenario. The previously isolated patches (marked A–F) would be connected to form larger and more physically connected habitat networks. Patch connection at the roots (the red ellipses) of the dendritic networks will dramatically increase structural connectedness of patch networks within the landscape

by 153% (2.5-fold) under A2 warming scenario and 106% (twofold) under B1 warming scenario by the year 2099. Most noticeably, moose habitat was predicted to penetrate into the river drainage systems to the north and west toward the arctic coastlines, expand greatly eastward on the North Slope toward the Canadian border, as well as increase in the Brooks Range to the south (Figures 4 and 5).

All three metrics for structural connectedness of shrub patches are predicted to increase with habitat expansion (Figure 6), as patches gradually coalesce to form larger and more connected patches (Figure 7). Our model indicates that connecting near-neighbor patches to the largest patch on the landscape will increase its area by 141% under A2 scenario and 83% under B1 scenario by the year 2099. Similarly, the total core area available to moose is projected to increase by 161% under A2 scenario and 111% under B1 scenario by the year 2099. Because the spatial configuration of moose habitat is a dendritic pattern, the area of connected patches is expected to dramatically increase due to coalescing roots of the dendritic patterns, instead of a gradual increase by connecting more patches incrementally (Figure 7).

4 | DISCUSSION

4.1 | Shrub habitat connectivity in a warming Arctic

Here we examined the predicted spatiotemporal patterns of shrub patches under warming and associated changes in habitat connectivity. Our results suggest that physical connectedness of shrub patches in river corridors will dramatically increase if the warming trend continues in the Arctic. With increased structural connectedness of shrub patch networks, the total area of spatially connected shrub patches will increase, and thus moose habitat will also increase. The 19 year moose survey showed that many patches in river corridors in our study area seemingly had sufficient shrub abundance but were not occupied by moose. A significant proportion of Alaskan moose migrate seasonally between habitats in different latitudes and elevations (Joly, Craig, Sorum, Mcmillan, & Spindler, 2015; Mauer, 1998). Increased connectivity of shrub patches in arctic river corridors will likely accelerate colonization of the newly created niche conditions by shrub-dependent species such as moose at the edge of their expanding ranges.

The moose distribution model showed a dendritic pattern that matches the pattern of tall-shrub habitat along river drainage systems in arctic Alaska (Beck, Horning, Goetz, Loranty, & Tape, 2011). Future expansion of tall-shrub distribution may show a similar dendritic pattern, and as such, herbivores that require tall-shrubs (e.g., moose and hares) will be limited to river corridors with abundant shrub patches. In river corridors, favorable conditions for expanding shrubs (such as early successional species like feltleaf willow) are created mainly by fluvial dynamics that produce new silt bars for shrub colonization (Butler et al., 2007). Floodplains in river corridors also provide continuous hyporheic supply of nutrients (Koyama & Kielland, 2011), which overall increases nutrient availability and ameliorates microsite growth condition for tall shrubs.

The dendritic expansion of tall-shrub habitat highlights the role of landscape patterns in spatial responses of species to climate change (Opdam & Wascher, 2004). Landscape structures, underpinned by physiographical patterns and hydrological regimes, clearly will exert significant control over patterns of shrub-habitat expansion under climate warming in arctic Alaska (Naito & Cairns, 2011b; Tape et al., 2012). We therefore emphasize the importance of examining patterns of range expansion rather than simple metrics of habitat change: whether the landscape structures synergistically enhance or hinder species range expansion with climate change (e.g., Saura, Bodin, & Fortin, 2014; Warren et al., 2001). Our findings suggest that dendritic patterns of shrub habitat in our study area will likely enhance the range expansion of shrub-dependent herbivores via increased structural connectivity of patch networks.

4.2 | Projected expansion of shrub habitat

Multiple lines of evidence, including warming manipulations, dendrochronology of shrubs, and spatial correlations, indicate that warming increases deciduous shrubs across the tundra biome (Arft et al., 1999; Blok et al., 2011; Elmendorf et al., 2012; Forbes et al., 2010; Hallinger et al., 2010; Myers-smith & Hik, 2018; Walker et al., 2006; Wang et al., 2019). Tall-shrubs in river valley systems may reach a tipping point of phase transition toward shrub dominance (Naito & Cairns, 2015), consistent with our analysis showing a distinct temperature threshold in feltleaf willow growth, marked by an abrupt increase in shrub size after mean July temperature surpasses 11.0°C. A shrub study in an adjacent region identified a remarkably similar temperature threshold for felfleaf willow growth of 11.8°C (Swanson, 2015). Currently, mean July temperature at most sites on the North Slope seldom exceeds 11.0°C, indicating the potential for increased growth of willow shrubs if summer temperature continues to rise.

The estimation of northern range limit of tall-shrubs by our temperature-threshold model is likely to be conservative. Influenced by the cold temperature of the Arctic Ocean, the lower segment of the Colville River (~80 km to the arctic coast) has relatively low summer temperature. However, a few sites along the corridor facilitate tall shrubs (Zhou et al., 2017). Field and browse surveys show that moose occasionally disperse into these sites, but our temperature-threshold model did not predict moose at these sites close to arctic coast, though our Maxent model did. Since projections of IPCC warming scenarios in our study area may also be conservative, we expect that moose may disperse further north in the lower floodplain areas than the estimation by our temperature-threshold model.

The shrub–temperature relationship that drives the model predictions does not account for several important indirect effects of warming, such as hydrological effects, which could alter shrub habitat predictions. Floodplain hydrologic disturbance (viz. a large flood) could at least locally modify tall-shrub patches (Butler et al., 2007) and corresponding growth trajectories. A lack of large floods could have a similar effect by permitting shrub patches to experience vegetation succession into graminoid-sedge tussock tundra. The observed peaks in daily mean discharge rates of the Colville River (Umiat station, 2003–2018), however, showed no patterns over the period (Figure S2). Earlier snow melt induced by spring warming could result in earlier occurrence of peak flow, but the available data during 2002–2019 (n = 18 years) showed no clear trend (Figure S3). Climate models on average predict moderate increases in annual precipitation at our shrub sampling sites (Figures S4 and S5), which could result in modest increases in discharge unaccounted for in our model. However, increased ground temperature via shrub trapped snow accumulation (Pomeroy et al., 2006) could lead to development of taliks at tall-shrub sites that allow water loss to the sub-permafrost region, resulting in a loss of stream water (Jafarov et al., 2018).

Permafrost thaw occurring in many Arctic locations (Liljedahl et al., 2016) could trigger disturbances that either enhance or curtail shrub growth, depending on microsite characteristics; these feedbacks are also not considered in our model. Whereas feltleaf willows can capitalize on in situ nutrients in floodplains with well-drained soil and higher soil pH (Swanson, 2015), areas with frequent tundra fires (Jones et al., 2015) and thermokarst and thaw slumps (Huebner & Bret-Harte, 2019; Lantz, Kokelj, Gergel, & Henry, 2009) also release nutrients and provide favorable conditions for establishment and growth of deciduous shrubs. An improved understanding of tundra fire and permafrost disturbance would likely improve the accuracy of projected tall-shrub distributions in tundra regions.

Herbivory in the floodplain also can potentially reduce shrub height and retard expansion rate for palatable species (Bryant, 1987; Bryant, Joly, Chapin, DeAngelis, & Kielland, 2014; Kielland et al., 1997; Olofsson et al., 2009; Olofsson & Post, 2018), though our model does not include these effects. Feltleaf willow is the preferred forage species of moose, hares, and ptarmigan (*L. lagopus*, *Lagopus muta*) in our study area (Zhou et al., 2017), and other arctic herbivores in the region, including muskox (*Ovibo moschatus*) and caribou, also prefer willows over well-defended species such as alder (Bryant & Kuropat, 1980; Christie et al., 2015). We observed that browsing by hares in the study area severely damaged and shortened willow shrubs more than alders (Zhou et al., 2017). Repeated browsing by moose in the floodplain areas facilitates a shift toward dominance of late successional species, such as alder, and suppresses palatable and early successional species like feltleaf willow (Butler et al., 2007; Kielland et al., 1997). A similar transition can be facilitated by hare browsing (Bryant, 1987). Furthermore, colonization by beavers, which currently occupy parts of the Brooks Range but are very rare or absent from the North Slope, could greatly alter the distribution of willow species in the riparian corridors by cutting them down for forage and engineering, while also flooding others (Tape, Jones, Arp, Nitze, & Grosse, 2018).

This local uncertainty is compounded when modeling moves from shrub habitat projection to dynamics of herbivore populations. Population performance and distribution are not solely determined by habitat condition (Soberón, 2007). For example, the North Slope moose population fluctuated in our study area since 1970 despite the ongoing shrub expansion. Snowshoe hare populations exhibit ~10 year cycles, seemingly independent of regional warming trends (Elton & Nicholson, 1942; Krebs, 2011). Biotic interactions such as predation and disease also influence herbivore distribution dynamics (Dussault et al., 2005; Jeffries & Lawton, 1984; Soberón, 2007). Although we expect the changes in habitat availability and connectivity projected by our models will be an important factor influencing the future distribution of moose, other limiting factors such as predation, harvest, and disease need to be accounted for as well.

The expansion patterns of habitats for shrub-dependent herbivores projected by environmental covariates in our model will thus be modulated by additional forces such as hydrology, permafrost or fire disturbance, and biotic interactions at fine scales. Species distribution models such as the Maxent model used here inherently assume a static, linear relationship between environmental variables and species distributions (Guisan & Thuiller, 2005). If these relationships vary across a species' range or over time, projections may be inaccurate (Van De Kerk, Verbyla, Nolin, Sivy, & Prugh, 2018). Despite these inherent uncertainties in projecting future changes of complex systems like the climate–shrub–herbivore system (Oreskes, Shrader-Frechette, & Belitz, 1994), the importance of environmental filters, such as temperature, increases with greater modeling scale for species distribution (Pearson, Dawson, Berry, & Harrison, 2002). Combined with river networks, climate change is predicted to control habitat expansion at large scales in the Arctic (Elmendorf et al., 2012; Forbes et al., 2010; Myers-smith & Hik, 2018; Naito & Cairns, 2011b; Walker et al., 2006; Wang et al., 2019), consistent with the findings presented here.

4.3 | Emergence of novel arctic ecosystems

Warming-induced expansion and increased connectivity of shrub habitat are likely reshuffling wildlife communities and reshaping community structure in the Arctic. With shrub expansion, moose, snowshoe hares, and beavers are expanding their ranges northward (Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016; Tape et al., 2018). Shrub expansion may reduce lichen forage availability and pasture quality for caribou in their arctic range (Fraser, Lantz, Olthof, Kokelj, & Sims, 2014; Joly, Jandt, & Klein, 2009). Shrub expansion may also alter communities of migratory songbirds (Boelman et al., 2015) and arthropods (Rich, Gough, & Boelman, 2013). Reshuffled wildlife community in the Arctic will likely alter the complexity of community structures and biotic interactions (Alexander, Diez, & Levine, 2015; Blois et al., 2013; Deacy et al., 2017; Harley, 2011) and influence ecosystem processes of element and nutrient cycling (Bryant, 1987; Buckeridge, Zufelt, Chu, & Grogan, 2010; Butler & Kielland, 2008; Jackson et al., 2002).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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