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Via Email To: sarah.canepa@usda.gov and online to the BHDL Comment Page

Re: Beaverhead-Deerlodge (BHDL) National Forest Plan Amendment for Canada Lynx Habitat

Supervisor Watson and Team Leader Canepa:

These comments and analysis are submitted on behalf of the Alliance for the Wild Rockies, Center for Biological Diversity, Bold Visions Conservation, Conservation Congress, Council on Wildlife and Fish, Gallatin Wildlife Association, Inland Empire Task Force, Native Ecosystems Council, Sage Steppe Wild, Swan View Coalition, Western Wildlife Conservancy, WildEarth Guardians, Wilderness Watch, and the Yellowstone to Uintas Connection. These organizations are public interest organizations that engage on public land issues affecting wildlife.

The comments respond to the March 4, 2025 Scoping Notice by taking a deep dive into the Biological Assessment (BA) for Canada lynx Effects of the 2009 Revised Forest Plan and the Northern Rockies Lynx Management Direction. Figure 2 of the Scoping Notice shows that the 2020 version of modeled habitat will be used as the basis for the plan amendment. The Plan Amendment process must include an alternative to ensure restoration of functionality of lynx habitat and connections, not limit the choice to the 2020 Model.

Some takeaways from our analysis include:

- Occupied Habitat designations appear to be arbitrary and a matter of convenience because they have omitted consideration of lynx habitat where historical observations revealed lynx presence.
- The absence of lynx from the BHDL following listing in 2000 has not been explained in relation to the massive deforestation occurring here in the last half of the past century and the explosion of motorized recreation.
- The BHDL analysis must address why, with its claimed 1,625,805 acres of lynx habitat, there were no lynx found for nearly 20 years following its listing as threatened.
- A view of the regional national forests using the Olson et al (2021) model shows that the BHDL is an important connection between the GYA and Northern Rockies.
- Forest Plan Standards must be established to identify, restore and maintain linkages and connecting habitats.
- The 2020 BHDL BA Model
    - The Model is flawed in that it uses the current modified forest structure to define "surrogate" habitat as opposed to the historical habitats used by lynx.

- The Model relied on modeled snow depths as criteria, and constrained habitat by aspect and elevation. Our analysis of 29 SNOTEL stations in and around the BHDL shows that snow depth is not a constraint for lynx in the BHDL.
  - Analysis of historical lynx observations in the BHDL show that slope, aspect and elevation are not constraints for lynx in the BHDL.
  - The Model used surrogates for habitat such as structural classes, e.g. stem exclusion rather than the actual habitat types where lynx were historically observed. It only focused on subalpine fir, spruce, and cool-moist Douglas-fir, yet both our analysis and the Montana Natural Heritage Program found that lodgepole pine forest was the dominant forest type.
  - The Model relied on VMAP and did a crosswalk with structural stages that includes major modifications from the historical forest vegetation types. This is an attempt to accept the modified forest as a baseline, rather than the habitats lynx have relied upon through the historical record. VMAP has a significant error rate which we illustrated using an aerial image showing the stem exclusion category is misrepresented.
  - The Model relies on the Wildland Urban Interface exemptions to NRLMD to request an exemption of 88,910 acres. Our analysis of WUI for the BHDL shows that instead of 1,644,663 acres of WUI, it should only be 34,663 acres. The Forest Plan amendment must correct this huge disparity with an analysis that accounts for building density.
- We compared the Montana Natural Heritage Program Inductive and Deductive models that relied on historical lynx observations, the Olson et al (2021) model that relied on tracking studies, and the 2020 BHDL Model. The BHDL Model was the only one that did not take into account historical observations or tracking data. Here, we repeat our Table 6 showing the differences.

Table 6. Area (acres) of Modeled Lynx Habitat on the Beaverhead-Deerlodge NF

BHDL		116,806 Secondary vegetation	1,509,146 Primary vegetation
MNHP	1,287,428 Generally Unsuitable	2,069,426 Low Suitability	257,089 Moderate Suitability
Olson	1,862,477 Low Probability	1,507,773 Moderate Probability	244,016 High Probability
Comparing the Model Acreage			
Beaverhead Deerlodge Models		2,711,422 acres (2001) 1,625,952 acres (2020) 2,134,741 acres* *Y2U 2001 BHDL model clipped to Forest Boundary	
Montana Natural Heritage Program Inductive Model		2,326,515 acres	
Olson et al (2021) Model		1,751,789 acres	

- To sum up, the BHDL 2020 model is too limited in its interpretation, leaving out much potential lynx habitat. It further did not consider historical observation locations and the historical vegetation types where those occurred. Instead, it used surrogates with cascading errors to eliminate major lynx habitats such as lodgepole pine and Douglas fir. The MNHP model used lynx observations combined with environmental variables to arrive at a habitat area of 2,326,515 acres, compared to the BHDL 2020 modeled 1,625,952 acres. This is less than the BHDL 2001 model, but that model would include the habitat in the Dillon Ranger District that was omitted from the 2020 model.

The MNHP Deductive model shows that the BHDL model eliminates major categories of vegetation types in its mapping. In the end, the BHDL 2001 model with 2,134,741 acres within the BHDL seems to capture the habitat better than the 2020 model and does include that habitat in the Dillon Ranger District. However, that said, the determination of lynx habitat must go back to the historical vegetation types where observations were made and map the extent of those across the BHDL. Since we have determined that snow depth, slope, aspect and elevation are not significant barriers within the constraint of the BHDL, these should not be part of the determination.

- We reviewed 2012 Planning Rule sections cited in the Scoping Notice, the ESA, and Forest Service Manual provisions that should apply.
    - While the Scoping Notice invites public comment, by including the 2020 lynx habitat map, it presupposes this is the lynx habitat that will be the basis for the plan amendment, thus pre-empting public input.
    - The Planning Rule expects the restoration of ecological integrity, diversity of plant and animal communities and species viability, multiple use, and listed timber requirements. All the elements listed in those sections will need specific standards in the plan amendment.
    - The ESA makes biological assessments "discretionary". These should be required in the plan amendment for all future projects.
    - The FSM cites the ESA to maintain species viability, and conduct activities to assist in the recovery of T&E species.
    - The FSM defines "Essential Habitat" to include areas needed for recovery of T&E species.
- Reflecting these Planning Rule, ESA and FSM provisions, we conclude, "The BHDL must now designate lynx habitat as Essential for recovery of lynx and maintaining connections within the BHDL and to adjacent public lands. It must determine the potential occupancy extent and home ranges and set population goals for a viable population within the BHDL to be established by a combination of habitat protection and introducing lynx as done in Colorado."

  We are not seeing National Forests conducting any analysis of linkages, or "suitable unoccupied habitat" or any effort to address its current vs historical condition. The Plan Amendment must correct this. The lack of adequate regulatory mechanisms to protect lynx habitat and connectivity has been implicated as a central issue for lynx being able to maintain populations. (FR p16052). The FSM described above makes the point that the Forest Service should establish through planning, objectives for habitat management and/or recovery of populations and prescribe measures to prevent adverse modification of habitat essential to the conservation of T&E species. This remains to be done with assurance that the BHDL land management plans are quantitatively addressing lynx habitat and connectivity needs with adequate standards.

- The BA Appendix H does a comprehensive review of NRLMD goals, objectives, standards, and guidelines and how existing Forest Plan provisions apply to each. We have seen no evaluation that the NRLMD has been effective, or for that matter, the 2009 BHDL RFP. Standards are missing for most of the NRLMD goals, objectives, and guidelines in the 2009 RFP. Goals, objectives and guidelines are without enforcement and need quantitative, not general, standards. The Forest Plan Amendment must now go through each of these NRLMD provisions and provide standards for each NRLMD Direction.

Sincerely,

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Scoping Comments Beaverhead Deerlodge Plan Amendment for Canada Lynx Y2U Et Al

The map of proposed lynx analysis units (LAUs) provided in the Scoping Letter (March 4, 2025) reflects the 2020 BHDL mapping analysis (BA).[1] This work was undertaken because of the Western Lynx Biology Team conclusion that the number of lynx detections on the forest met provisions for changing the BHDL from unoccupied to occupied, thereby triggering the Northern Rockies Lynx Management Direction Standard S1 for changing LAU boundaries based on site-specific habitat information. A problem emerges in that in 2001 the BHDL modeled lynx habitat and found 2,711,422 acres. The 2020 model reduced that to 1,625,952 acres. In these comments we have focused on the BA, its rationale, and modeling.

The Occupied Habitat Problem

We have been analyzing lynx habitat for many years and are dismayed at the deflection around human impacts on lynx and lynx habitat. When one looks at the historical records there have been thousands of lynx observations in the Rocky Mountains from Montana, Idaho, Wyoming, Utah and Colorado. Those are being discounted as unverified because there is no DNA evidence under a protocol that has only been in existence in recent years. The BA:11 declares that "Detections prior to 2018 are considered 'unverified' as eDNA or photographs do not exist."

Occupied habitat is described in the BA Attachment 1 as:

> In order to implement this agreement, the FWS and FS will jointly identify 'occupied lynx habitat' as a subset of mapped lynx habitat. The identification of occupied lynx habitat will include consideration, as appropriate, of the Science Report, the LCAS, FWS's final listing decision documents, any information used to designate critical habitat, and new scientific information regarding the ecology and distribution of lynx, and population data. (BA:85).
>
> The Lynx Conservation Assessment and Strategy identities 17 lynx risk factors in 4 different categories - factors affecting lynx productivity, lynx mortality, lynx movements, and other large-scale risk factors. Risk factors identified activities or existing conditions that could adversely affect either individual or groups of lynx. (BA:85).
>
> Factors identified include timber management; wildland fire management; recreation; forest/backcountry roads and trails; livestock grazing; other human developments; trapping; predator control; incidental or illegal shooting;

[1] Gatlin, J. 2021. Biological Assessment for Canada lynx Effects of the 2009 Revised Forest Plan and the Northern Rockies Lynx Management Direction. Beaverhead-Deerlodge National Forest. January 4,2021.

> competition and predation as influenced by human activities; highways (vehicular collisions); highway, railroad and utility corridors; land ownership patterns; ski areas and large resorts; fragmentation and degradation of lynx refugia; lynx movement and dispersal across shrub steppe habitats; and habitat degradation by non-native invasive plant species. (BA:85).

The Final Rule listing Canada lynx as threatened was enacted in 2000.[2] The National Lynx Survey took place in that same time frame.[3] Despite evidence that lynx persisted over historical times, the "unoccupied" status results from failing to find current evidence of lynx long after habitats have been fragmented by mines, high road density, an explosion in motorized recreation, timber and fuel reduction projects, and including habitat alteration by livestock grazing. (Where do the major areas of disturbance by invasive plants come from across the landscape except disturbance and removal of natives by livestock that lead to the invasive species?)

The problem with this concept of "occupied habitat" is that it makes optional the application of the Northern Rockies Lynx Management Direction in "unoccupied habitat". The direction only says it "should be 'considered''. In our experience in such places as the Caribou Targhee NF, the Uinta Wasatch Cache NF, the Ashley NF, in linkage and peripheral habitat, but habitat historically used by lynx, it is met with deflection and no analysis. Meanwhile the practices listed above as detrimental to lynx proceed apace.

We have prepared multiple sets of mapping and analysis comments for Canada lynx. These include comments on the 2017 Species Status Assessment, the Draft Recovery Plan, and the recent 2024 Revised Designation of Critical Habitat. In those comments we have addressed the deflection around human activities as the cause of lynx abandoning habitats and the resultant negative effects on habitat that result from both the "unoccupied" status and the weakness of the NRLMD which provides inadequate standards. For example, the explosion in motorized recreation, and deforestation by timber related projects in the latter half of the 1900s.

As an example, we provide Figure 1 which illustrates the history of timber harvest in the National Forest System and Region One. Note that it only came down to today's levels after a huge amount of deforestation between about 1950 and 2000. A time when lynx observations were declining across much of the Rocky Mountains, and they were no longer being observed in some areas. We are unsure as to whether the Region One harvest data includes fuel reductions, silviculture treatments, and other manipulations that may not fall under the umbrella of timber sales. These historically logged areas take decades to return to lynx and snowshoe hare habitat, which have affected large areas of historical lynx habitat. This is a cumulative impact.

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[2] DOI Fish and Wildlife Service. 2000. Endangered and Threatened Wildlife and Plants; Determination of Threatened Status for the Contiguous U.S. Distinct Population Segment of the Canada Lynx and Related Rule. Federal Register Vol. 65, No. 58:16052 – 16086.

[3] McElvey, K.S., Claar, J.J., McDaniel, G.W., and Hanvey, G. 1999. National Lynx Detection Protocol.

The the BA, with its stand structure analysis reveals to some extent the scope of this altered forest ecosystem and relies on this altered structure to define a new baseline rather than address the actual habitat (vegetation) types where lynx were historically observed. We address this later in these comments showing these forest types where historical observations occurred. We used the Landfire database, where the Montana Natural Heritage Program used the Montana Land Use/Land Cover Dataset.

In the recent FWS Revised Designation of Critical Habitat, we saw Colorado go from "unoccupied" to "occupied" habitat. We saw critical habitat in the northern Rockies diminished by 12%, and in the Greater Yellowstone Area by 88%.[4] Yet, these last two areas were widely inhabited by lynx when you look at historical observations. (Figure 2). In the comments we cited above we have looked back at historical accounts and obtained the McElvey (1998) data, Montana, and Wyoming data for historical observations. There are thousands of these, for example, the Montana Natural Heritage data contains 2,414 records up to the present. The McElvey data contained over 3,000 records, and the Wyoming database contained 315 records. Some are duplicates, and there are missing records we know of. But, overall, thousands of records exist across the Rockies.

With this as background, the BA:77 acknowledges that there were 109 observations on the BHDL "that McKelvey and others (Ibid) considered 'reliable', but unverifiable". This is the unfortunate consequence of inventing a criterion (DNA) that didn't exist at the time. If "reliable" is not reliable to be used, can we infer anything other than the abandonment of the precautionary principle is at work? Is it the need to accommodate logging, off-road vehicles, snowmobiles, trapping, and mining? This is a legitimate question. It also leads to the question as to why lynx were not observed in the BHDL until recently if these factors were not at play? In the meantime, did the BHDL modify its projects or recreational use to accommodate lynx? How much lynx habitat was lost due to human activities during the period before listing? After listing? These are all questions needing an analysis and answer in the plan amendment process.

[4] Department of the Interior, Fish and Wildlife Service. 2024. Endangered and Threatened Wildlife and Plants; Revised Designation of Critical Habitat for the Contiguous U.S. Distinct Population Segment of the Canada Lynx. Federal Register 89 No. 230 (pp 94656 – 94680) dated November 29, 2024.

Figure 1.

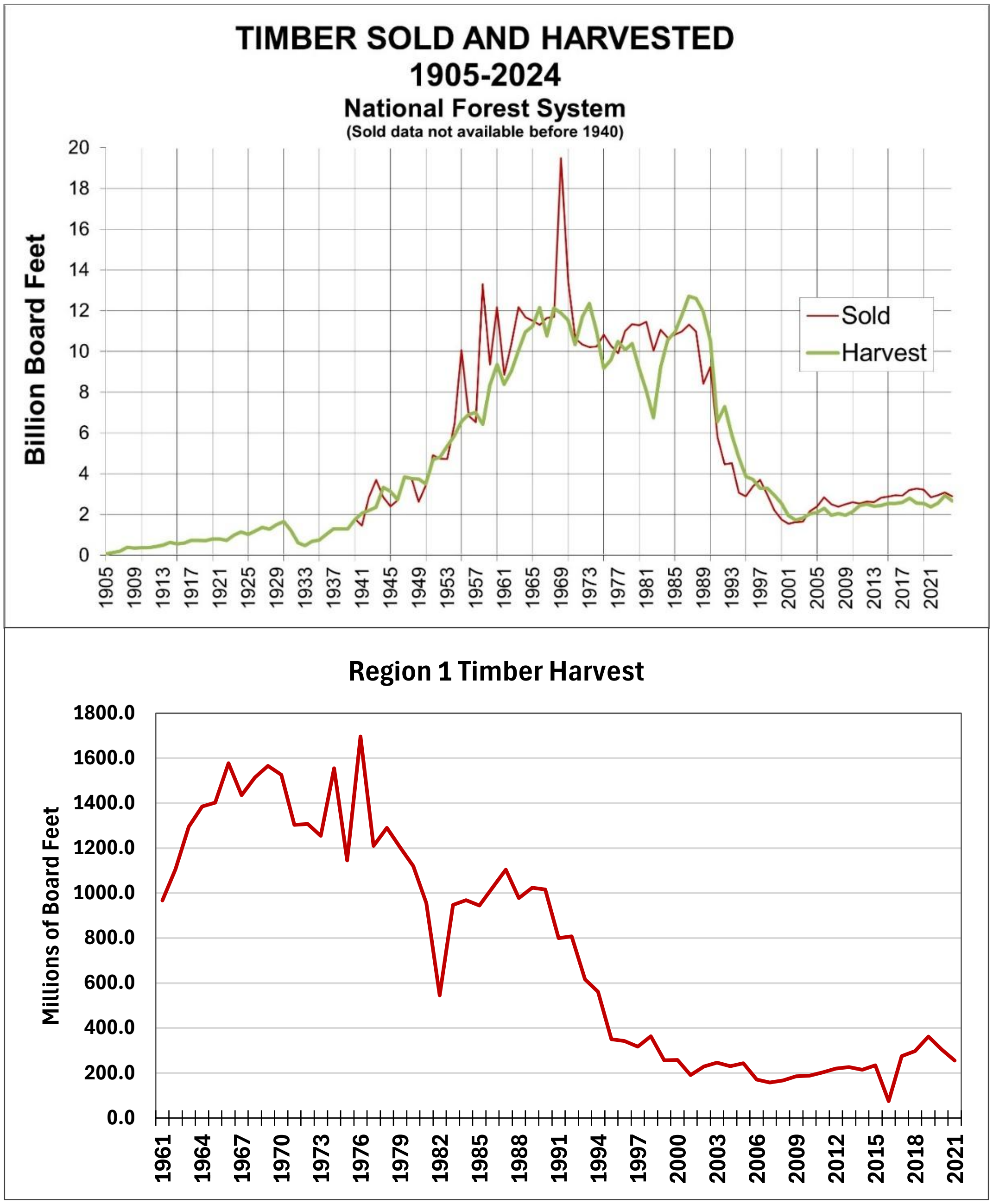
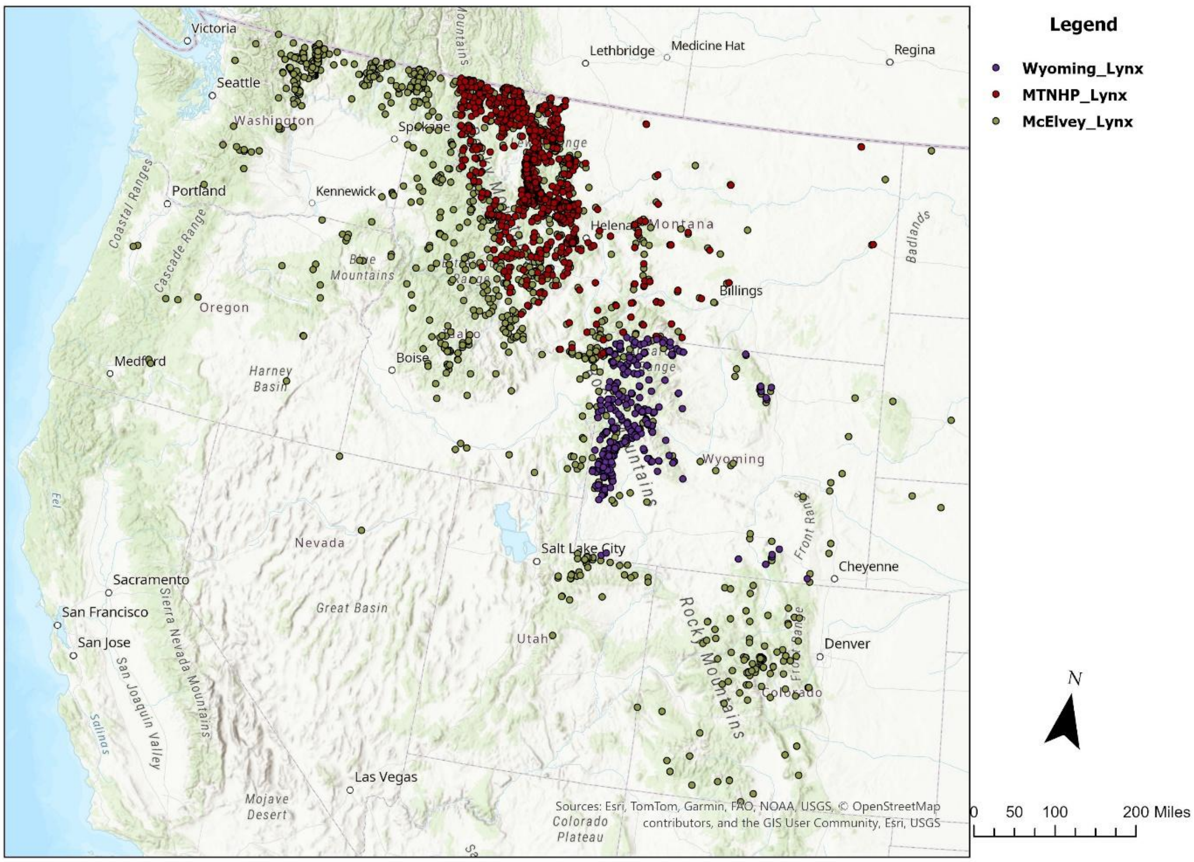

TIMBER SOLD AND HARVESTED
1905-2024
National Forest System
(Sold data not available before 1940)
Billion Board Feet
Sold
Harvest
Region 1 Timber Harvest
Millions of Board Feet

Figure 2. Lynx Observations in the Rocky Mountains



The Federal Register Notice to revise lynx critical habitat addressed the Colorado critical habitat being added, when in the 2014 critical habitat designation, that Federal Register Notice[5] did not designate critical habitat. The reasons for not designating included: "the last lynx verified record was from 1974 (no verified records from 1875 to 1999) despite large-scale snow tracking efforts… .". "We concluded at the time that there were 'few if any' native lynx in Colorado at the time of listing… .". The 2024 Federal Register Notice stated the rational for designating critical habitat as: "At the time of listing, this unit was occupied by lynx translocated from Canada and Alaska and it is currently occupied by the descendants of those released lynx. It is uncertain whether this unit historically supported a resident population or if lynx presence was naturally ephemeral and intermittent." But millions of acres of critical habitat were proposed for designation in Colorado.

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[5] Department of the Interior, Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and Plants; Revised Designation of Critical Habitat for the Contiguous United States Distinct Population Segment of the Canada Lynx and Revised Distinct Population Segment Boundary; Final Rule. Federal Register 79 No. 177 (pp 54782 - 54846) dated September 2, 2014.

Occupied habitat appears to be an arbitrary construct used as a matter of convenience to include or exclude areas with habitat that could support, or historically supported lynx, rather than addressing lynx habitat in a holistic manner across its historical range.

The BA:107 – 108 describes a very large effort in the BHDL that failed to detect lynx between 1999 and 2019. Passive, but "unverified" observations were made in 2016, 2018, and camera trap observations in 2017 and 2019 by MFWP were verified. "A single lynx was observed in the Thompson Park area in June of 2019 and a pair of lynx were observed in the same area again in August. The Thompson Park observations have not been verified but are considered to be reliable by Montana Fish, Wildlife, and Parks."

So, here "reliable" observations are okay while historical "reliable" observations are dismissed. Table 1 of the BA:110 summarizes these efforts, finding no verified observations between 1999 – 2017, with 5 verified observations between 2018 – 2020. The BA:11 Table 5 states there are 1,625,805 acres of lynx habitat on the BHDL. If this is the case, then why were lynx not detected during the nearly 20 years of intensive surveys from 1999 forward?

The BHDL analysis must address why, with its claimed 1,625,805 acres of lynx habitat, there were no lynx found for nearly 20 years following its listing as threatened.

Comments Specific to the BA

Connections. We appreciate the effort of the BHDL and Gatlin to arrive at some approximation of lynx habitat. However, we find issues with the analysis and its seeming intent to eliminate potential or historical lynx habitat by setting a baseline of lynx habitat using forest structure modified by logging and other manipulations rather than the historical habitats where lynx were observed. It failed to include analysis of local and regional connectivity, or linkages. In our recent comments on the USFWS 2024 Proposed Critical Habitat, we mapped National Forests, Ranger Districts, Wilderness Areas, National Parks, and Inventoried Roadless Areas using the Olson et al (2021) model that the Fish and Wildlife Service uses.[6]

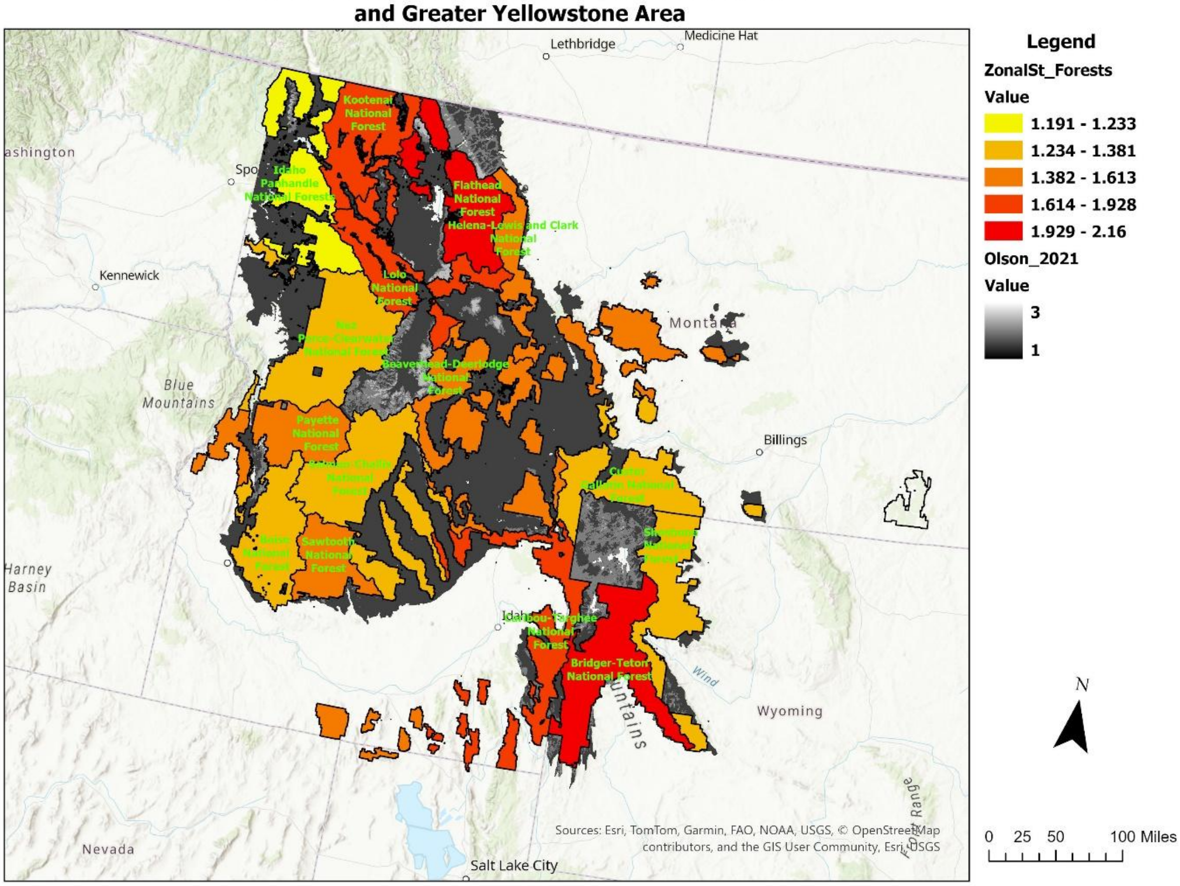
While we have issues with that model, it provides information we can use to relate or compare areas across the Rockies for lynx habitat and link those areas together to provide paths for connectivity. The color scheme goes from yellow (low probability habitat) to red (high probability habitat) (Figure 3). This shows the entire BHDL is in the middle range of habitat probability for these National Forests. It is accepted that lynx habitat becomes less suitable as you move south, but it still can support resident lynx, albeit at lower densities than more northern populations (overlooking human habitat alterations).

[6] Olson, L.E., Squires, J.R., DeCesare, N.J., and Kolbe, J.A. 2011. Den Use and Activity Patterns in Female Canada Lynx (Lynx canadensis) in the Northern Rocky Mountains. Northwest Science, Vol. 85, No. 3, 2011. https://research.fs.usda.gov/treesearch/44989

The analysis also shows the BHDL is extremely important to regional connectivity and emphasizes that the areas excluded as lynx habitat in the BA, such as the area in the Dillon Ranger District in (BA:30:Figure 2) are important for connectivity. This area is shown as linkage but eliminated as habitat south of Hwy 324 and Interstate 15 (BA:95). If linkages are not mapped with defined corridors as lynx habitat, and given standards, then they have no protection against fragmentation.

Connectivity and linkage must be identified locally within the BHDL and regionally in the Northern Rockies and Greater Yellowstone Area National Forests. Habitat, linkages and regional connections must be given strict Forest Plan standards to ensure lynx persistence and connectivity. In addition, highway crossings should be identified so that planning for crossing structures will be an element of the Plan Amendment.

Figure 3. National Forests Olson Probability Northern Rockies and Greater Yellowstone Area



Snow Depth. "In 2020, the BDNF updated the lynx habitat model and associated LAUs based on improved vegetation and snow-depth datasets (Appendix C)." (BA:11). "Denning habitat is generally abundant across the coniferous forest landscape of northwest Montana and is not likely to be limiting for lynx (Squires et al. 2008;2010)." (BA:10). "Preferred forests have a multistory structure with dense horizontal cover provided by the young trees in the understory and conifer boughs touching the snow surface, which could support snowshoe hare populations at varying snow depths throughout the winter." (BA:10).

A search of the BA did not turn up any definition of, or criteria for, denning habitat. Nor was it mapped to determine its extent or vulnerability. What does "generally abundant" mean? The logic of habitat with snow touching the lower boughs fails to recognize that hares are present before it snows, during snow cover, and after snowmelt. Other prey such as red squirrels, grouse, and small mammals are present. Squires et al (2010) also tracked habitat use by lynx in summer, noting they "broadened" their habitat use during summer.[7] So, if there is less snow as occurs in the transition to and from spring or summer, lynx are still using that habitat. It is not a black and white proposition of habitat vs no habitat, it's a gradation, like an ecotone. In fact, the paragraph above shows the BHDL knows that snow depth varies throughout the winter and snowshoe hares are supported.

The BA:AppC:7 described the process for updating LAUs for the BHDL. Using Squires et al (2010) it was determined that lynx selected habitats with a minimum snow depth of 50 cm (20 inches) in winter. To determine the lower threshold elevation for habitat based on snow depth, the BA used model data from SNODAS to determine this threshold based on **average** snow depth greater than 50 cm for the December to May periods for the years 2009 – 2019. This reduced habitat in nine HUC10 watersheds. (Figure 4). SNODAS is a modeling and data assimilation system developed by NOHRSC to "provide the best possible estimates of snow cover and associated parameters to support hydrologic modeling and analysis." Note that the output data are estimates and the data is for hydrologic modeling, not defining lynx habitat. The selection of the December to May period of six months and average snow depth is arbitrary. The BA acknowledged above that snowshoe hares occupy their habitat as snow levels vary.

We analyzed actual, not estimated, snow depths at snow monitoring stations (SNOTEL) over a 21-year period ending in March 2024. (Table 1, Figure 5). There were 29 monitoring stations covering all elevations and areas within and adjacent to the BHDL. This analysis illustrates that in most years, at all elevations, sufficient snow depth is available to accommodate lynx if the Squires et al (2010) minimum snow depth is used. While the onset and end of the 20-inch depth varies, there are long time periods in nearly all cases where it is exceeded. Even at the lowest elevations, there is sufficient snow in nearly half to 100% of the years. Charts of these SNOTEL stations are provided in Appendix I. It must also be remembered that Squires et al (2010) tracked use during summer as well. What about snow depths then?

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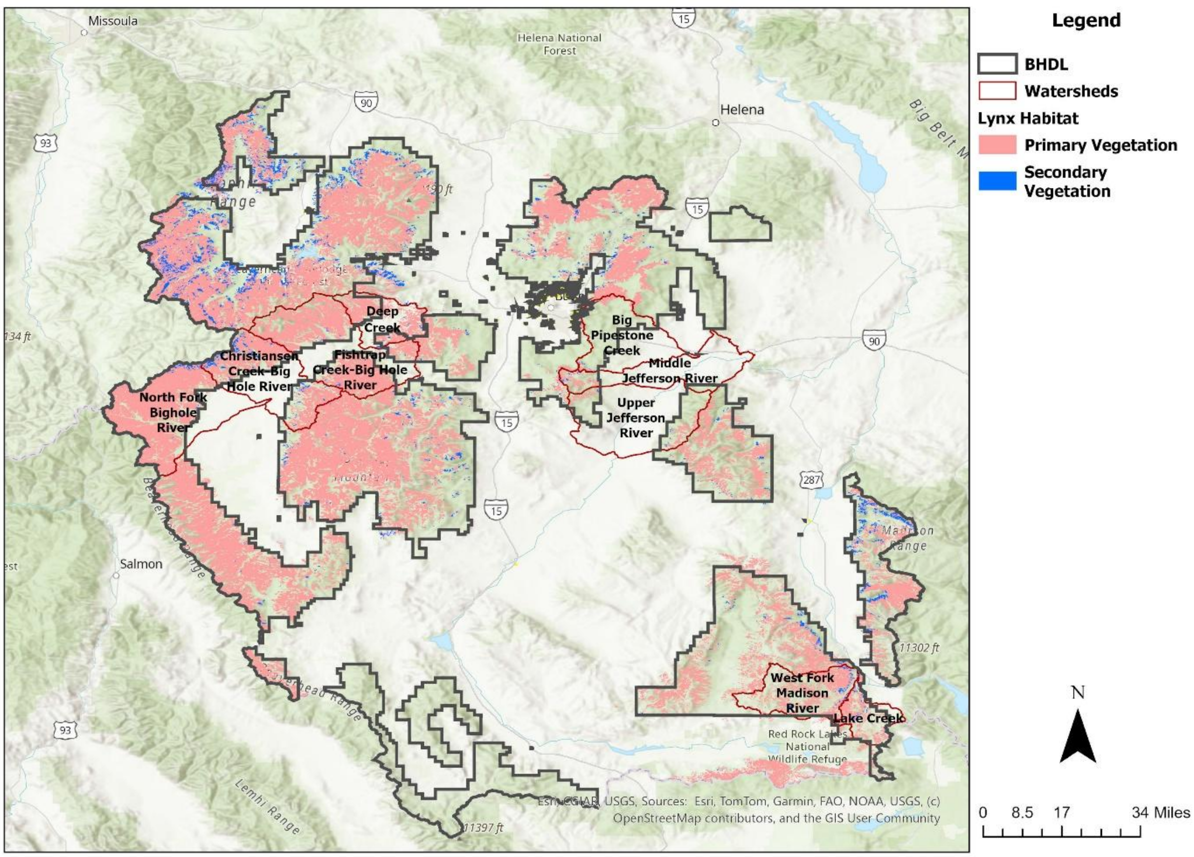
[7] Squires, John R.; DeCesare, Nicholas J.; Kolbe, Jay A.; Ruggiero, Leonard F. 2010. Seasonal resource selection of Canada lynx in managed forests of the northern Rocky Mountains. Journal of Wildlife Management. 74(8): 1648-1660. https://research.fs.usda.gov/treesearch/50160

Olson et al (2011) identified three seasons of female reproduction.[8] Pre-denning occurred in February – April, denning occurs in May to July, and post-denning in August – October. The pre-denning period is the breeding period. Denning is during parturition/lactation period. Post-denning is when kittens can travel. We remain to be convinced that the December – May (6 months) period average snow depth is meaningful. How is this applicable when denning can last until July? These denning seasons or others don't line up with a static December - May period.

Figure 4. Watersheds with Lower Elevations Omitted from Lynx Habitat



Since hares and other prey are available year-round as snow levels rise, recede, and disappear at all elevations, the agencies are stuck on static habitat parameters, not dynamic conditions as experienced throughout the year. Snow levels should not be used to discount habitat in the BHDL.

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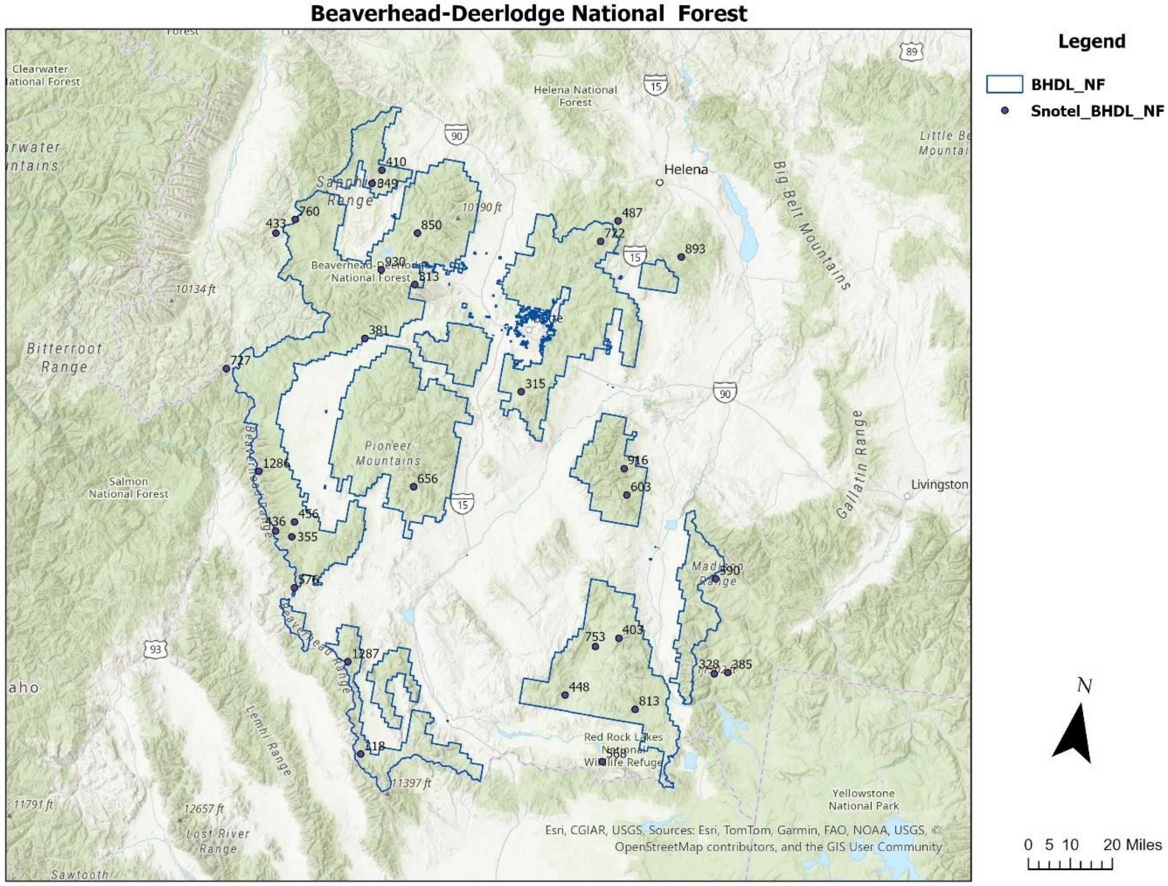
[8] Olson, L.E., Squires, J.R., DeCesare, N.J., and Kolbe, J.A. 2011. Den Use and Activity Patterns in Female Canada Lynx (Lynx canadensis) in the Northern Rocky Mountains. Northwest Science, Vol. 85, No. 3, 2011. https://research.fs.usda.gov/treesearch/44989

Table 1. Years at or Above Minimum Snow Depth of 20 Inches in or near the BHDL

Station	Elevation, ft	Count of Years/percent of 21-year record
Combination 410	5600	9/43%
Daly Creek 433	5780	21/100%
Calvert Creek 381	6430	18/85%
Frohner Meadow 487	6480	21/100%
Tizer Basin 893	6880	21/100%
11 Stations	7000 - 8000	21/100%
13 Stations	8000 – 9000	21/100%

Figure 5. SNOTEL Stations
Beaverhead-Deerlodge National Forest



Slope, Aspect, and Elevation: The BA Appendix C: Updated Lynx Habitat Mapping Process Paper describes aspect being used for structural stage classification and the use of aspect and elevation being used in the "modeling process to classify lynx habitat". (AppC:5 – 6). The BA:8

describes lynx habitat elevations as, “In the northern Rockies, this habitat generally occurs between 3,500 and 8,000 feet in elevation (USDA 2007b).” “In winter, lynx forage primarily in mid- to high-elevation forests (4,134 – 7,726 feet)… and in summer they use slightly higher elevations composed of mature, large diameter (greater than 11 inches DBH) trees and select forests with relatively dense horizontal cover, more abundant hares, and deeper snow (Squires et al. 2010).” (BA:10). These elevation ranges argue against the snow depth limitations used for the BHDL. Note here the BA acknowledges use by lynx down to 4,134 feet.

The BA Appendix C (Table 3) describes model parameters for the disturbed and non-disturbed habitat stands for regeneration harvest. These were applied to the Early Stand Initiation and Stand Initiation stages and used more northerly aspects for the more recent time periods and more southerly aspects for the longer-term regeneration harvests. Appendix A:Table A -1 then described the modified stand structure for Mature; Multi-Storied, and Other modified structures constrained by aspect. We are concerned that the BHDL is artificially reducing lynx habitat by placing these limiting criteria into an already uncertain modeling exercise. We will address the VMAP concerns in the following section.

We obtained McKelvey lynx observation data from the BHDL through FOIA (February 21, 2024). We also obtained historical lynx observation data from the Montana Natural Heritage Program in April 2024. There were 3,493 records of observations in the McKelvey database provided by the BHDL and 2,414 records of observations in the MNHP database. There were 158 occurrences of the McKelvey observations within the BHDL. There were 35 locations within the BHDL in the MNHP database. The MNHP data included 81 observations between 1977 and 2023. The MNHP data includes a location uncertainty value. The MNHP Predictable Suitable Habitat Modeling incorporated records with ≤1600 meters of locational uncertainty.[9]

We used the MNHP location uncertainty <100 meters and a digital elevation map to determine slope, aspect and elevation ranges and means for Montana and then for the BHDL. There were 1,817 records for Montana that met this criterion. (Table 2). The aspect included all directions with an average nearly at true South (192°). Elevations ranged from 1,876 to 7,716 feet with an average of 5,320 feet. Slopes averaged 19 degrees and ranged from flat to 74 degrees. The mean elevation value reflects numerous locations during tracking studies in and around the Seeley Lake area and may not represent the BHDL.

Table 2 . MNHP Observation Locations (location uncertainty <100m)

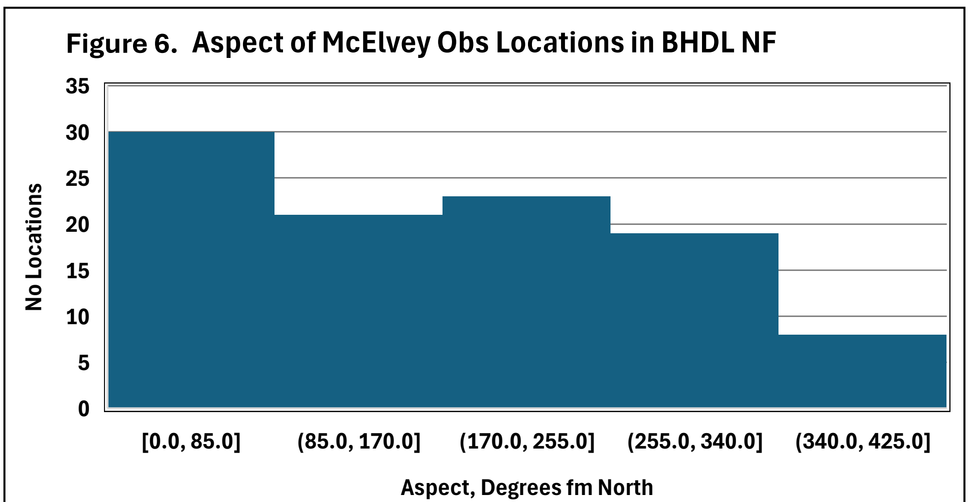
	Mean	Minimum	Maximum
Elevation, ft.	5,320	1,876	7,716
Slope, %	19.0	0	74
Aspect, degrees	192	0	360

[9] Burkholder, B. 2022. Canada Lynx (Lynx Canadensis) Predicted Suitable Habitat Modeling. Montana Natural Heritage Program, Montana State Library. https://mtnhp.org/models/files/Canada_Lynx_AMAJH03010_20220519.pdf

When we used the 35 MNHP locations within the BHDL we found a mean elevation of 7,304 feet, an aspect of 160 degrees, and a slope of 20 percent. (Table 3). Finally, we analyzed the McElvey observation locations within the BHDL. The distribution of aspect, slope and elevations are shown in Figures 6 – 8. Aspect is relatively evenly divided, slopes less than 22% are dominant, and elevations used are mostly in the 6,000 to 8,000 feet range.

Table 3. MNHP Records for the Beaverhead Deerlodge NF

Records Included	Elevation, ft	Aspect, degrees	Slope, Percent
35	Mean 7304 Range 5672 – 10317	Mean 160 Range 2 - 356	Mean 20 Range 0 - 54
7 < 1000-meter uncertainty	Mean 7174 Range 6461 - 8070	Mean 187 Range 54 - 323	Mean 19 Range 9 - 47



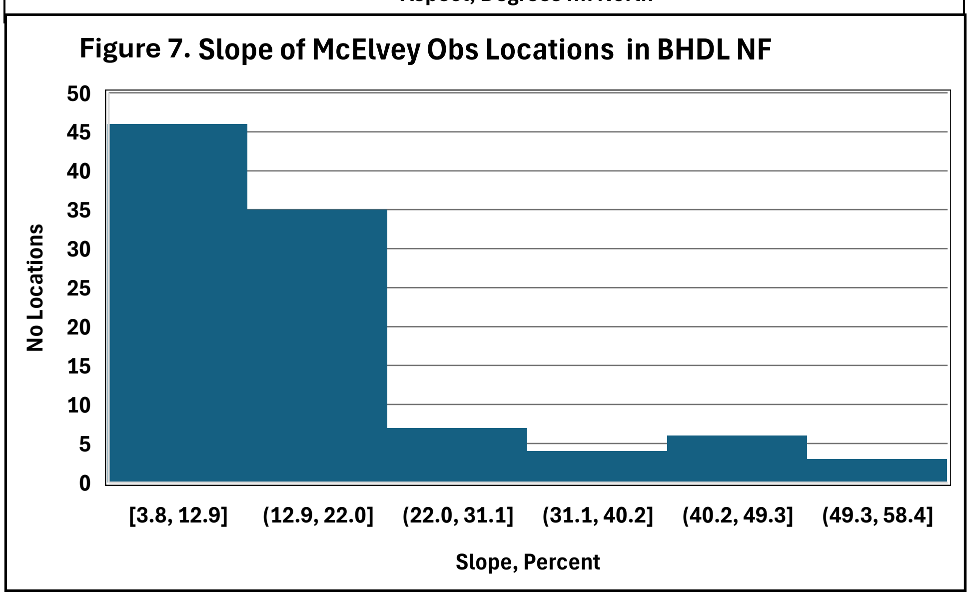
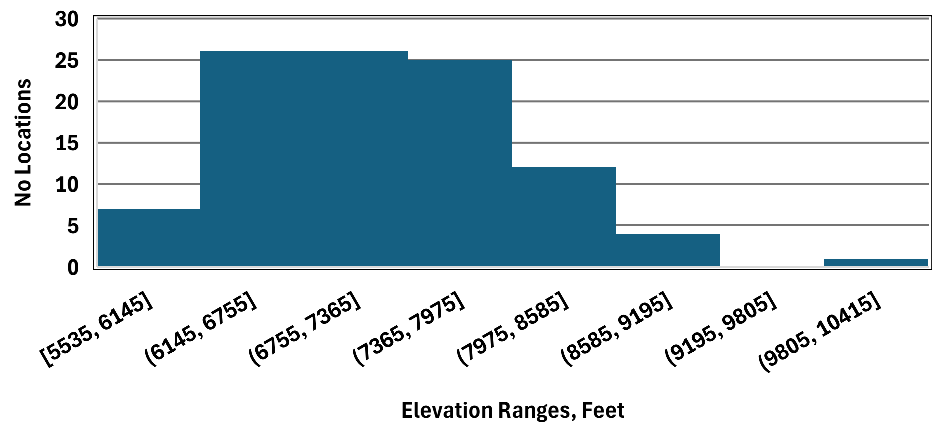


Figure 8. Elevation of McElvey Obs Locations in BHDL NF



What is being lost in the BHDL modeling process is any description of the habitats historically used by lynx. The BA analysis is divorced from historical observations. What is needed is to use locations where lynx have been observed and describe those vegetation or forest types. These should be used to map the habitat across the BHDL. Areas that have been logged or burned should not count in the mapping of habitat. Only potential or historical forest or vegetation types need to be included. Disturbance should only be included later when analyzing project proposals and compliance with the NRLMD and this Plan Amendment.

The BHDL Mapping Process.

Data Sources: The BA summarizes the background of its mapping analysis:

> Although the LCAS recommended specific habitat types most preferred by lynx for mapping lynx habitat on National Forests in Montana, habitat type data sets where not available on the BDNF when the Forest initially mapped habitat in 2000; thus, biologists and silviculturists on the Forest utilized SILC-3 cover type and aspect combinations as a proxy for mapping lynx habitat, which resulted in a very conservative approach that included many acres of non-boreal forest habitat types that do not support lynx. The BDNF's 2020 mapping update utilized the same habitat mapping direction provided in the 2000 LCAS for mapping lynx habitat on the forest, but incorporated improved vegetation data sets and refined Geographic Information System (GIS) mapping tools to more accurately identify and spatially delineate the boreal forest habitat types (subalpine fir, Engelmann spruce, and other mesic habitat types) that are capable of supporting lynx on the BDNF. (BA:113).

> At that time, the BDNF did not have a consistent habitat mapping method but determined the best data source combined two existing geospatial products: remotely-sensed satellite imagery (SILC-3) and aspect from 30-meter digital elevation models (DEMs). Satellite imagery land classification, version 3 (SILC-3) delineates existing vegetation attributes (cover type) across the entire landscape, and, when combined with aspect from the DEMs, created a surrogate for habitat types that represented potentially suitable habitat for Canada lynx. Using this guidance, the Forest used attributes from existing vegetation datasets, namely subalpine fir, spruce, and cool-moist Douglas-fir habitat types, to identify lynx habitat. (Appendix C:1).

The assumption that lynx habitat is only boreal forest types continues a long-standing error that boreal forests like those occupied by lynx in Canada occur in the continental US. These should not be compared to our western forests. A recent paper has analyzed the extent of the North American boreal zone.[10] This is shown in Figure 9.[11] It occurs in Maine, Michigan, and Minnesota. It does not occur in the western US. There have been thousands of verified and reliable lynx observations in Colorado, Idaho, Montana, Utah, Washington, and Wyoming beginning in the mid-1800s. These did not occur in boreal forest, but in the Kuchler forest types that would include Douglas fir, Englemann spruce, lodgepole pine, mixed conifer, whitebark pine, limber pine, and other associated types that are intermixed therein. The characteristics of these forest types constitute what should be used for habitat evaluations for the BHDL.

The BA:95 (Attachment 2) limits primary habitat types to subalpine fir and spruce and excludes the broader suite of habitats described above that lynx historically used. Secondary habitat is considered Grand Fir types. This is a major flaw. We mapped the MNHP observations against the Landfire database (LANDFIRE 2022 Existing Vegetation Type (EVT) CONUS). (Table 4 and Figure 10).

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[10] Brandt, J.P. 2009. The extent of the North American boreal zone. Environ. Rev. 17: 101–161 (2009) doi:10.1139/A09-004 Published by Natural Resources Canada Research Press.

[11] Geography Realm. https://www.geographyrealm.com/boreal-forests-north-america-shrinking/ Accessed January 25, 2024.

Table 4 . Landfire Cover Type for Montana Natural Heritage Program Lynx Locations

Cover Type	Locations	Percent
Lodgepole Pine Forest and Woodland	712	29%
Douglas-fir-Ponderosa Pine-Lodgepole Pine Forest and Woodland	499	21%
Spruce-Fir Forest and Woodland	320	13%
Douglas-fir Forest and Woodland	186	8%
Transitional Forest Vegetation - Conifer	174	7%
Western Riparian Woodland and Shrubland	133	6%
Deciduous Shrubland	104	4%
Douglas-fir-Grand Fir-White Fir Forest and Woodland	75	3%
Big Sagebrush Shrubland and Steppe	31	1%
Other	180	7%
Total	2414	

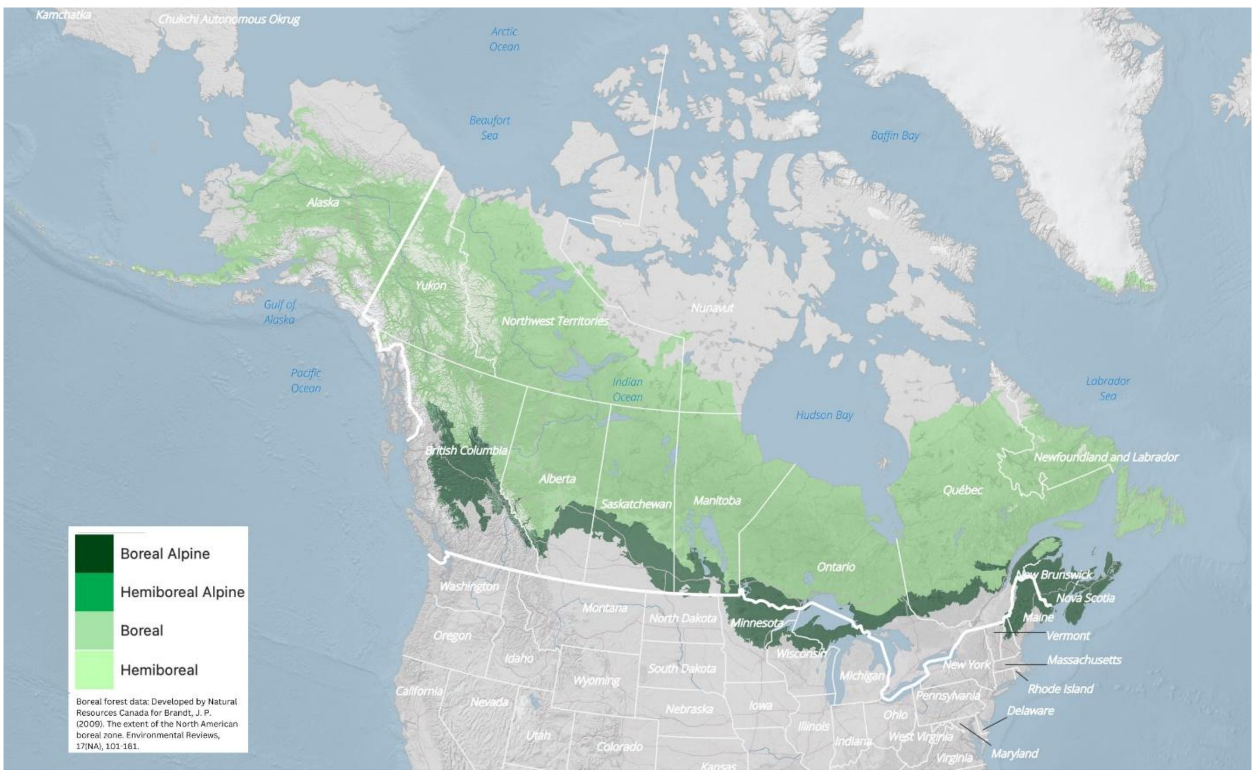
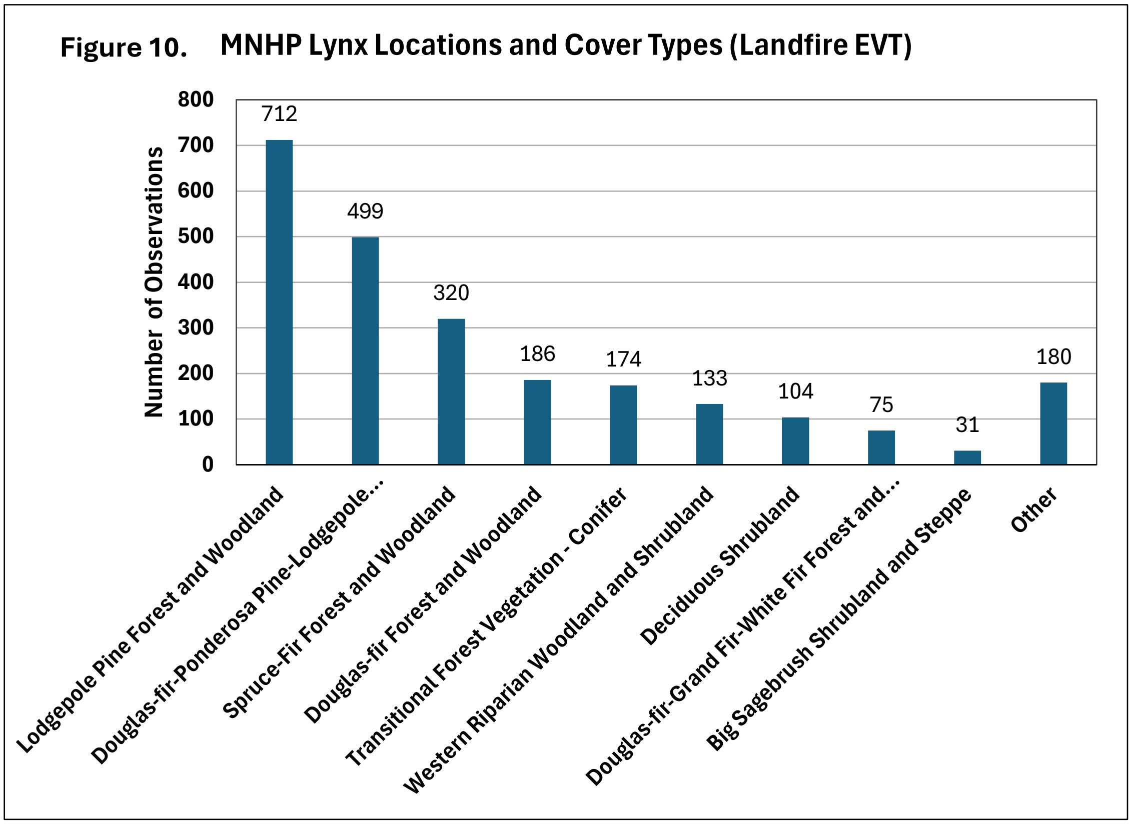


Figure 9. Map of the North American boreal zone



This Landfire comparison reveals a much broader habitat use by lynx dominated by lodgepole pine and Douglas fir with less use in spruce-fir and grand fir. We looked at the publication Ecology and Conservation of Lynx in the United States for more description of lynx habitat. Ruediger et al (2000).[12]

The BA:91, also relying on the Ruediger et al (2000), provided this narrative. "Mapped lynx habitat consists primarily of mesic coniferous forests that have cold, snowy winters and provide a prey base of snowshoe hare. The vegetation types and elevations that provide lynx habitat vary somewhat across the U.S. The specific descriptions are listed on pages 4 and 5 of the Glossary in the LCAS, by geographic area (i.e. Northeastern U.S., Great Lakes states and Western U.S.)." In the Ecology and Conservation of Lynx in the United States (p380), lynx habitat associations in Montana were described.

> In Montana, Koehler et al. (1979) reported that 26 of 29 lynx locations for two radio-marked lynx were in densely stocked lodgepole pine stands where hares

[12] Ruggiero, Leonard F.; Aubry, Keith B.; Buskirk, Steven W.; Koehler, Gary M.; Krebs, Charles J.;McKelvey, Kevin S.; Squires, John R. 2000.. Ecology and conservation of lynx in the United States. General Technical Report RMRS-GTR-30WWW. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://www.fs.usda.gov/research/treesearch/50623 Accessed on January 21, 2023.

were abundant; the remainder were in Douglas-fir and western larch stands. Selection by lynx of dense lodgepole pine stands containing high numbers of snowshoe hares has also been demonstrated in north-central Washington (Koehler 1990). Lodgepole pine is a seral, fire-dependent species in boreal forests of the western mountains (Chapter 3) and appears to be preferred by lynx in northern portions of the Cascade Range and Rocky Mountains (Koehler et al. 1979; Koehler 1990; Chapter 10).

The LCAS describes lynx habitat for western forests.

> LCAS[13] Glossary pp4-5, "Western US: Most lynx occurrences (83%) were associated with Rocky Mountain Conifer Forest, and most (77%) were within the 1500 – 2000 m (4920 – 6,560 ft) elevation zone (McKelvey et al 2000b). There is a gradient in the elevational distribution of lynx habitat from the northern to the southern Rocky Mountains, with lynx habitat occurring at 2,330 – 3,500 m (8,000 – 11,500ft) in the southern Rockies. Primary vegetation that contributes to lynx habitat is lodgepole pine, subalpine fir, and Englemann spruce (Aubry et al. 2000).
>
> Primary vegetation is considered necessary to support lynx reproduction and survival. Secondary vegetation includes other vegetation types that, when intermingled with or immediately adjacent to primary habitat, may also contribute to lynx habitat. Mapping of lynx habitat and delineation of LAUs involves consideration of the amount and arrangement of primary vegetation and secondary vegetation, land ownership pattern, lynx occurrence records and snow depth information. After lynx habitat is mapped, there is no distinction between primary and secondary vegetation. Conservation measures generally apply only to lynx habitat on federal lands within LAUs.

Note that BA:95 provides a map showing the primary and secondary habitat derived from their modeling process. It does not include the historical vegetation types used. In addition, the BA fails by distinguishing primary and secondary vegetation. It should be designated lynx habitat and include the historically used types described above.

The LCAS also states that "dry forest types (e.g., ponderosa pine, climax lodgepole pine) do not provide lynx habitat. We have no definition of these "dry forest types" nor any mapping information that delineates them. If the BHDL is eliminating climax lodgepole pine under this umbrella, it must show lynx observations never occurred in them.

---

[13] Ruediger, Bill, Jim Claar, Steve Gniadek, Bryon Holt, Lyle Lewis, Steve Mighton, Bob Naney, Gary-Patton, Tony Rinaldi, Joel Trick, Anne Vandehey, Fred Wahl, Nancy Waren, Dick Wenger, and Al Williamson. 2000. Canada Lynx Conservation Assessment and Strategy. USDA Forest Service, USDI Fish and Wildlife Service, USDI Bureau of Land Management, and USDI National Park Service. Forest Service Publication #R1-00-53, Missoula, Mt. 142 pp.

The BHDL must analyze these forest types for all historic observations, how they have been altered by fire and management, rather than total reliance on modeling. While modeling can supplement these observations, it is not acceptable to avoid describing and using the actual forest or vegetation types where the observations were made.

VMAP Crosswalk: Gatlin et al (2020) provide a summary of the modeling process in the BA.[14] VMAP was used to derive the characterizations for lynx habitat as seen in Appendix A Table A-1 as BDNF modified structure. These categories include Stand Initiation, Early Stand Initiation, Other, Mature; Multi-storied, and Stem Exclusion. For the 2020 LAU modeling, these are shown in BA Figure B-4. This is flawed in that it includes disturbance in a baseline for mapping habitat. Disturbance should only be used to characterize impacts, whether historical, or later in the project evaluation stage. This is a planning effort. Perhaps this scheme could be used to explain the absence of lynx in the BHDL.

VMAP Region 1 Metadata describes the process of generating the map using satellite imagery to capture vegetation patterns and stand boundaries. "In 2018, an updated VMap database was produced for the Beaverhead-Deerlodge National Forest (B-D). The VMap database consists of four primary spatially explicit attributes that include descriptions of 1) lifeform, 2) tree canopy cover class, 3) tree size class, and 4) tree dominance type. These attributes can be mapped and used to support mid and base-level analysis and planning."

VMAP Accuracy was described in the metadata as, "After draft products were inspected and adjusted, an accuracy assessment was conducted to provide a quantitative validation of the database. Estimates of overall map accuracy and confidence measures of individual map classes can be inferred from the error matrix derived from the comparison of known reference sites to mapped data, for each attribute. The stated accuracy assessment results are applicable to the entire B-D, and ranged from 63-93%, depending on the attribute in question."

VMAP Use Limitations are described in the metadata as, "The USDA Forest Service manages resource information and derived data as a service to USDA Forest Service users of digital geographic data. The USDA Forest Service is in no way condoning or endorsing the application of these data for any given purpose. It is the sole responsibility of the user to determine whether or not the data are suitable for the intended purpose. It is also the obligation of the user to apply those data in an appropriate and conscientious manner. The USDA Forest Service provides no warranty, nor accepts any liability occurring from any incorrect, incomplete, or misleading data, or from any incorrect, incomplete, or misleading use of these data."

From the BA Habitat Modeling Documentation section of the metadata as, "Habitat or Structural Stage Errors": "In some cases, ground-verification reveals inaccurate habitat

---

[14] Gatlin et al. 2020. Habitat Mapping Documentation for Canada Lynx (Lynx canadensis) on the Beaverhead-Deerlodge National Forest – 2020 Update.

mapping or structural stage determinations. This generally occurs when field specialists verify the existing conditions within a project area prior to analysis. If mapped habitat or structural stage in the updated geospatial layer differs from existing on-the-ground conditions, updates will be made to the lynx habitat polygon or structural stage attributes to reflect the current conditions. Per guidance in the NRLMD, maps of lynx habitat would be reviewed and updated based on local information during site-specific project analysis (USDA Forest Service 2007)."

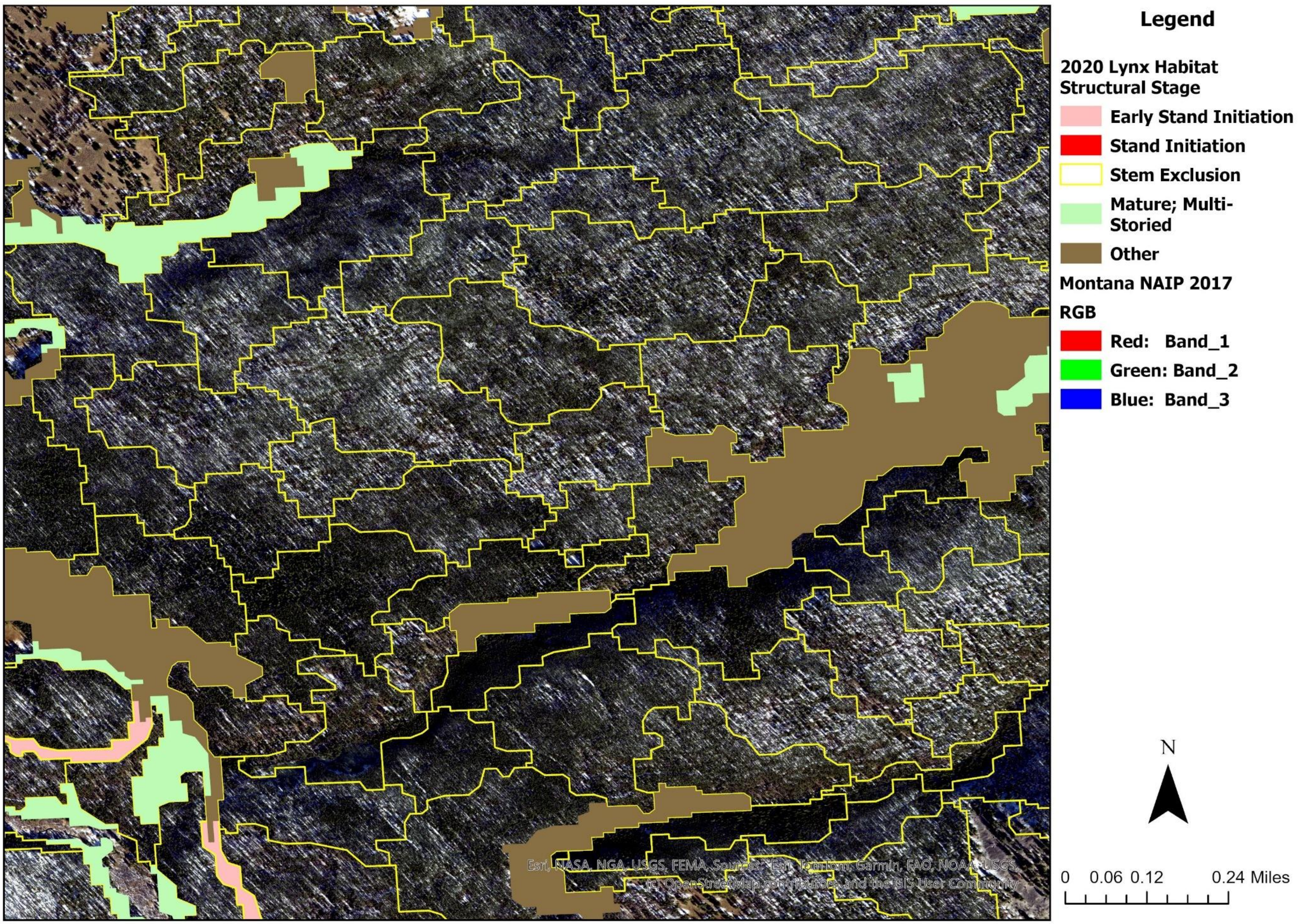
We obtained the model output from the BHDL and did an analysis of the occurrence of lynx observations in the BHDL to these VMAP-derived modified stand structures. (Table 5). Only 17 of 35 past observations in the MNHP database for the BHDL fell within the BHDL 2020 model. There were observations within every category which compels reconsideration of eliminating habitat based on the stem exclusion or other stand structure category and instead, focusing on the vegetation type in its unmodified state. Figure 10 is an example showing the VMAP stem exclusion category superimposed on the Montana 2017 NAIP image. It shows areas of sparse canopy throughout and a few areas of closed canopy. The closed canopy areas are a small portion of the whole. There is apparent solar exposure and openings between the trees over most of the image that should allow an understory of tree seedlings, shrubs, and herbaceous vegetation to develop. This should support snowshoe hares and lynx.

Table 5. MNHP Observations within BHDL 2020 Model

Habitats	Observations
Primary Habitat	17
Secondary Habitat	0
Early Stand Initiation	1
Mature, multi-storied	4
Other	9
Stand Initiation	1
Stem Exclusion	2

These qualifications to use of VMAP point out the risk of this modeling-only approach. The risk is of underestimating habitat by the cascading limitations included in the analysis. An overestimate of habitat would be protective, whereas an underestimate could lead to exclusion and loss of habitat that is critical to lynx. This is why reliance should be placed on the actual vegetation types historically used by lynx, not modified to different stand structures by logging, thinning, burning and so forth. Later field verification can take place at the project stage. It also precludes omitting areas that should be habitat but would then not be required to meet standards under the NRLMD.

Figure 10. Example of Stem Exclusion Area in the BHDL



Wildland Urban Interface Exemptions. The BA:39 described NRLMD fuels treatment project exemptions. The NRLMD exempts fuels treatment projects from VEG S1, S2, S5,and S6 to no more than 6% of lynx habitat on a forest. There are 155,433 acres of foraging habitat and 417,638 acres of non-foraging habitat. "If all exemptions are used, 57% of foraging habitat within WUI in stand initiation and mature could be removed from the WUI area." Table 9 (BA:18) shows the area and percentage of modeled lynx habitat in WUI. Of 1,481,830 acres of modeled lynx habitat 573,071 acres (39%) are in the WUI. Table D-1 shows there are 154,400 identified exemption acres and the requested exemption is 88,910 acres. With this in mind, we used the BHDL WUI GIS data we received under our FOIA request to get a handle on the extent of WUI in the BHDL based on the actual criteria defining WUI.

Using ArcGIS Pro 3.4, we clipped the BHDL's WUI layer to the boundary of the BHDL and calculated the area, which was 1,644,663 acres of WUI in the 3,613,855 acres within the BHDL. This means that WUI designations cover 45.5% of the Forest. This is a striking amount, like this is an urban park, rather than a forest ecosystem with a full complement of fish, wildlife, and native vegetation attributes. A cynical person would interpret this as manipulating the meaning of WUI to ease restrictions on timber harvest and related forest manipulations. However, we have chosen to analyze the situation.

The Federal Register defines WUI thus[15]:

> Wildland Urban Interface, Intermix and Interface Communities as:
> The urban wildland interface community exists where humans and their development meet or intermix with wildland fuel.
>
> The **Intermix Community** exists where structures are scattered throughout a wildland area. There is no clear line of demarcation; wildland fuels are continuous outside of and within the developed area The development density in the intermix ranges from structures very close together to one structure per 40 acres. Fire protection districts funded by various taxing authorities normally provide life and property fire protection and may also have wildland fire protection responsibilities. An alternate definition of an intermix community emphasizes a population density of 28 - 250 people per square mile.
>
> The **Interface Community** exists where structures directly abut wildland fuels. There is a clear line of demarcation between residential, business, and public structures and wildland fuels. Wildland fuels do not generally continue into the developed area. The development density for an interface community is usually 3 or more structures per acre, with shared municipal services. Fire

[15] Federal Register. 2001. Urban Wildland Interface Communities Within the Vicinity of Federal Lands That Are at High Risk from Wildfire. Fed. Register Vol 66(3):751-777.

protection is generally provided by a local government fire department with the responsibility to protect the structure from both an interior fire and an advancing wildland fire An alternative definition of the interface community emphasizes a population density of 250 or more people per square mile.

The Healthy Forest Restoration Act elucidates further in Section 101 by defining (1) At Risk Community as an area:

> (A) that is comprised of—
>
> (i) an interface community as defined in the notice entitled ''Wildland Urban Interface Communities Within the Vicinity of Federal Lands That Are at High Risk From Wildfire'' issued by the Secretary of Agriculture and the Secretary of the Interior in accordance with title IV of the Department of the Interior and Related Agencies Appropriations Act, 2001 (114 Stat.1009) (66 Fed. Reg. 753, January 4, 2001); or
>
> (ii) a group of homes and other structures with basic infrastructure and services (such as utilities and collectively maintained transportation routes) within or adjacent to Federal land;
>
> (B) in which conditions are conducive to a large-scale wildland fire disturbance event; and
>
> (C) for which a significant threat to human life or property exists as a result of a wildland fire disturbance event.

The key in the HFRA definition above is that the focus is on Interface Communities. It does not address Intermix Communities. Carlson et al (2022) translates this for modeling the WUI. [16]

> WUI is where building density exceeds 6.17 units/km^2 and where land cover is either (1) at least 50% wildland vegetation (intermix) or (2) under 50% wildland vegetation but within 2.4 km (1.5 miles) of a patch of wildland vegetation at least 5 km^2 in area that contains at least 75% vegetation (interface).

The Carlson et al (2022) source for building density was The Microsoft data set (available at https://github.com/microsoft/USBuildingFootprints. The vegetation information was the 2016 National Land Cover Dataset (NLCD), a 30-m resolution satellite image classification (Yang, Jin, et al., 2018). [17] We took a closer look at building density relative to the WUI definition to analyze this on a site-specific basis for the BHDL.

[16] Carlson, Amanda R., David P. Helmers, Todd J. Hawbaker, Miranda H. Mockrin, and Volker C. Radeloff. 2022. "The Wildland–Urban Interface in the United States Based on 125 Million Building Locations." Ecological Applications e2597. https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2597

[17] Yang, L., S. Jin, P. Danielson, C. Homer, L. Gass, S. M. Bender, A. Case, et al. 2018. "A New Generation of the United States National Land Cover Database: Requirements, Research Priorities, Design, and

We applied the Carlson et al (2022) model output to arrive at the WUI for these communities. (Figure 11). Carlson et al (2022) recommends using the 500-meter WUI output "because changes in WUI area and number of WUI buildings were minimal, and because smaller neighborhoods offer greater precision around building locations. The maps based on the 500-m neighborhood therefore are most ideal for general purposes." The Value = 1 (green) areas are Intermix areas where structures are intermixed with forested areas. Figure 11 also shows these are not Interface communities.

We also mapped the USGS 500-meter building density. (Figure 12). This shows that the building density is concentrated outside the BHDL and that is where home hardening and defensible space should be the focus, not log and burn the forest. When we calculated the area of the Intermix and Interface communities, we found that there are 34,663 acres of intermix and 149 acres of interface within the BHDL. This exposes the WUI as a false proposition when the BHDL has imposed HFRA on 1,644,663 acres with no apparent justification based on actual building densities.

The Forest Plan amendment must correct this huge disparity in WUI acres with an analysis that accounts for these facts of building density.

Implementation Strategies." ISPRS Journal of Photogrammetry and Remote Sensing 146: 108–23. https://pubs.usgs.gov/publication/70227947

Figure 11. Beaverhead Deerlodge NF with Wildland Urban Interface and USGS Modeled WUI 500 Meter Neighborhood

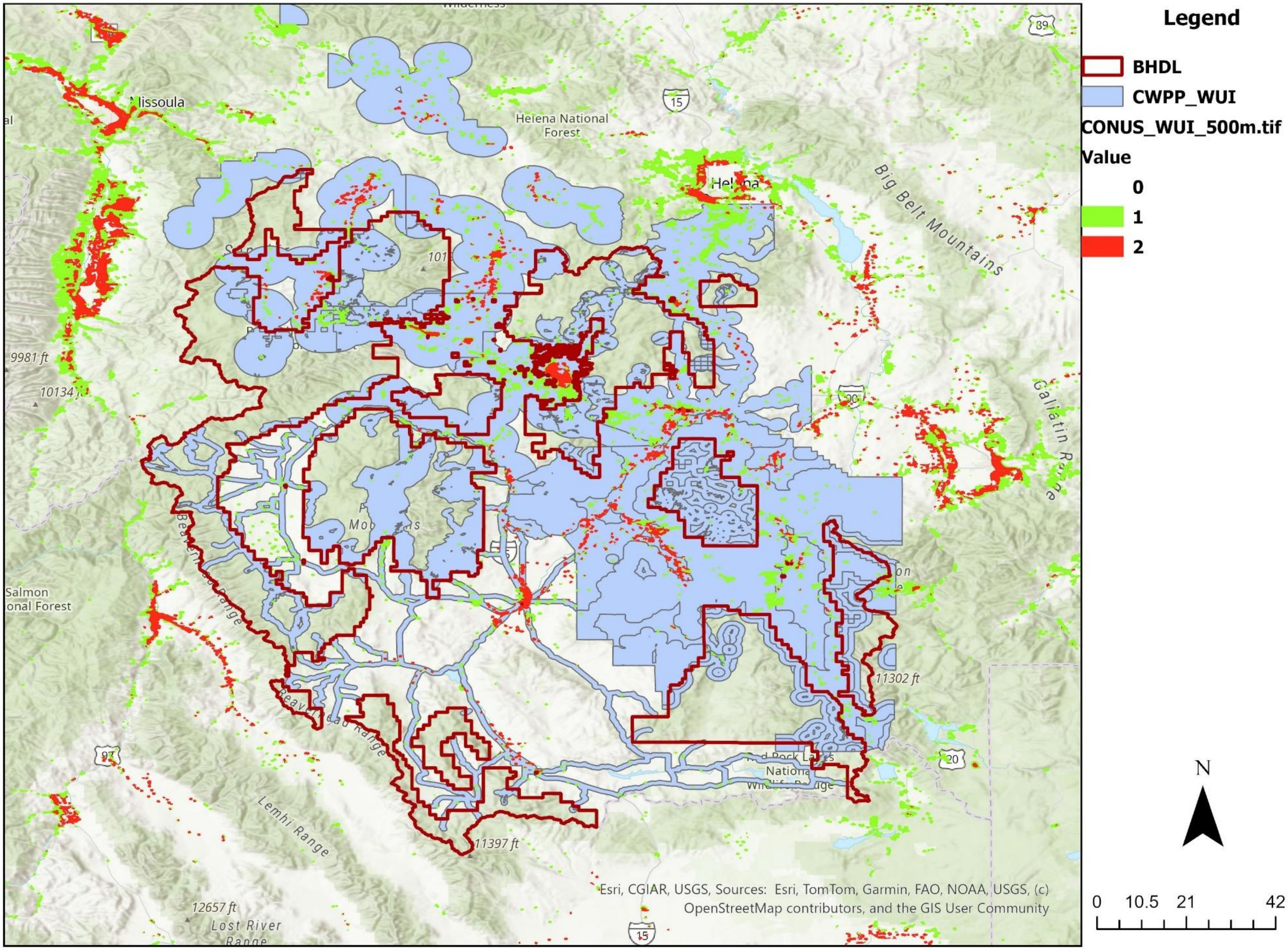
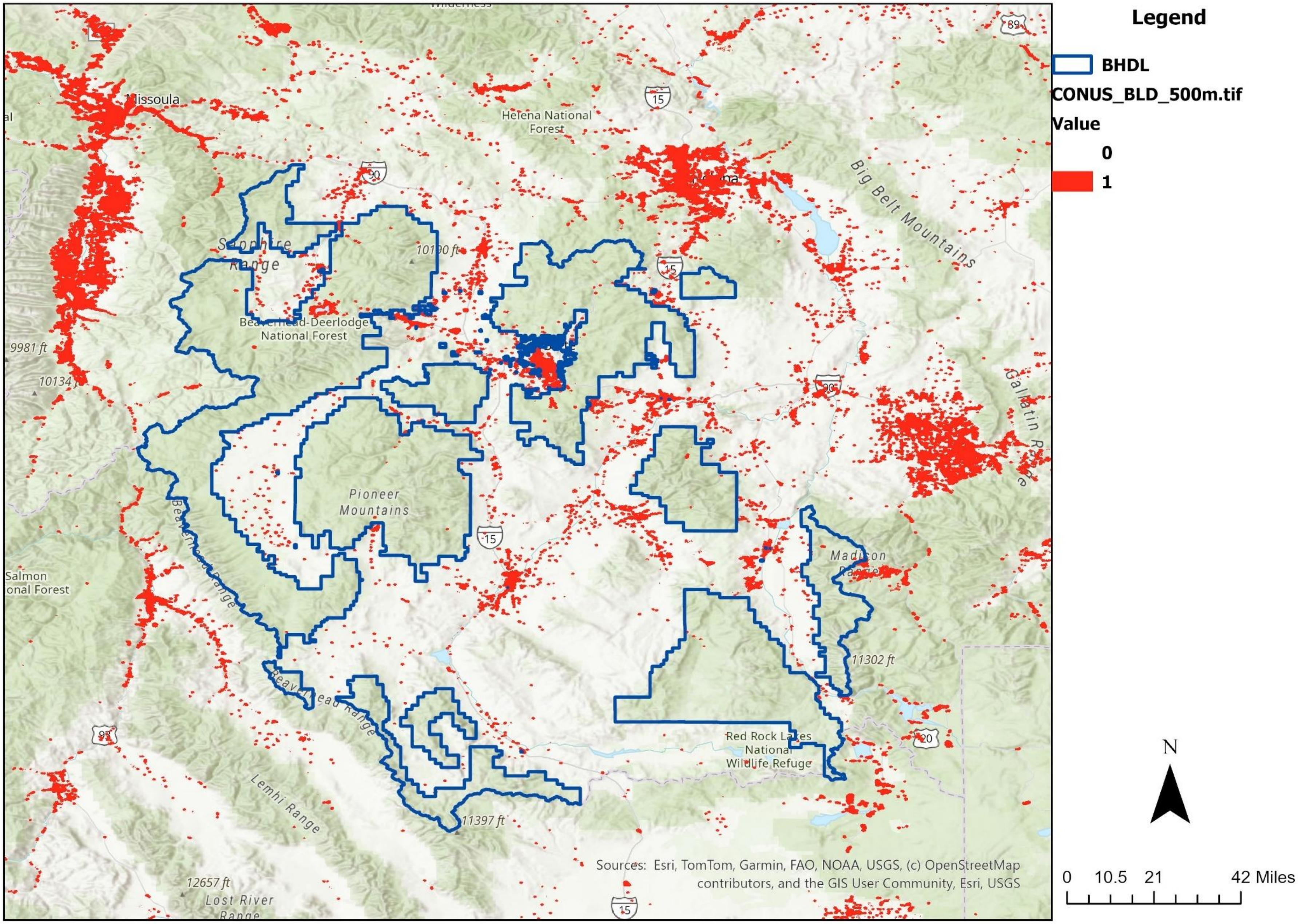


Figure 12. Beaverhead Deerlodge NF with USGS Modeled 500 Meter Building Density



Comparing Lynx Habitat Models for the BHDL

Montana Natural Heritage Program Models. The Montana Natural Heritage Program provided both Inductive and Deductive models. The Inductive Model used a combination of lynx observations in Montana with a suite of 44 environmental factors with a goal "To predict the current distribution and relative suitability of general year-round habitat for Canada Lynx at large spatial scales across its presumed current range in Montana." [18] (Figure 13). Their report is provided as Attachment 1. When we clipped this model to the BHDL we found a total lynx habitat of 2,326,515 acres consisting of the Low and Moderate suitability categories.

We also looked at their Deductive Model which used statewide land cover classifications and Level 3 Ecological Systems and determined the number of lynx observations associated with each ecological system. Their table is copied below. Interestingly, this data shows categories of forest that are downplayed or completely omitted in the BHDL model analysis in the BA but are aligned with what we found when comparing lynx observations to Landfire data.

Deductive Model Results

Table 6: Ecological Systems Associated with Canada Lynx

Ecological System	Code	Association	Count[a]
Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	4232	Common	28
Rocky Mountain Lodgepole Pine Forest	4237	Common	28
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	4242	Common	24
Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	4243	Common	21
Rocky Mountain Mesic Montane Mixed Conifer Forest	4234	Common	18
Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland	9155	Common	18
Rocky Mountain Montane Douglas-fir Forest and Woodland	4266	Common	9
Rocky Mountain Subalpine Deciduous Shrubland	5326	Common	7
Insect-Killed Forest	8700	Common	4
Harvested forest-tree regeneration	8601	Common	3
Harvested forest-shrub regeneration	8602	Common	3
Rocky Mountain Poor Site Lodgepole Pine Forest	4267	Common	0
Rocky Mountain Subalpine-Montane Riparian Woodland	9171	Common	0
Rocky Mountain Subalpine-Montane Riparian Shrubland	9187	Common	0
Recently burned forest	8501	Occasional	15
Rocky Mountain Ponderosa Pine Woodland and Savanna	4240	Occasional	5
Post-Fire Recovery	8505	Occasional	5
Aspen Forest and Woodland	4104	Occasional	3
Rocky Mountain Montane-Foothill Deciduous Shrubland	5312	Occasional	2
Rocky Mountain Subalpine-Montane Mesic Meadow	7118	Occasional	2
Aspen and Mixed Conifer Forest	4302	Occasional	1
Rocky Mountain Subalpine Woodland and Parkland	4233	Occasional	0
Rocky Mountain Conifer Swamp	9111	Occasional	0
Rocky Mountain Wooded Vernal Pool	9162	Occasional	0

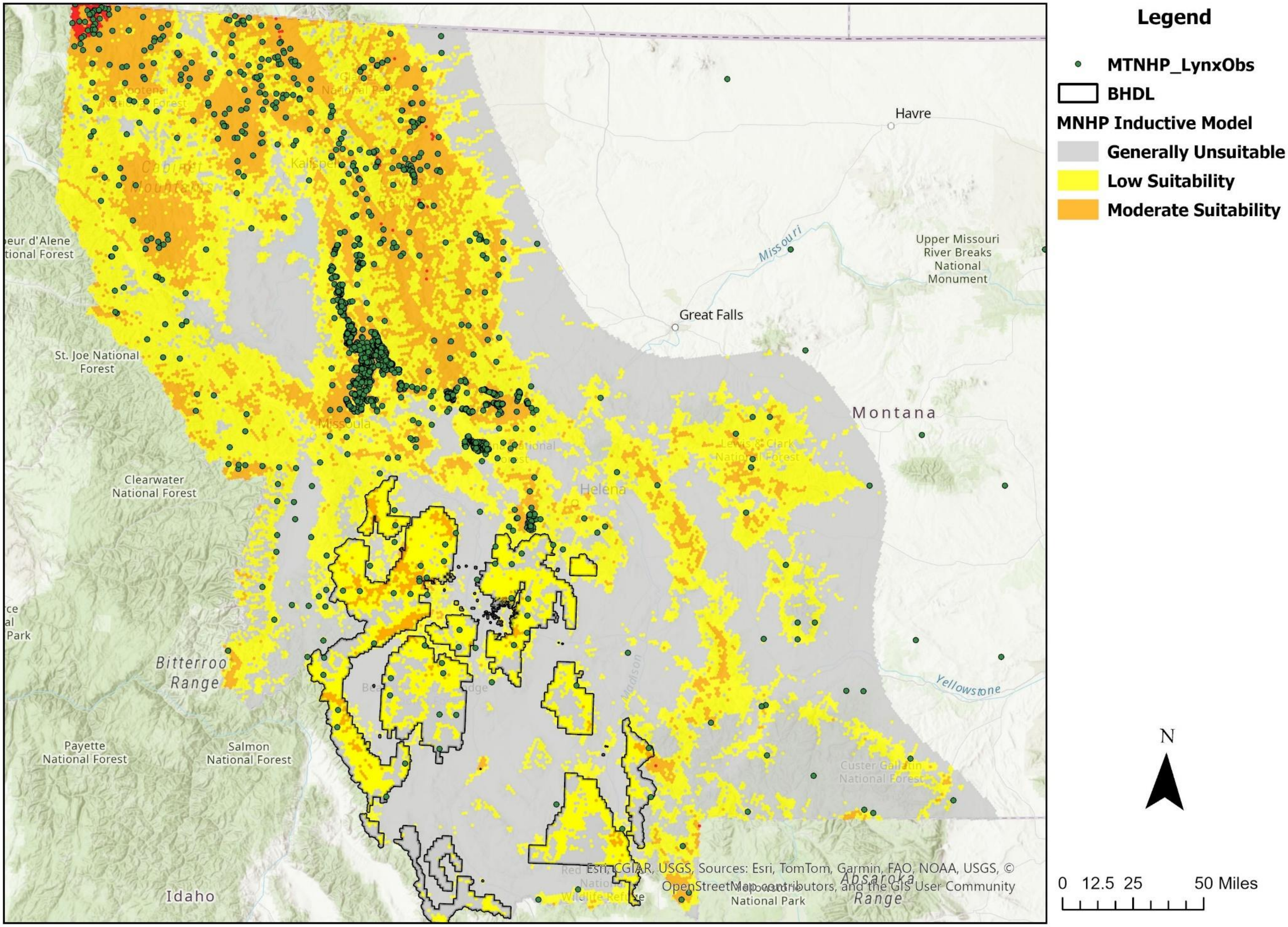
[a] A count of the observation records intersecting each ecological system, based on the 272 observation records used in the inductive model (see Table 1). This may be zero if the number of observations is low or if the ecological system is patchily distributed.

---

[18] Montana Natural Heritage Program. 2022. Canada Lynx (Lynx canadensis) predicted suitable habitat models created on May 19, 2022. Montana Natural Heritage Program, Helena, MT. 20 pp.

Figure 13.

Montana Natural Heritage Program Canada Lynx Inductive Model Output



<u>The Olson et al (2021) Model</u>. We received this model output from the USDA Forest Service Rocky Mountain Research Station.[19] It is mapped for the Northern Rockies and GYA in Figure 14. Lighter colors are higher habitat probability. The paper is included here in Attachment 2. The Olson paper described some of the limitations of species distribution modeling in terms of uncertainty, variations in geographically distinct populations in their responses to local conditions, complex models with "excessive environmental covariates" may be less generalized to novel areas and landscapes. The Olson model used 16 covariates, including climate, topographic, anthropogenic (road density), and vegetative covariates along with GPS collared lynx locations to define habitat suitability. The vegetative component used NDVI during the growing season to characterize vegetation presence. Thresholds applied to the Olson Model included 90% of GPS locations as high probability and 85% as medium probability lynx habitat. These are extremely restrictive criteria, eliminating consideration of anything but the most perfect habitat, at least by their model's apparent philosophy.

We clipped the Olson raster to the BHDL and determined the area of low, moderate, and high habitat probability. (Table 6) The area of moderate and high probability combined were 1,751,789 acres. Table 6 compares the three models and their total habitat acres. BA:Figure B-3 shows 1,509,146 acres of primary vegetation and 116,806 acres secondary vegetation for the 2020 BHDL model. This is a total of 1,625,952 acres of lynx habitat. Figure B-1 shows a total of 2,711,422 acres of lynx habitat for the 2001 BHDL model, however, some of that habitat is outside the BHDL. We clipped the modeled lynx habitat to the BHDL and found 2,134,741 acres within the BHDL.

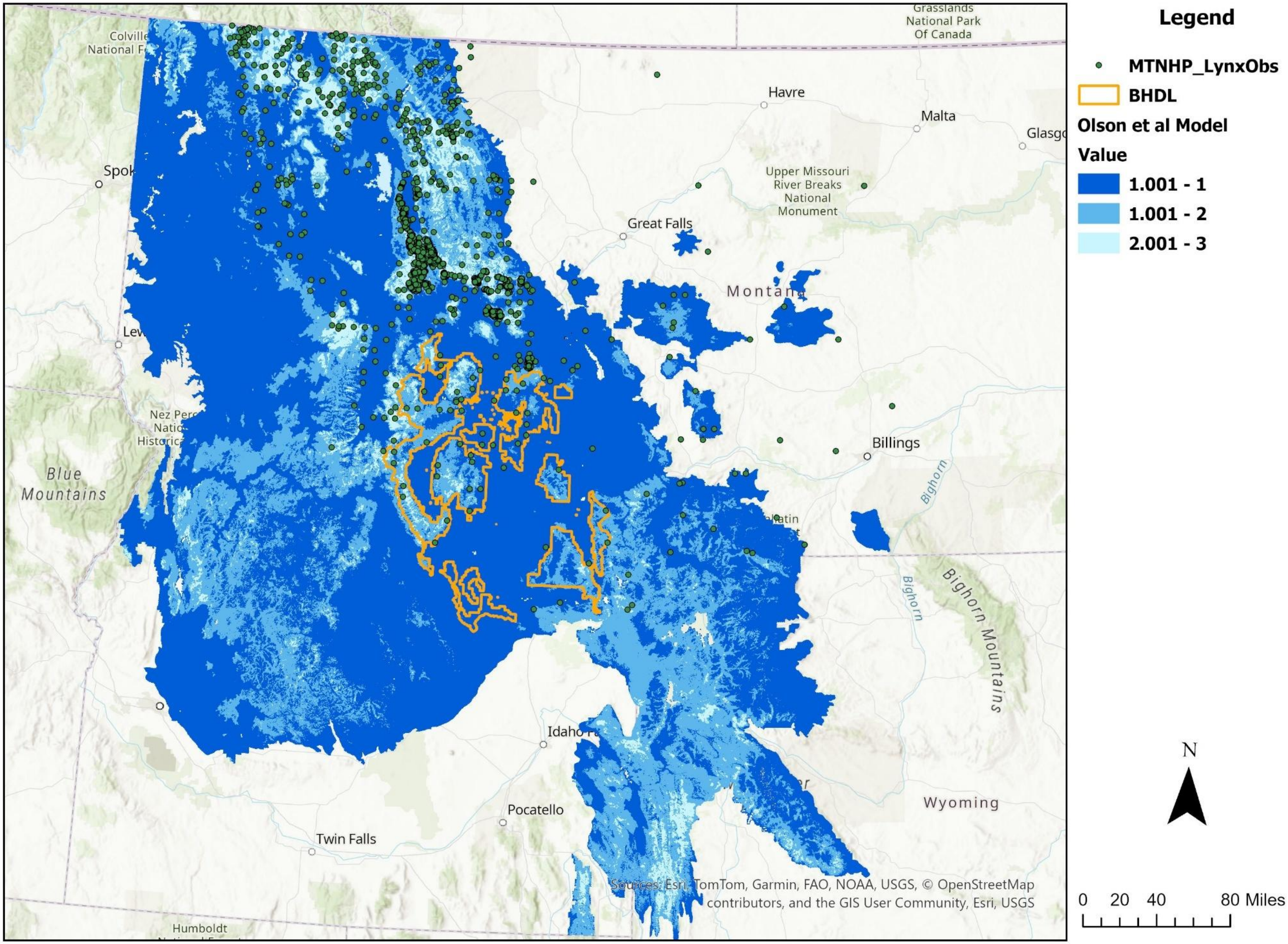
Table 6. Area (acres) of Modeled Lynx Habitat on the Beaverhead-Deerlodge NF

BHDL		116,806 Secondary vegetation	1,509,146 Primary vegetation
MNHP	1,287,428 Generally Unsuitable	2,069,426 Low Suitability	257,089 Moderate Suitability
Olson	1,862,477 Low Probability	1,507,773 Moderate Probability	244,016 High Probability
Comparing the Model Acreage			
Beaverhead Deerlodge Models		2,711,422 acres (2001) 1,625,952 acres (2020) 2,134,741 acres* *Y2U 2001 BHDL model clipped to Forest Boundary	
Montana Natural Heritage Program Inductive Model		2,326,515 acres	
Olson et al (2021) Model		1,751,789 acres	

[19] Olson et al. 2021. Improved prediction of Canada lynx distribution through regional model transferability and data efficiency. Ecology and Evolution 11:1667 – 1690.

Figure 14.

Olson et al (2021) Categorical Lynx Habitat Probability



From Table 6, we see that the BHDL 2020 version provides the least habitat of all the models. It was the only one that did not consider historical lynx observations or tracking data. A note on lynx observations is, however, in order. In our comments on the Federal Register Notice to revise lynx critical habitat, we analyzed the MNHP observations in Glacier National Park, and the Bob Marshall and Mission Mountain Wilderness in Montana relative to areas outside these special designations. To wit:

Squires et al (2010)[20] studied lynx in the Swan River drainage near Seeley Lake, Montana. The area was bordered by the Mission Mountain and Bob Marshall Wilderness areas. See Figure 15 for a map using MNHP observations to illustrate how studies or areas accessible to people, or used in tracking studies, can result in more observations compared to areas such as wilderness where human presence is low in winter and mechanized travel or trail cameras are not allowed. Does this mean, therefore, that the wilderness is not a suitable habitat?

We looked at MNHP observations in Glacier National Park (GNP). (Figure 15). Here we see scattered lynx observations that are lower in density than areas outside the park. Does this mean the park has little suitable lynx habitat? Note the observations are along valleys where people may have access in winter, but not across the wider area. A park-wide occupancy survey using motion activated cameras found a mean of 52 individual lynx and density of 1.28/100 km^2. Later, when we looked at the Olson et al (2021) Model and its mean habitat probabilities across management areas, we saw that Glacier NP is not rated high, yet it has a significant population. This argues for an expanded interpretation of Olson et al (2021) to include areas with lower modeled habitat probabilities or risk eliminating important lynx habitat from further consideration.

The Dillon Ranger District Issue: BA Figure B-3 shows an absence of lynx habitat in the Dillon Ranger District south of HWY 324. Yet, the 2001 modeled habitat area is significant there. When we clipped the 2001 BHDL model habitat to that area, we found 83,265 acres of lynx habitat south of HWY 324. The 2020 model omits this area in its entirety, yet Figure 16 shows it provides potential linkage to the western half of the BHDL without crossing Interstate 15. We have reproduced the map of 2001 modeled habitat as well for comparison. (Figure 17).

To sum up briefly, the BHDL 2020 model is too conservative in its interpretation, leaving out much potential or historical lynx habitat. It further did not consider historical observation locations and the actual vegetation types where those occurred. Instead, it used surrogates with cascading errors to eliminate major lynx habitats such as lodgepole pine and Douglas fir. The MNHP model used lynx observations combined with environmental variables to arrive at a habitat area of 2,326,515 acres, compared to the BHDL 2020 modeled 1,625,952 acres. This is

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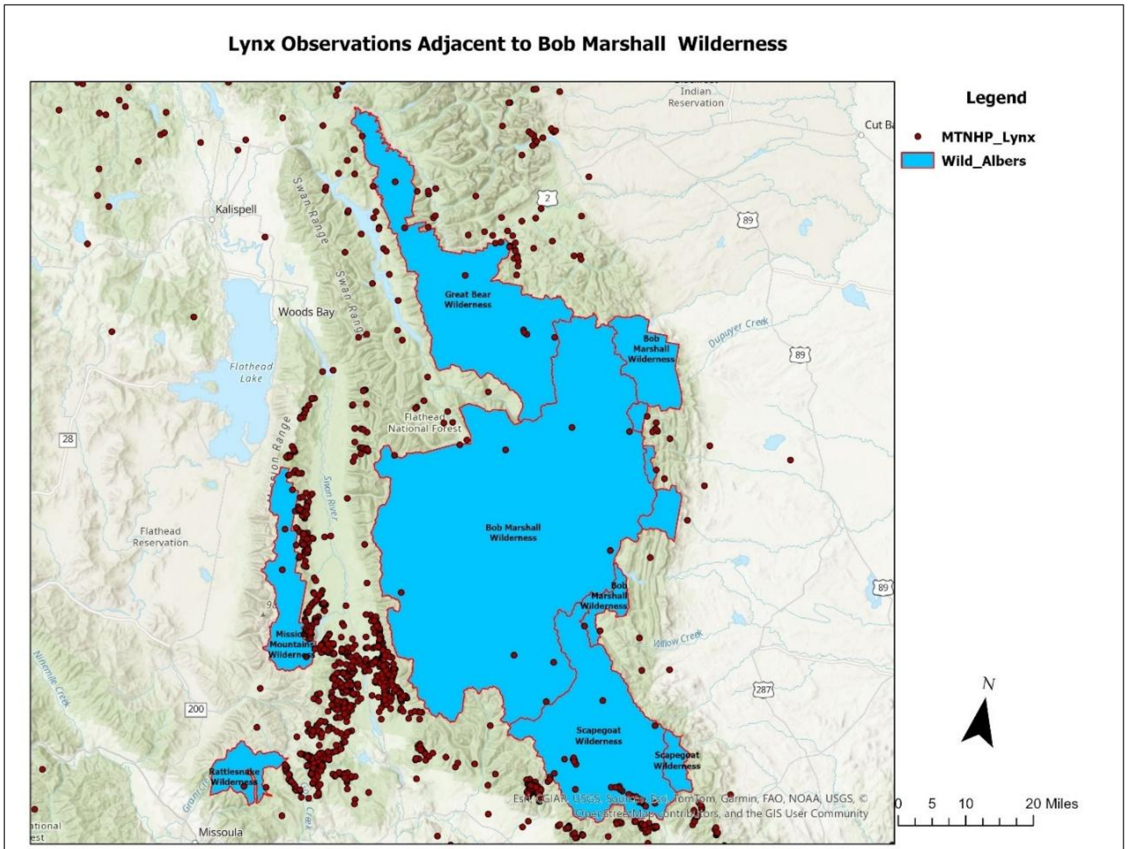
[20] Squires, J.R., Decesare, N.J., Kolbe,J.A., and Ruggiero, L.F. 2010. Seasonal Resource Selection of Canada Lynx in Managed Forests of the Northern Rocky Mountains. Journal of Wildlife Management, 74(8):1648-1660. 2010. Published By: The Wildlife Society DOI: 10.2193/2009-184 URL: http://www.bioone.org/doi/full/10.2193/2009-184

less than the BHDL 2001 model, but that model would include the habitat in the Dillon Ranger District that was omitted from the 2020 model. The MNHP Deductive model shows that the BHDL model eliminates major categories of vegetation types in its mapping. In the end, the BHDL 2001 model with 2,134,741 acres within the BHDL seems to capture the habitat better than the 2020 model and does include that habitat in the Dillon Ranger District. However, that said, the determination of lynx habitat must go back to the actual forest or vegetation types where observations were made and map the extent of those across the BHDL. Since we have determined that snow depth, slope, aspect and elevation are not significant barriers within BHDL, these should not be part of the determination.

Figure 15.


Lynx Observations Adjacent to Bob Marshall Wilderness
Legend
MTNHP_Lynx
Wild_Albers
Great Bear Wilderness
Bob Marshall Wilderness
Bob Marshall Wilderness
Bob Marshall Wilderness
Scapegoat Wilderness
Scapegoat Wilderness
Rattlesnake Wilderness
Flathead National Forest
Flathead Reservation
Flathead Lake
Kalispell
Woods Bay
Missoula
Swan Range
Swan River
0 5 10 20 Miles
N
Esri, CGIAR, USGS, Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

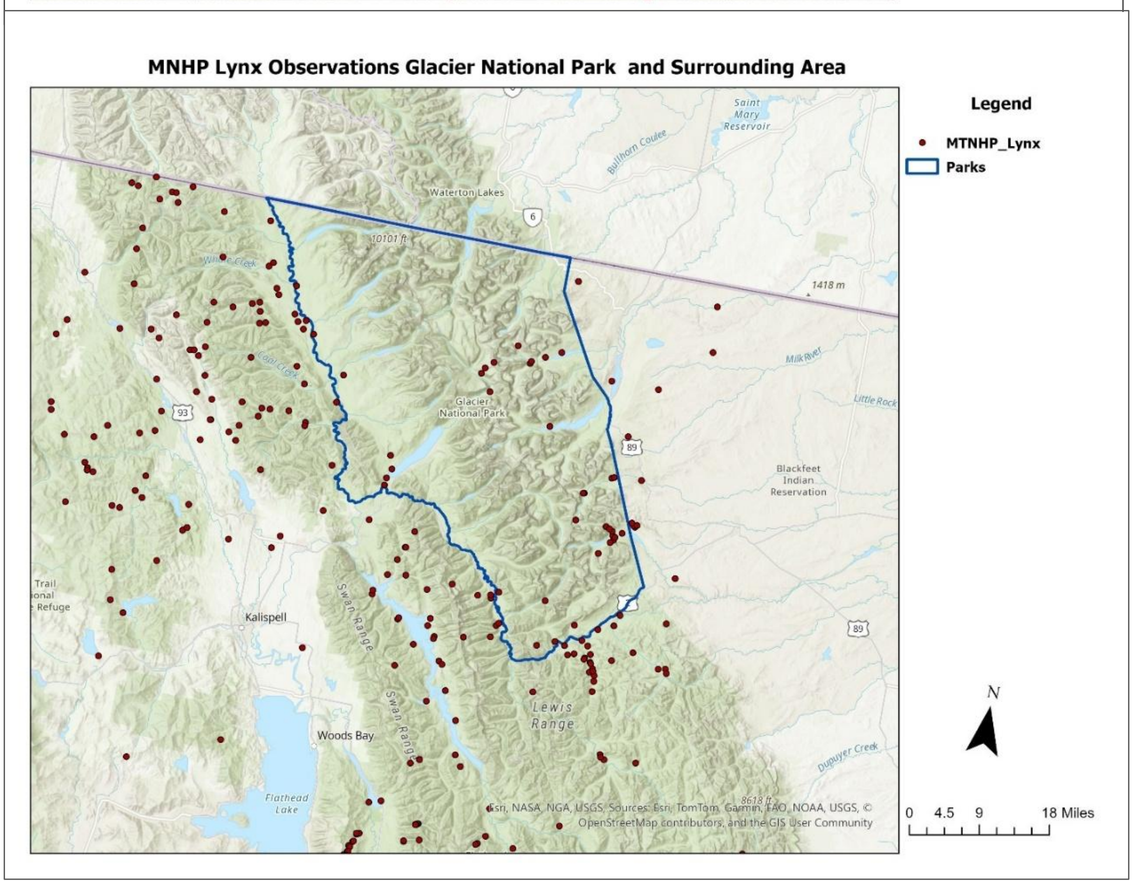

MNHP Lynx Observations Glacier National Park and Surrounding Area
Legend
MTNHP_Lynx
Parks
Waterton Lakes
Glacier National Park
Blackfeet Indian Reservation
Saint Mary Reservoir
Kalispell
Woods Bay
Flathead Lake
Swan Range
Lewis Range
Milk River
0 4.5 9 18 Miles
N
Esri, NASA, NGA, USGS, Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

Figure 16.

BHDL 2001 Modeled Lynx Habitat and Ranger Districts

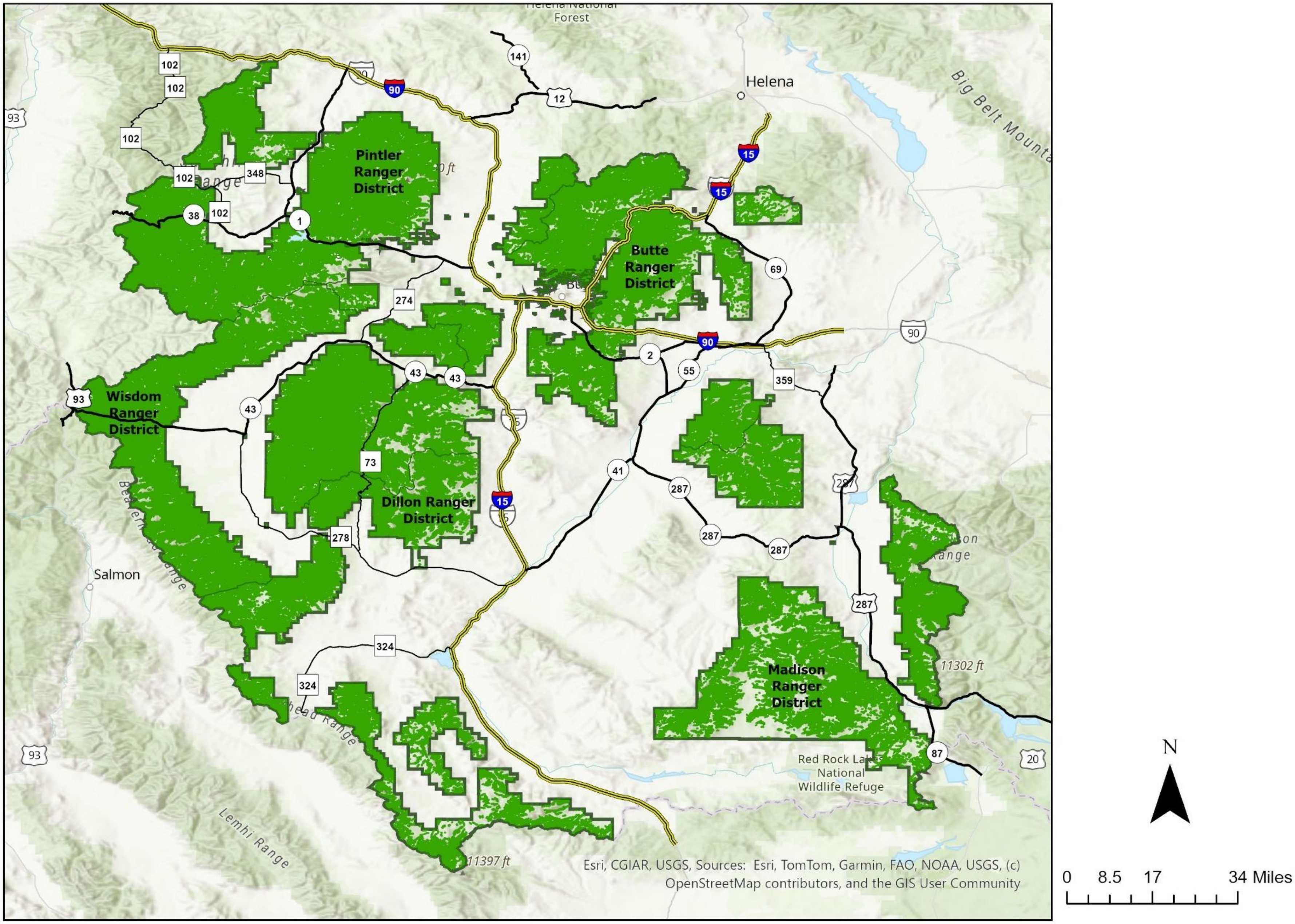
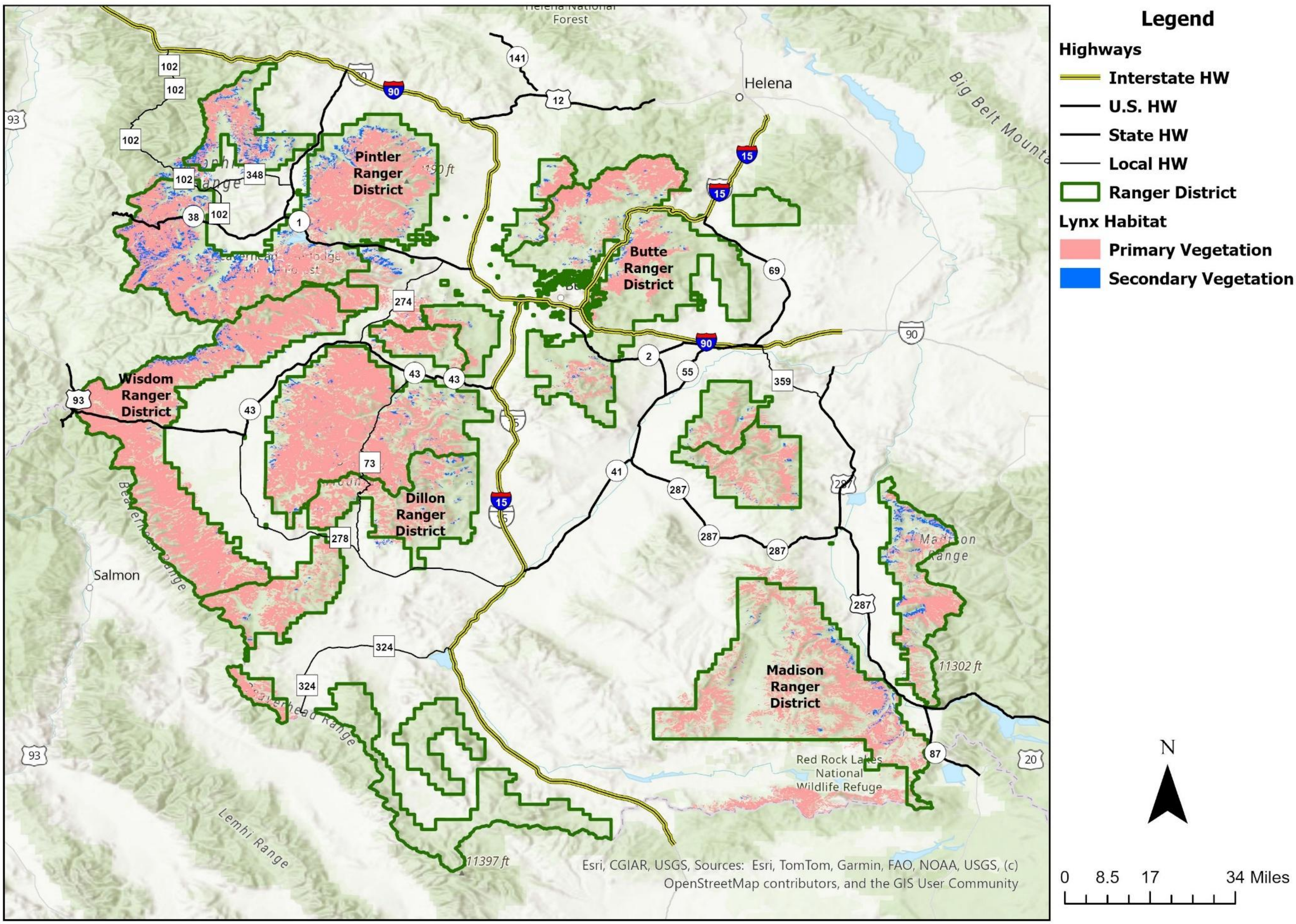


Figure 17.

BHDL 2020 Modeled Lynx Habitat and Ranger Districts



Forest Plan Standards

<u>Purpose</u>. The Scoping Notice states the Purpose for the proposed plan amendment is "to identify lands on the Forest that meet the criteria for Canada lynx habitat and to delineate where the Forest Plan standards will apply". It cites Figure 2 of the Scoping Notice. Inspection of that figure reveals that the BHDL has assumed the 2020 mapping of LAUs and lynx habitat constitute the lands that meet the criteria for Canada lynx habitat. The analysis we have provided above clearly shows that the 2020 BHDL model has many flaws and is not clearly identifying lynx habitat. A new analysis must be done that takes into account historical lynx observation locations and the vegetation types in which those occurred, not an altered forest baseline containing the outcomes of timber manipulations.

Rather than the BHDL claimed habitat of 1,625,952 acres stemming from that 2020 modeling exercise, the plan amendment must consider the 2,134,741 acres represented by the 2001 BHDL model that occur within the BHDL itself combined with the MNHP Inductive Model that found 2,326,515 acres of lynx habitat within the BHDL. The analysis must rely on the vegetation types represented in the MNHP Deductive Model in which lynx observations occurred. Taking this approach combines the strengths of these models and corrects the missing habitat in the Dillon Ranger District which is a critical linkage in the western half of the BHDL.

<u>Need for the Project</u>. The Scoping Notice expresses the need for a plan amendment to include new information on lynx habitat, the change in occupied status to identify where NRLMD standards and guidelines apply, and to respond to the public's desire for involvement in the habitat mapping effort. In these comments we have provided a detailed critique of the current (2020) habitat map. The Scoping Notice appears to preclude that involvement by using the flawed habitat map shown in the Notice Figure 2, an apparent decision already made.

<u>The 2012 Planning Rule</u>. The Scoping Notice references 36 CFR 219.8 through 36 CFR 219.11 as "directly related to the plan direction being added." These sections of the law address Sustainability (§ 219.8), Diversity of plan and animal communities (§ 219.9), Multiple Use (§ 219.10), and Timber Requirements based on NFMA (§ 219.11).

<u>§ 219.8 Sustainability</u> requires for ecosystem integrity, "The plan must include plan components, including standards or guidelines, to maintain or restore the ecological integrity of terrestrial and aquatic ecosystems and watersheds in the plan area, including plan components to maintain or restore structure, function, composition, and connectivity…" It then describes the elements such as air, soil, water, and riparian areas that must be taken into account. Each of these elements must be fully addressed with analysis of monitoring data and other science that describes the current and potential conditions on the BHDL, and the factors driving those conditions. Along with timber manipulations, recreation, roads and trails, we are concerned about the existing conditions of the riparian areas, meadows, and forested communities that have been altered by livestock grazing. The degradation of these habitats deprives snowshoe hares of their forage and

cover, removes herbaceous vegetation and ground cover in aspen and conifer communities, subsequently altering forest structure and lynx habitat.

§ 219.9 Diversity of plant and animal communities has the same requirement for ecosystem integrity as § 219.8. In addition, it requires that ecosystem diversity be maintained or restored, a determination as to whether plan components, "provide the ecological conditions necessary to: contribute to the recovery of federally listed threatened and endangered species, conserve proposed and candidate species, and maintain a viable population of each species of conservation concern within the plan area." Species viability must be addressed in the plan amendment analysis by presenting the trend of the special status species on the BHDL, their habitat requirements and the current and potential condition of those habitats as supported by monitoring data.

§ 219.10 Multiple use requires, "The plan must include plan components, including standards or guidelines, for integrated resource management to provide for ecosystem services and multiple uses in the plan area." Ten elements are listed which must be addressed under "Integrated resource management for multiple use." These must be addressed by analyzing BHDL monitoring data and science.

In the section "(b) Requirements for plan components for a new plan or plan revision." Six elements are outlined. It outlines "designated" areas such as wilderness, wild and scenic rivers, areas of tribal importance, cultural and historic resources, and sustainable recreation. While designated areas are certainly important, it is critical that the entire BHDL have standards and guidelines for Canada lynx that recognize the impact of human uses, including recreation, on their habitat and use of that habitat. Road density, habitat security, connectivity within the BHDL and adjacent National Forests must be analyzed. Special concerns are high motorized road and trail density that must also include non-system, illegal, or user created roads. Groomed snowmobile trails and play areas are of major concern and the analysis must identify lynx habitat with protection and security from these winter uses. The effectiveness of BMPs, standards and guidelines must be specifically addressed for each element.

§ 219.11 Timber requirements based on the NFMA. In section "(a) Lands not suited for timber production." Six elements are described. One of these is restocking within 5 years of harvest, another is timber harvest not compatible with DFCs. The analysis should provide data showing the restocking success and whether these harvest areas have become thickets of conifers or have not regenerated that may preclude use by snowshoe hares and Canada lynx. It should also show how any harvest, or vegetation treatment it has authorized has met the DFCs for lynx habitat and special status species habitat.

Another provision is described, "(c) Timber harvest for purposes other than timber production." In this section "Examples of using timber harvest to protect other multiple use values may include improving wildlife or fish habitat, thinning to reduce fire risk, or restoring meadow or savanna ecosystems where trees have invaded." We have described the massive exaggeration of WUI above and that is the first thing to correct. The analysis should include monitoring data, reports and scientific studies demonstrating that these non-production values have been achieved on the BHDL by reviewing past projects and their outcomes. Maps, charts, and data all need to be presented to show whether project objectives were achieved or not.

(d) Limitations on timber harvest elements are described. This includes general requirements such as lands not suitable or with sensitive watershed conditions. We would add that timber harvest for any purpose should not be allowed in Canada lynx habitat until past harvests have regenerated and snowshoe hares have re-occupied disturbed areas. The current status of lynx habitat should be mapped by forest type (lodgepole, fir, spruce, aspen, riparian) and analyze departures from optimal or potential conditions. No exceptions to standards or guidelines should be allowed so the forest can complete its successional pathway. Lynx and snowshoe hare (and other species) have evolved to coexist with natural disturbance. Old growth forests should be protected and mature forests allowed to progress to old growth.

Lynx, the ESA and Forest Service Manual. The ESA promulgated regulations at 50 CFR § 402.12 delineate the purpose of a Biological Assessment (BA) as to *"evaluate the potential effects of the action on listed and proposed species and designated and proposed critical habitat…"*. It describes the contents as *"discretionary"* and depends on the nature of the federal action with consideration for including (1) results of on-site inspections; (2) views of recognized experts; (3) review of the literature; (4) analysis of the effects of the action on species and habitat, including cumulative effects and the results of related studies; and (5) analysis of alternate actions considered by the Federal agency. This Forest Plan Amendment should preclude making BA's "discretionary". They should be required of all future activities/projects affecting lynx habitat.

The Forest Service Manual[21] cites the ESA as *"the Act directs federal departments and agencies to ensure that actions authorized, funded, or carried out by them are not likely to jeopardize the continued existence of any threatened or endangered species or result in the destruction or adverse modification of their critical habitats."* (FSM 2670.11). The FSM (2679.12) cites Departmental Regulation 9500-4 as (1*) "Manage 'habitats for all existing native and desired nonnative plants, fish and wildlife species in order to maintain at least viable populations of such species.'"* (2*) "Conduct activities and programs 'to assist in the identification and recovery of threatened and endangered plant and animal species.'"* (3) *"Avoid actions 'which may cause a species to become threatened or endangered'"*. We have seen for Canada lynx, as we described above, that "occupied habitat" has been arbitrarily applied and led to the exclusion of peripheral habitat, connections and linkages remaining without regulatory protection and are seldom addressed in project analyses. These connections and linkages are part of lynx habitat and should be identified, mapped and then designated as protected with appropriate standards.

[21] USDA Forest Service. 2005. Forest Service Manual National Headquarters (WO) Washington DC. FSM 2600 – Wildlife, Fish, and Sensitive Plan Habitat Management Chapter 2670 – Threatened, Endangered and Sensitive Plants and Animals (September 23,2005).

FSM 2670.31 provides additional guidance for T&E species.

> (1) *"Place top priority on conservation and recovery of endangered, threatened, and proposed species and their habitats."* (2) *"Establish, through the Forest planning process, objectives for habitat management and/or recovery of populations."* (4) *"Avoid all adverse impacts on threatened and endangered species and their habitats, except when it is possible to compensate adverse effects totally through alternatives identified in a biological opinion."* (6) *"Identify and prescribe measures to prevent adverse modification or destruction of critical habitat and other habitats essential for the conservation of endangered, threatened, and proposed species. Protect individual organisms or populations from harm or harassment as appropriate."*

The FSM 2670.5 provides definitions of terms that are useful in interpreting the efficacy of the agency analysis. An **adverse effect** includes *"Any action that directly alters, modifies, or destroys, critical or essential habitats or renders occupied habitat unsuitable for use by a listed species, or that otherwise affects its productivity, survival, or mortality."* **Essential habitat** is defined as *"Those areas designated by a regional forester as possessing the same characteristics as critical habitat without having been declared as critical habitat by the Secretary of the Interior or Commerce. The term includes habitats necessary to meet recovery objectives for endangered, threatened, and proposed species and those necessary to maintain viable populations of sensitive species."* A **viable population** is defined as *"A population that has the estimated numbers and distribution of reproductive individuals to ensure the continued existence of the species throughout its existing range (or range required to meet recovery for listed species) within the planning area."*

The BHDL must now designate lynx habitat as Essential for recovery of lynx and maintaining connections within the BHDL and to adjacent public lands. It must determine the potential occupancy extent and home ranges and set population goals and Plan standards for a viable population within the BHDL to be established by a combination of habitat protection and introducing lynx as done in Colorado.

FSM 2671.44 describes determination of the effects on listed species. Biological evaluations are to *"conduct and document the program and activities review necessary to ensure that any action … is not likely to jeopardize the continued existence of any listed or proposed species or to result in the destruction or adverse modification of critical or proposed critical habitat."* Internal *"biological expertise"* and *"informal consultation"* are to be used to reach *"supportable determinations of effect"*. Finally, *"Consider effects on suitable unoccupied habitat essential to recovery of the species when doing the biological evaluation."*

We are not seeing National Forests conducting any analysis of linkages, or "suitable unoccupied habitat" or any effort to address its current vs historical condition. The Plan Amendment must correct this. The lack of adequate regulatory mechanisms to protect lynx habitat and connectivity has been implicated as a central issue for lynx being able to maintain populations.[22]

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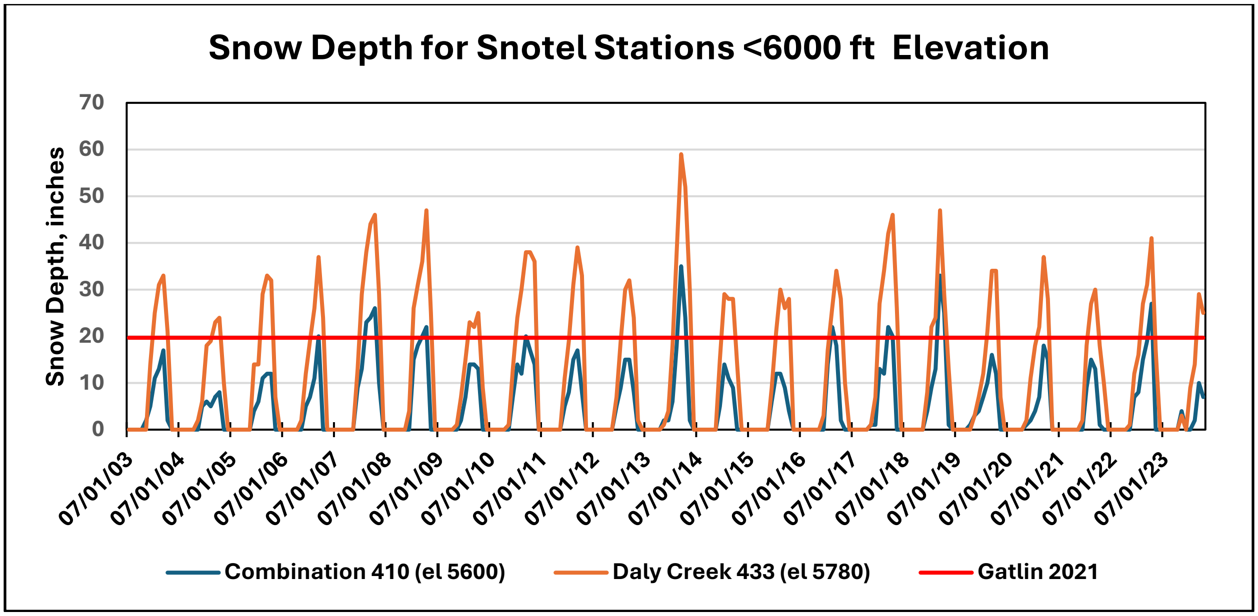
[22]DOI USFWS. 2000. Endangered and Threatened Wildlife and Plants; Determination of Threatened Status for the Contiguous U.S. Distinct Population Segment of the Canada Lynx and Related Rule. Fed. Register Vol. 65, No. 58.

(FR p16052). The FSM described above makes the point that the Forest Service should establish through planning, objectives for habitat management and/or recovery of populations and prescribe measures to prevent adverse modification of habitat essential to the conservation of T&E species. This remains to be done with assurance that the BHDL land management plans are quantitatively addressing lynx habitat and connectivity needs.

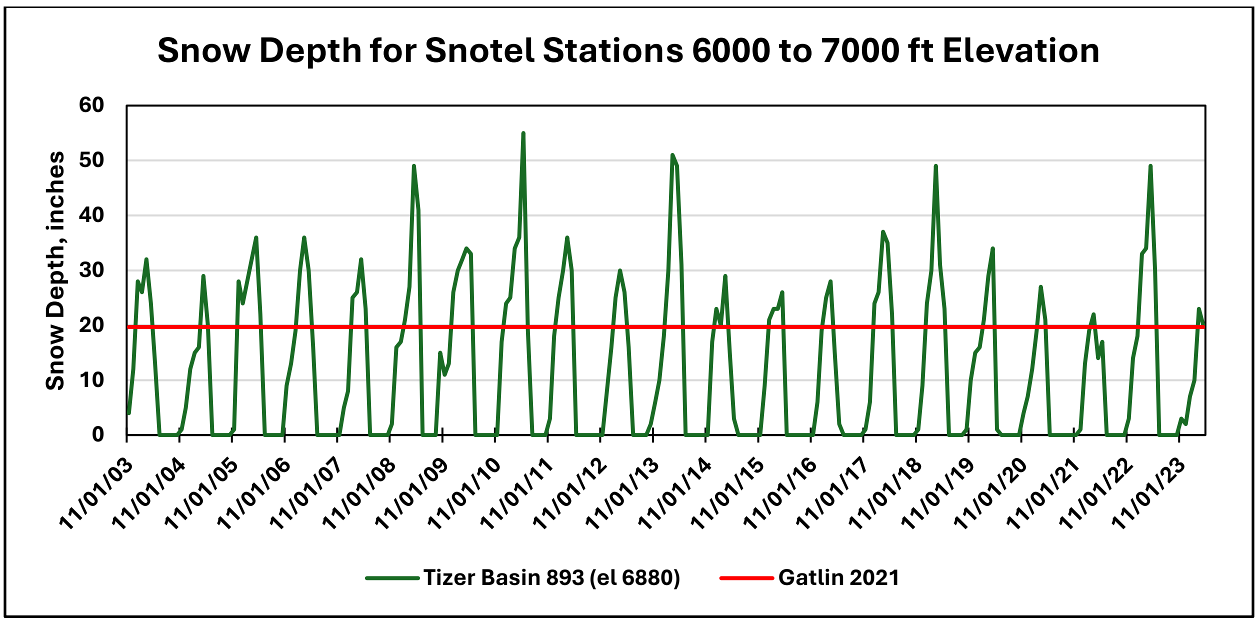
The BA:Appendix H provides a comprehensive review of the NRLMD goals, objectives, standards and guidelines with a comparison to the BHDL 2009 RFP provisions. Standards are missing for most of the NRLMD goals, objectives, and guidelines in the 2009 RFP. Goals, objectives and guidelines are without enforcement and need quantitative, not general, standards. The Forest Plan Amendment must now go through each of these NRLMD provisions and provide standards for each NRLMD Direction. As we pointed out in our comments on the lynx SSA, and draft Recovery Plan cited above, the listing of lynx as threatened was driven by the need for adequate regulatory mechanisms. To date there has been no analysis of the effectiveness of the NRLMD or any forest plans we are aware of. Lynx have disappeared across much of its previously occupied landscape. The NRLMD has not provided adequate protections for lynx and much of its direction is general and lacks enforceable standards.

The BHDL must analyze its Forest Plan and the activities allowed therein and determine why no lynx were found following listing until nearly 20 years later. It has not determined that the handful of lynx found on the Forest the past few years are resident, have home ranges, denning habitat, or are reproducing and persisting. The process for the plan amendment must carry out this analysis. The BHDL must designate areas not included in critical habitat as Essential Habitat. This includes linkages, connections, and all lynx habitat. Existing and potential highway crossings must be analyzed and located with a goal of achieving their implementation.

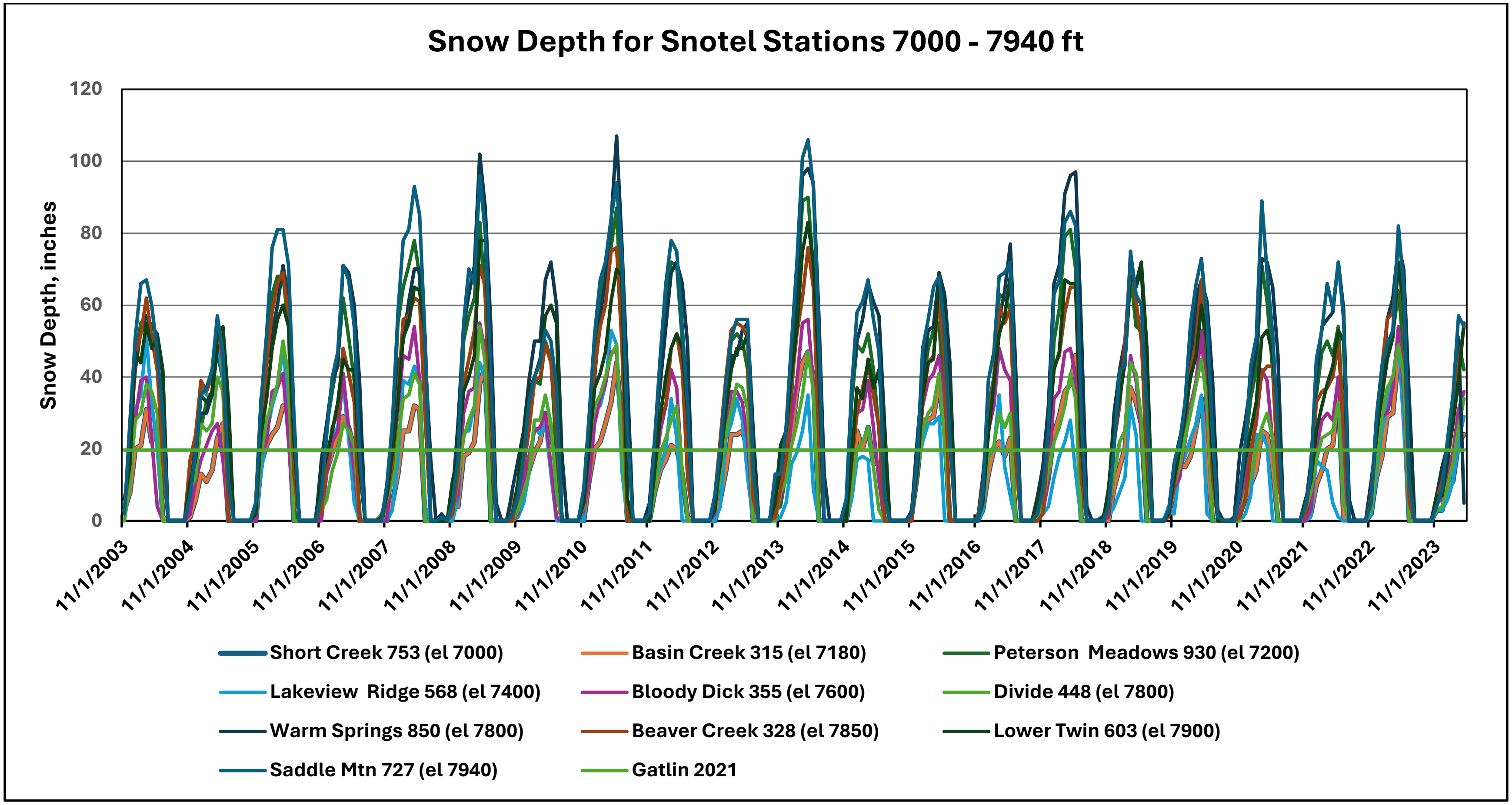
Appendix I

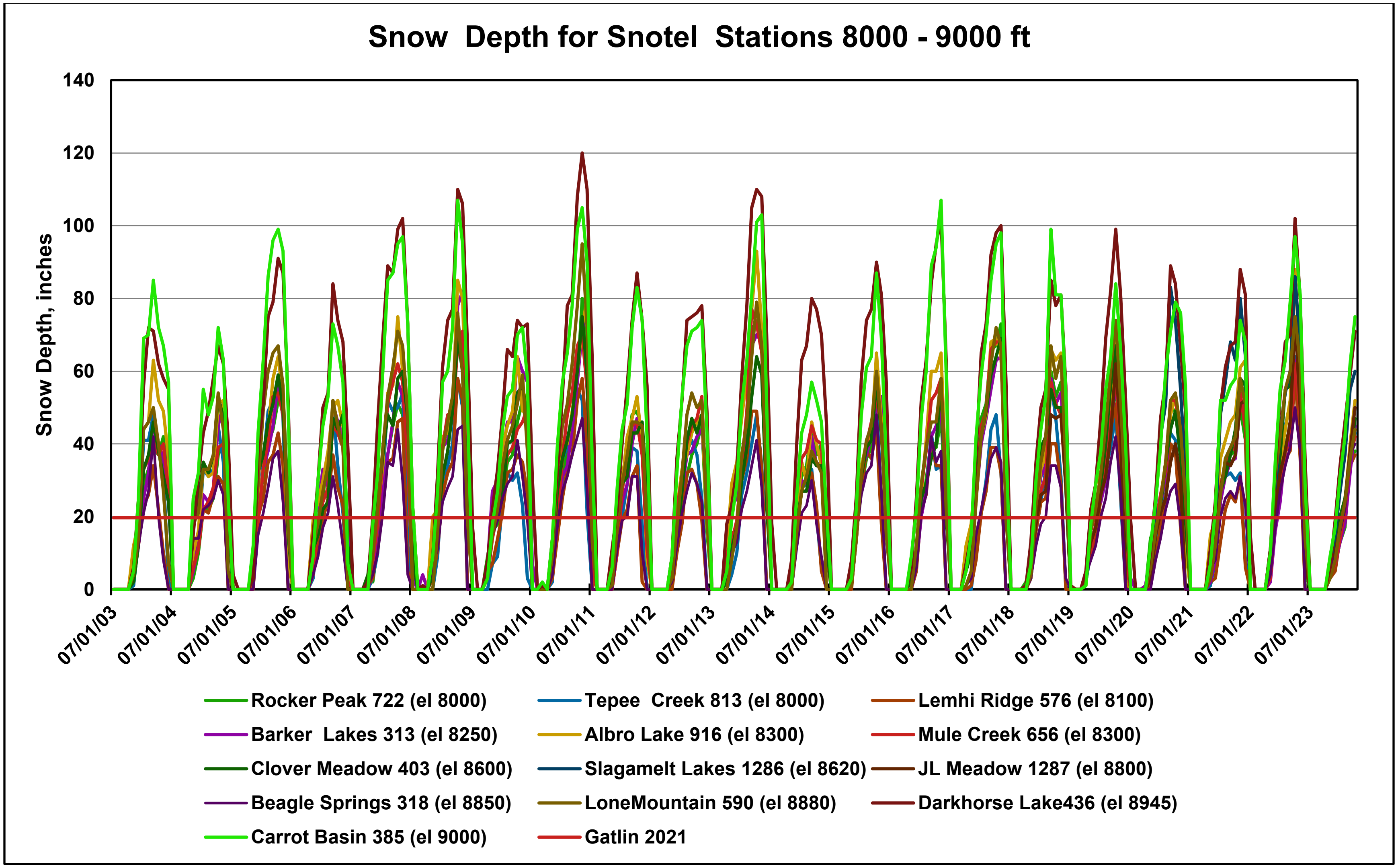


Snow Depth for Snotel Stations <6000 ft Elevation
Snow Depth, inches
70
60
50
40
30
20
10
0
07/01/03
07/01/04
07/01/05
07/01/06
07/01/07
07/01/08
07/01/09
07/01/10
07/01/11
07/01/12
07/01/13
07/01/14
07/01/15
07/01/16
07/01/17
07/01/18
07/01/19
07/01/20
07/01/21
07/01/22
07/01/23
Combination 410 (el 5600)
Daly Creek 433 (el 5780)
Gatlin 2021



Snow Depth for Snotel Stations 6000 to 7000 ft Elevation
Snow Depth, inches
60
50
40
30
20
10
0
11/01/03
11/01/04
11/01/05
11/01/06
11/01/07
11/01/08
11/01/09
11/01/10
11/01/11
11/01/12
11/01/13
11/01/14
11/01/15
11/01/16
11/01/17
11/01/18
11/01/19
11/01/20
11/01/21
11/01/22
11/01/23
Tizer Basin 893 (el 6880)
Gatlin 2021


Snow Depth for Snotel Stations 7000 - 7940 ft
Snow Depth, inches
120
100
80
60
40
20
0
11/1/2003
11/1/2004
11/1/2005
11/1/2006
11/1/2007
11/1/2008
11/1/2009
11/1/2010
11/1/2011
11/1/2012
11/1/2013
11/1/2014
11/1/2015
11/1/2016
11/1/2017
11/1/2018
11/1/2019
11/1/2020
11/1/2021
11/1/2022
11/1/2023
Short Creek 753 (el 7000)
Basin Creek 315 (el 7180)
Peterson Meadows 930 (el 7200)
Lakeview Ridge 568 (el 7400)
Bloody Dick 355 (el 7600)
Divide 448 (el 7800)
Warm Springs 850 (el 7800)
Beaver Creek 328 (el 7850)
Lower Twin 603 (el 7900)
Saddle Mtn 727 (el 7940)
Gatlin 2021



Snow Depth for Snotel Stations 8000 - 9000 ft
Snow Depth, inches
140
120
100
80
60
40
20
0
07/01/03
07/01/04
07/01/05
07/01/06
07/01/07
07/01/08
07/01/09
07/01/10
07/01/11
07/01/12
07/01/13
07/01/14
07/01/15
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07/01/20
07/01/21
07/01/22
07/01/23
Rocker Peak 722 (el 8000)
Tepee Creek 813 (el 8000)
Lemhi Ridge 576 (el 8100)
Barker Lakes 313 (el 8250)
Albro Lake 916 (el 8300)
Mule Creek 656 (el 8300)
Clover Meadow 403 (el 8600)
Slagamelt Lakes 1286 (el 8620)
JL Meadow 1287 (el 8800)
Beagle Springs 318 (el 8850)
LoneMountain 590 (el 8880)
Darkhorse Lake436 (el 8945)
Carrot Basin 385 (el 9000)
Gatlin 2021

Attachment 1

Canada Lynx (*Lynx canadensis*)
Predicted Suitable Habitat Modeling

Distribution Status: Resident Year Round
State Rank: S3 (Species of Concern)
Global Rank: G5

Modeling Overview

Created by: Braden Burkholder
Creation Date: May 19, 2022
Evaluator: Dan Bachen
Evaluation Date: May 25, 2022

Inductive Model Goal: To predict the current distribution and relative suitability of general year-round habitat for Canada Lynx at large spatial scales across its presumed current range in Montana.
Inductive Model Performance: The model appears to adequately reflect the current distribution and relative suitability of general year-round habitat for Canada Lynx at larger spatial scales across its presumed current range in Montana. Evaluation metrics indicate a moderate model fit with elevated average deviance but acceptable AVI values and the delineation of habitat suitability classes is well supported by the data.
Inductive Model Output: http://mtnhp.org/models/files/Canada_Lynx_AMAJH03010_20220519_modelHex.lpk

Deductive Model Goal: To represent the ecological systems commonly and occasionally associated with Canada Lynx year-round, across its presumed current range in Montana.
Deductive Model Performance: Ecological systems that Canada Lynx is commonly and occasionally associated with seem to overpredict the amount of suitable habitat across its presumed current range in Montana.

Suggested Citation: Montana Natural Heritage Program. 2022. Canada Lynx (*Lynx canadensis*) predicted suitable habitat models created on May 19, 2022. Montana Natural Heritage Program, Helena, MT. 20 pp.

Montana Field Guide Species Account: http://fieldguide.mt.gov/speciesDetail.aspx?elcode=AMAJH03010

Species Model Page: http://mtnhp.org/models/?elcode=AMAJH03010

Other Models or Spatial Products for this Species:
Olson, L.E., N. Bjornlie, G. Hanvey, J.D. Holbrook, J.S. Ivan, S. Jackson, B. Kertson, T. King, M. Lucid, D. Murray, R. Naney, J. Rohrer, A. Scully, D. Thornton, Z. Walker, and J.R. Squires. 2021. Improved prediction of Canada lynx distribution through regional model transferability and data efficiency. Ecology and Evolution 11 (4), 1667–1690. https://doi.org/10.1002/ece3.7157

Inductive Modeling

Model Limitations and Suggested Uses

This model is based on statewide biotic and abiotic environmental layers originally mapped at a variety of spatial scales and standardized to 90×90-meter raster pixels. The spatial accuracy of the training and testing data are varied (typically 20-400 meters) and may result in additional statistical noise in the model. As a result, model outputs may not be appropriate for use on smaller areas or at fine spatial scales. **Model outputs should not typically be used for planning efforts on land areas smaller than one quarter of a public land survey system (PLSS) section (<64 hectares)** and model outputs for some species may only be appropriate for broader regional level planning efforts. Models should be interpreted as landscape-level habitat suitability (fundamental niche) and not as estimated distributions of the species (realized niche) since suitable habitat may be unoccupied (Pulliam 2000). **Consequently, model outputs should not be used in place of on-the-ground surveys for species**, and wildlife and land management agency biologists should be consulted about the value of using model output to guide habitat management decisions for regional planning efforts or local projects. See Suggested Contacts for Natural Resource Agencies listed at the end of this report or on our website. In general, we have found across a large number of species representing a wide variety of plant and animal taxa that experts believe optimal and moderate suitability classes represent landscapes where suitable habitat is often more continuous while the low suitability class represents landscapes where suitable habitat is often less continuous, scattered, or patchy (see definitions in the Model Outputs and Evaluation section below). We encourage use of these classes for management, planning, permitting, survey, and other decisions accordingly.

Inductive Model Methods

Modeling Process

Presence-only data were extracted from Montana Natural Heritage Program Databases, which serve as a clearinghouse for animal and plant observation data in Montana. These data were then filtered to ensure spatial and temporal accuracy and to reduce spatial autocorrelation (summarized in Table 1). The spatial extent of this model was limited to the presumed geographic range of the species, by season when applicable, in order to accurately assess potentially available habitat.

We then used these data and 44 statewide biotic and abiotic environmental layers at a 90×90-meter pixel scale (Table 2) to construct the model using a maximum entropy algorithm employed in the modeling program Maxent (Phillips et al. 2006, Phillips et al. 2017). Entropy maximization modeling functions by calculating constraint distributions and then applies those constraints to the environmental layers to estimate a predicted suitable habitat distribution. The mean and variance of the environmental layer values (environmental variables) at the training data locations are used to estimate the constraint distributions. Maxent requires that the final predicted distribution fulfills these constraints. Maxent avoids overfitting models to the training data by “regularizing” or relaxing the constraints so that modeled distributions only have to be close to, rather than exactly equal to, the constraint distributions (Elith et al. 2011). The default regularization multiplier of 1.0 was used since species-specific tuning was impractical given the diversity and volume of species modeled in this effort (Merow et al. 2013, Radosavljevic and Anderson 2014). Additionally, we did not use hinge or threshold features at any sample size to minimize potential overfitting by overly complex models (Syfert et al. 2013, De Marco and Nóberga 2018). The Maxent algorithm can successfully train models even when collinearity exists between environmental variables and the practices of removing collinear variables and/or reducing variables results in limited improvement in Maxent model performance (De Marco and Nóberga 2018, Feng et al. 2019); neither method was employed here.

Maxent fits a model by assuming the predicted distribution is uniform in geographic space and moves away from this distribution only to the extent that it is forced to by the constraints of the training data. To do this, Maxent successively modifies the coefficients for each environmental variable via random walk, accepting the modified coefficient if it increases the gain. Gain is a measure of the closeness of the model concentration around the presence samples that is similar to goodness of fit in generalized linear models. The random walk of coefficients continues until either the increase in the gain falls below a set convergence threshold (0.00001) or a set maximum number of iterations are performed (50,000). The gain value at the end of a model run indicates the likelihood of suitability of the presence samples relative to the likelihood for random background points.

We employed a k-folds cross validation methodology, in this case using ten folds for model training and validation (Elith et al. 2011). Each fold consists of 90% of the data designated for training and 10% of the data reserved for testing. Each record is used for training nine times and testing once. Ten models are estimated and averaged to produce the final model presented here.

Model Outputs and Evaluation

The overall gain associated with individual environmental variables (Table 3) can be used as a measure of the relative importance of each variable (Merow et al. 2013). However, the importance of individual environmental variables should be interpreted with caution due to collinearity between variables. The jackknife assessment of contribution by individual environmental variables to training gain (Figure 1) may be more useful in interpreting the relative importance of individual variables. The response curves for the top four contributing environmental variables are shown for reference (Figure 2). These response curves should also be interpreted cautiously because the observation data used to train the models was not gathered under a probabilistic sampling scheme. If enough observations were available to train and evaluate the model, thresholds are estimated for low, moderate, and optimal habitat suitability; details of this process are presented in Table 4 and Figure 3.

The initial model output is a spatial dataset of continuous logistic values that ranges from 0-1 with lower values representing areas predicted to be less suitable habitat and higher values representing areas predicted to be more suitable habitat (Figures 4 & 5). The standard deviation in the model output across the averaged models is also calculated and plotted as a map to examine spatial variance of model output (Figure 6). The continuous output is reclassified into suitability classes and aggregated within 259-hectare hexagons (Figures 7-9).

In addition to the map of spatial variance in model output, we also evaluated the output of the Maxent model with absolute validation index (AVI) (Hirzel et al. 2006) and deviance (Phillips and Dudik 2008). These metrics are described below in the results (Table 5). True skill statistic (TSS) (Allouche et al. 2006), symmetric extremal dependence index (SEDI) (Wunderlich et al. 2019), and Area Under the Curve (AUC) values are also displayed for reference but are not used for evaluation (Lobo et al. 2008). Finally, a deviance value was calculated for each test data observation as a measure of how well model output matched what the model predicted for the location of test observations and this was plotted with larger symbols indicating larger deviance (see Figure 5). In practice, we have found large deviance values to be associated with records that are incorrectly or imprecisely mapped, problematic areas in underlying environmental layers, regions where species have few observations outside of the core portion of their range, or insufficient models with poor performance.

Table 1: Model Data Selection Criteria and Summary

Location Data Source	Montana Natural Heritage Program Databases
Total Number of Records	901
Location Data Selection Rule 1 – Valid and Accurate Records	Records with <= 1600 meters of locational uncertainty
Number of Locations Meeting Selection Rule 1	461
Location Data Selection Rule 2 – Spatially Unique Records	No overlap in locations within 1600 meters in order to avoid spatial autocorrelation
Observation Records used in Model (Locations Meeting Selection Rules 1 & 2)	272
Season Modeled	Year-round
Number of Model Background Locations[a]	23,991

[a] Background locations are chosen at random and in proportion to the percent of the state covered by a species' geographic range, with a maximum of 60,000 locations. Although these locations only represent ~0.1% of the pixels in any modeled area, this level of sampling is sufficient to estimated distributions of environmental conditions present (Phillips and Dudik 2008).

Table 2: Environmental Layers and Corresponding Variables[a]

Layer Name	Variable		Layer Name	Variable
LC_AgDry_97	Developed - Dry Agriculture		NED_AspectEW	Aspect (East-West)
LC_AgIrr_97	Developed - Irrigated Lands		NED_AspectNS	Aspect (North-South)
LC_Alpine_97	Alpine		NED_Elevation	Elevation
LC_Barren_97	Sparse and Barren		NED_Ruggedness	Ruggedness
LC_Developed_97	Developed - All Other		NED_Slope	Slope
LC_ForestBurn_97	Forest - Burned		NED_SRISummer	Summer Solar Radiation
LC_ForestConif_97	Forest - Conifer		NED_SRIWinter	Winter Solar Radiation
LC_ForestDecid_97	Forest - Deciduous		NED_TPI	Topographic Position Index
LC_ForestHarv_97	Forest - Harvested		NHD_Dist2WaterEdge	Distance to Water Edge
LC_ForestInsct_97	Forest - Insect Killed		NHP_AnthroInfl	Anthropogenic Influence
LC_Grassland_97	Grasslands		NRCS_FrostFreeDays	Frost Free Days
LC_IntroVeg_97	Introduced Vegetation		NRCS_REAP	Relative Effective Annual Precipitation
LC_ShrubBurn_97	Shrublands - Burned		PRISM_Precipitation	Annual Precipitation
LC_Shrubland_97	Shrublands		PRISM_WinPrecip	Percent Winter Precipitation
LC_WetRip_97	Wetland & Riparian		SoilGrid_BD	Bulk Density
LC_Dist2Forest	Distance to Forest		SoilGrid_Clay	Percent Clay
MCO_DegreeDays	Degree Days		SoilGrid_EC	Electric Conductivity
MCO_MaxSumTemp	Maximum Summer Temp		SoilGrid_OrgC	Organic Carbon
MCO_MinWinTemp	Minimum Winter Temp		SoilGrid_pH	Soil pH
MCO_NDVI	Normalized Difference Vegetation Index		SoilGrid_Sand	Percent Sand
MTGeol_Dist2Alluv	Distance to Alluvium		SoilGrid_Silt	Percent Silt
MTGeol_Dist2C03	Distance to Carbonate Rock		SoilGrid_TotN	Total Nitrogen

[a] Additional details and sources available in Appendix.

Inductive Model Results

Table 3: Top Ten Contributing Environmental Variables to Model Fit

Variable	Percent Contribution[a]	Variable	Percent Contribution[a]
Forest - Conifer	12.8%	NDVI	3.7%
Developed - All Other	10.7%	Slope	3.5%
Distance to Carbonate Rock	7.9%	Annual Precipitation	3.5%
% Winter Precipitation	6.5%	Wetland Riparian	3.3%
Grasslands	3.7%	Degree Days	3.3%

[a] Relative contributions of the variables to the model based on changes in fit (gain) during iterations of the training algorithm.

Table 4: Habitat Suitability Thresholds and Areas of Suitable Habitat

Measure	Value
Optimal Logistic Threshold[a]	0.722
Moderate Logistic Threshold[b]	**0.225**
Low Logistic Threshold[c]	0.050
Area of predicted optimal habitat within modeled range	1,814.8 km^2
Area of predicted moderate suitability habitat within modeled range	**22,981.6 km^2**
Area of predicted low suitability habitat within modeled range	48,601.0 km^2
Total area of predicted suitable habitat within modeled range	73,397.3 km^2
Area of entire modeled range (percent of Montana)	152,154.5 km^2 (40.0%)

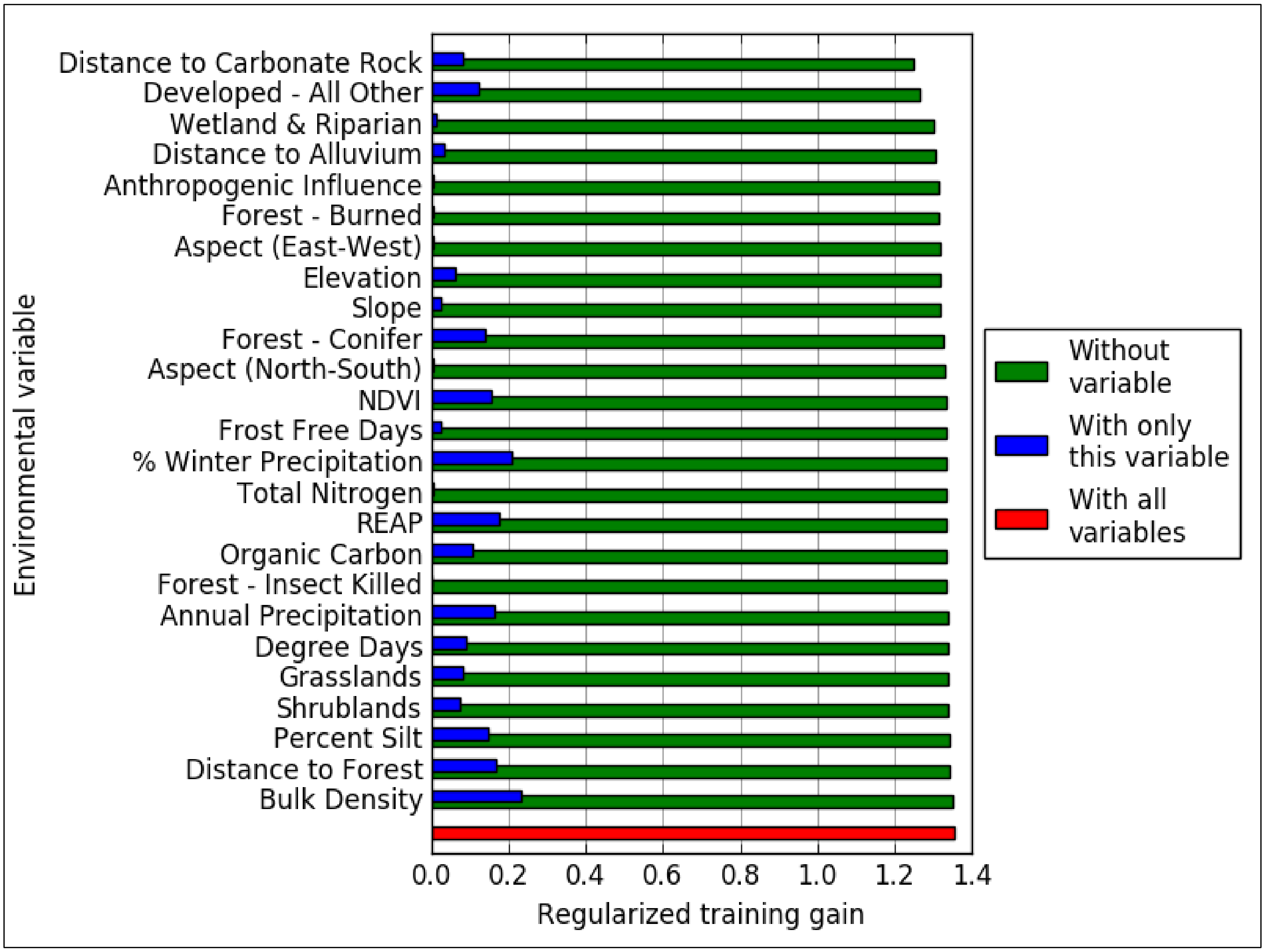
[a] The logistic threshold where the percentage of test observations above the threshold is 10 or more times higher than would be expected if the observations were randomly distributed across logistic value classes (Hirzel et al. 2006) (see Figure 3). When sample sizes are small, it may be undetermined.
[b] **This is the cutoff recommended for use in management decisions.** The logistic threshold value where the percentage of test observations above the threshold is greater then what would be expected if the observations were randomly distributed across logistic value classes - in other words, when the modeled habitat is used more often than expected from its proportional availability on the landscape (Hirzel et al. 2006). When sample sizes are small, it may be undetermined.
[c] The logistic threshold between unsuitable and low suitability as determined by Maxent which balances data omission error with minimizing predicted suitable area (Phillips et al. 2017). This is a conservative threshold that should encompass nearly all potentially suitable habitat for a species. In practice, habitat with low suitability may represent landscapes of marginal or discontinuous habitat where suitable habitat patches of various sizes are isolated by unsuitable habitat.

Table 5: Evaluation Metrics

Metric	Value
Low AVI[a]	86.8%
Moderate AVI[a]	61.4%
Optimal AVI[a]	23.5%
Average Testing Deviance ($\bar{x} \pm sd$)[b]	2.996 ± 2.999
TSS (Sensitivity + Specificity - 1)[c]	0.4508 (0.6140 + 0.8368 -1)
SEDI[c]	0.6117
Training AUC[d]	0.917
Test AUC[e]	0.814

[a] Absolute Validation Index: The proportion of test locations that fall above the low, moderate, or optimal logistic threshold (see Table 4).
[b] A measure of how well model output matched the location of test observations. In theory, everywhere a test location was located, the logistic value should have been 1.0. The deviance value for each test location is calculated as -2 times the natural log of the associated logistic output value. For example, the equivalent deviance values for the low, moderate and optimal logistic thresholds of this model would be 6.008, 2.982 and 0.652, respectively. Deviances for individual test locations are plotted in Figure 5. Average Testing Deviance less than the Moderate Deviance typically indicates good model performance.
[c] Ranges from -1 to 1, with a random or null model performing at a value of 0 and values 0.65 indicating moderate performance (0.8 generally good performance). The moderate threshold (0.225) is used to develop the confusion matrix for Sensitivity and Specificity metrics. Note that Specificity is calculated based on pseudo-absences (not true absences) and may be biased when large areas are modeled as moderate or optimal suitable habitat.
[d] The area under a curve obtained by plotting the true positive rate against 1 minus the false positive rate for model training observations (averaged over 10 folds). Values range from 0 to 1 with a random or null model performing at a value of 0.5.
[e] The same metric described in [d], but calculated for test observations.

Figure 1. Jackknife assessment of contribution by individual environmental variables to training gain. Variables are ordered by reduction in gain without that variable (green), from greatest to least impact. Only the 25 most influential variables[a] are shown.



[a] Interpretation of individual environmental variables should be approached cautiously and may be inappropriate due to covariance between variables.

Figure 2. Response curves for the top four contributing environmental variables, mean value in red, +/- one standard deviation in blue. Response curves for additional environmental variables are available upon request.

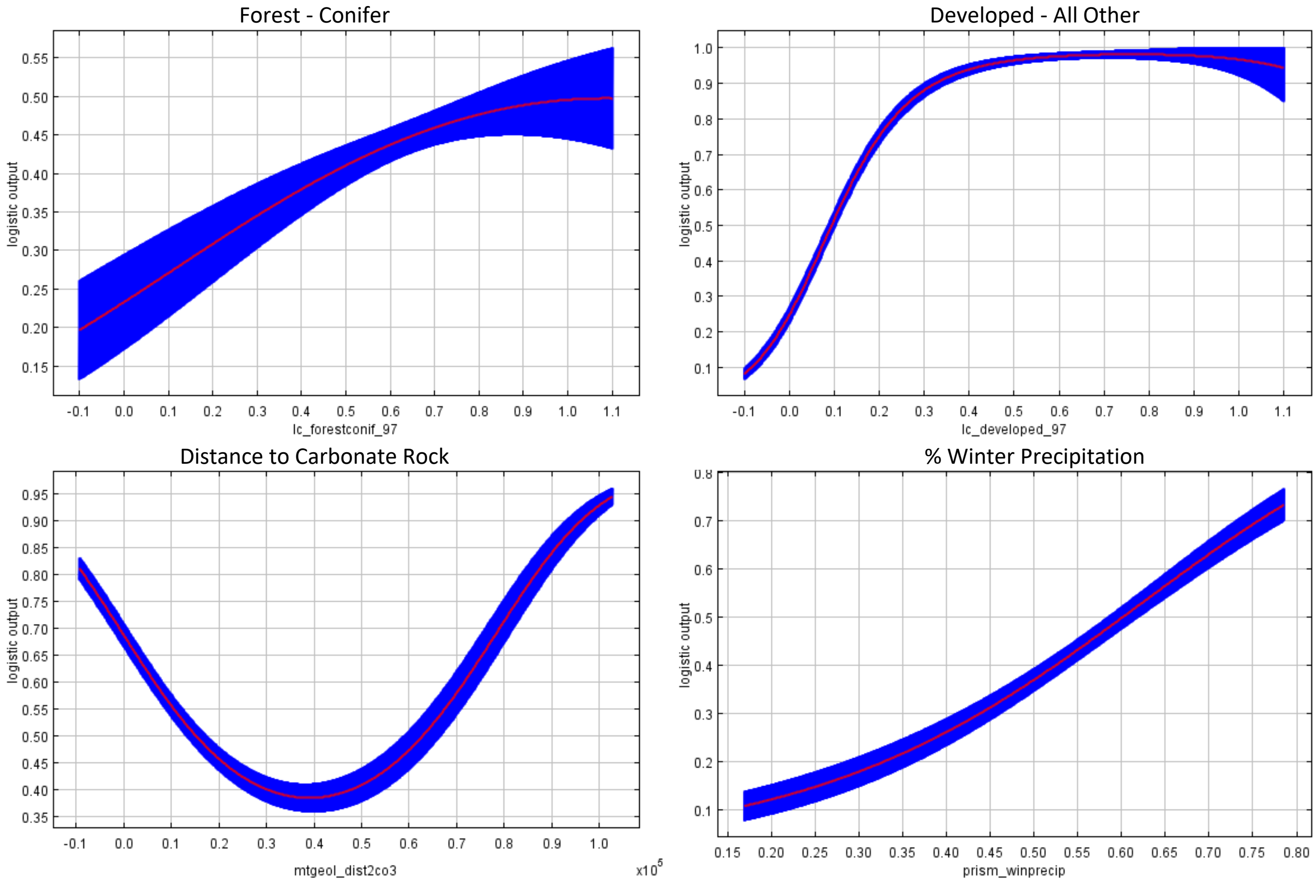
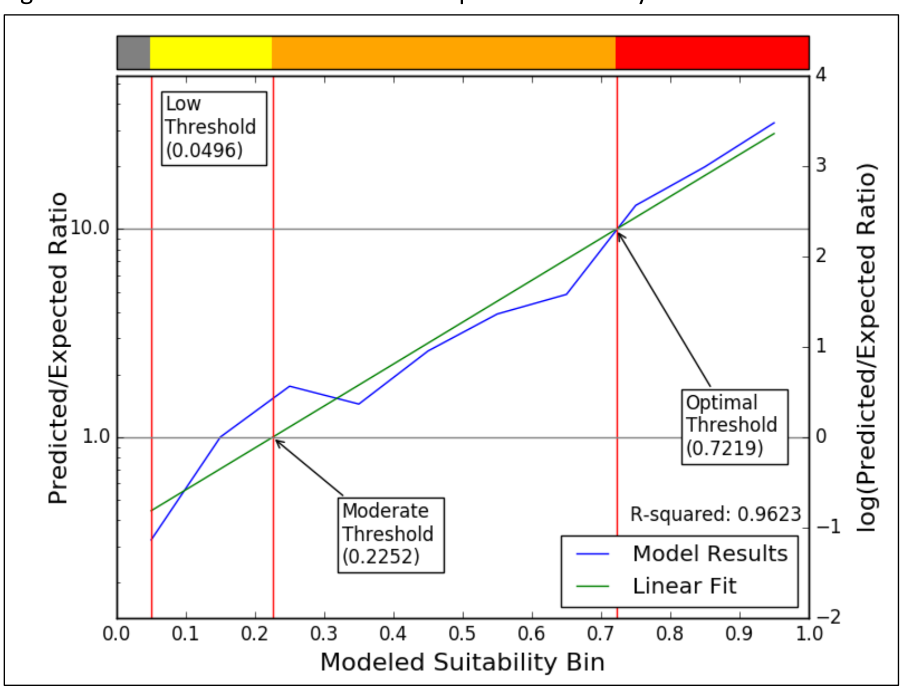


Figure 3. Thresholds for moderate and optimal suitability classes as determined by linear fit.



Inductive Model Map Outputs

Figure 4. Continuous habitat suitability model logistic output (90-meter pixels); white area is not modeled.

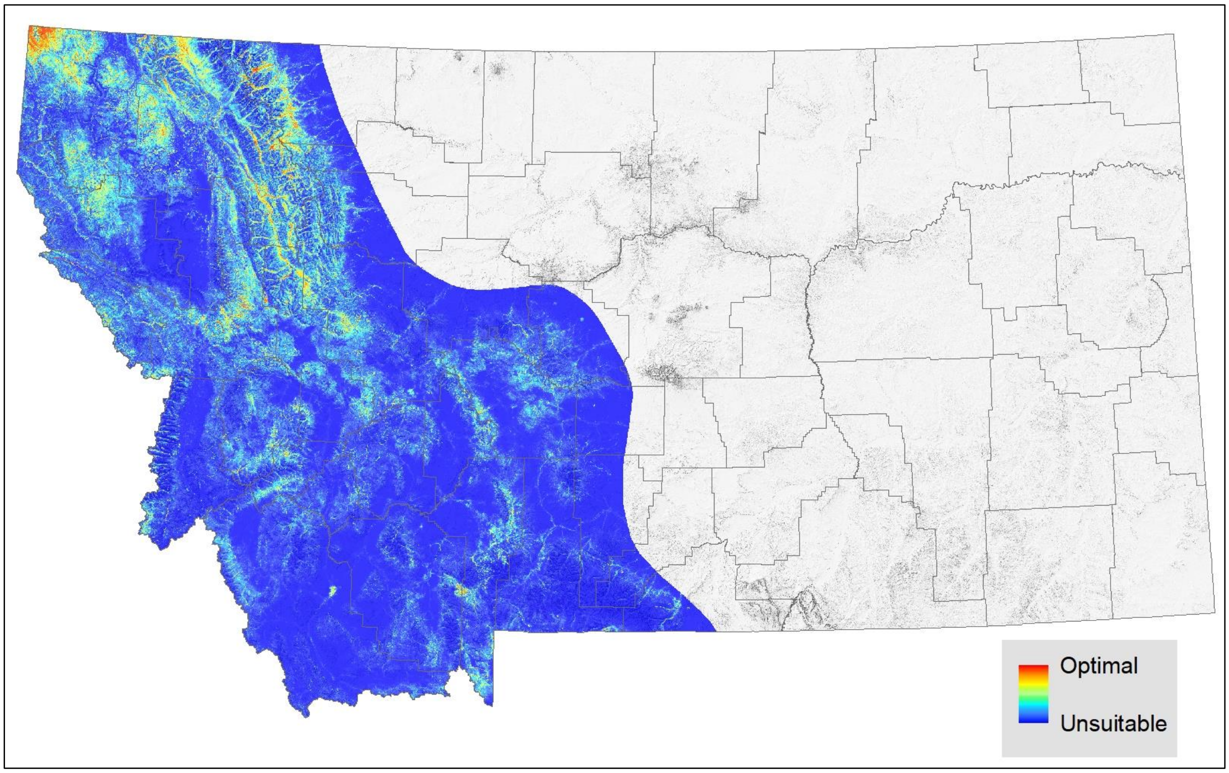


Figure 5. Continuous habitat suitability model output with relative deviance for each observation. Low deviance points fall within optimal or moderate habitat; high deviance points are in generally unsuitable habitat.

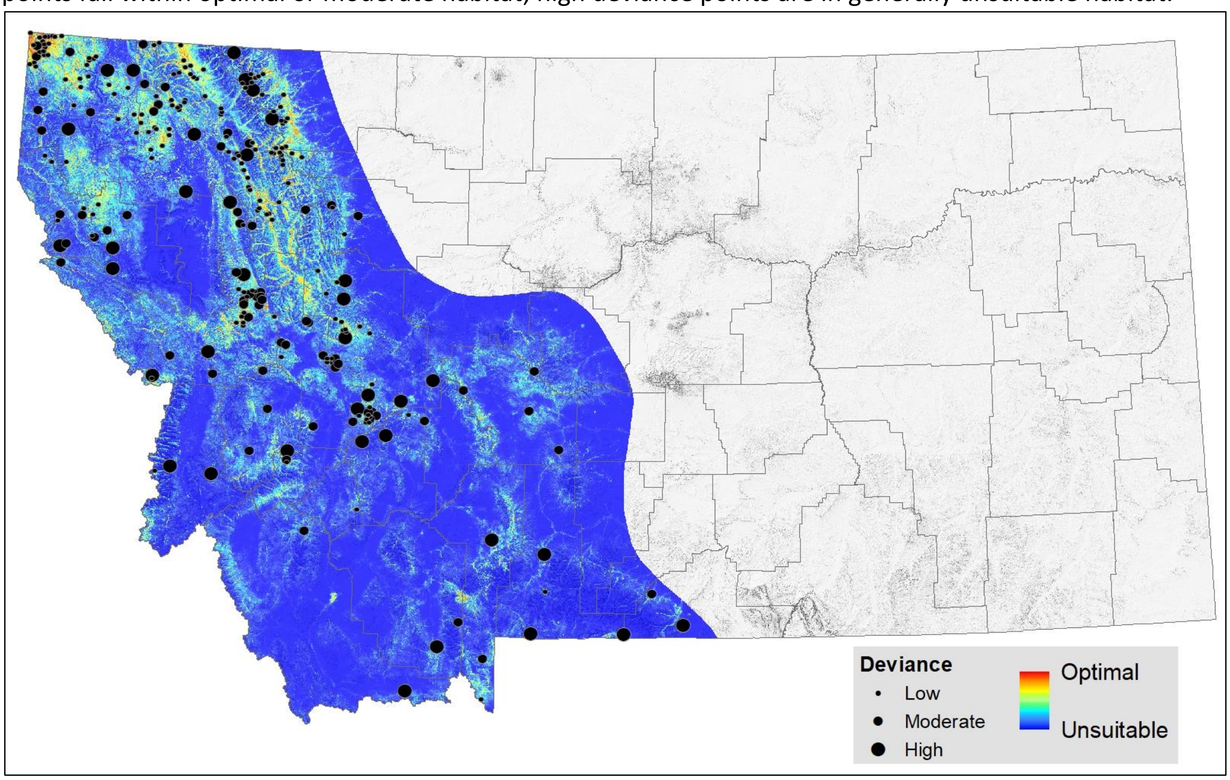


Figure 6. Standard deviation in the model output across the averaged models. Lower deviance (a solid blue map) indicates a better fitting model with lower variability between model iterations.

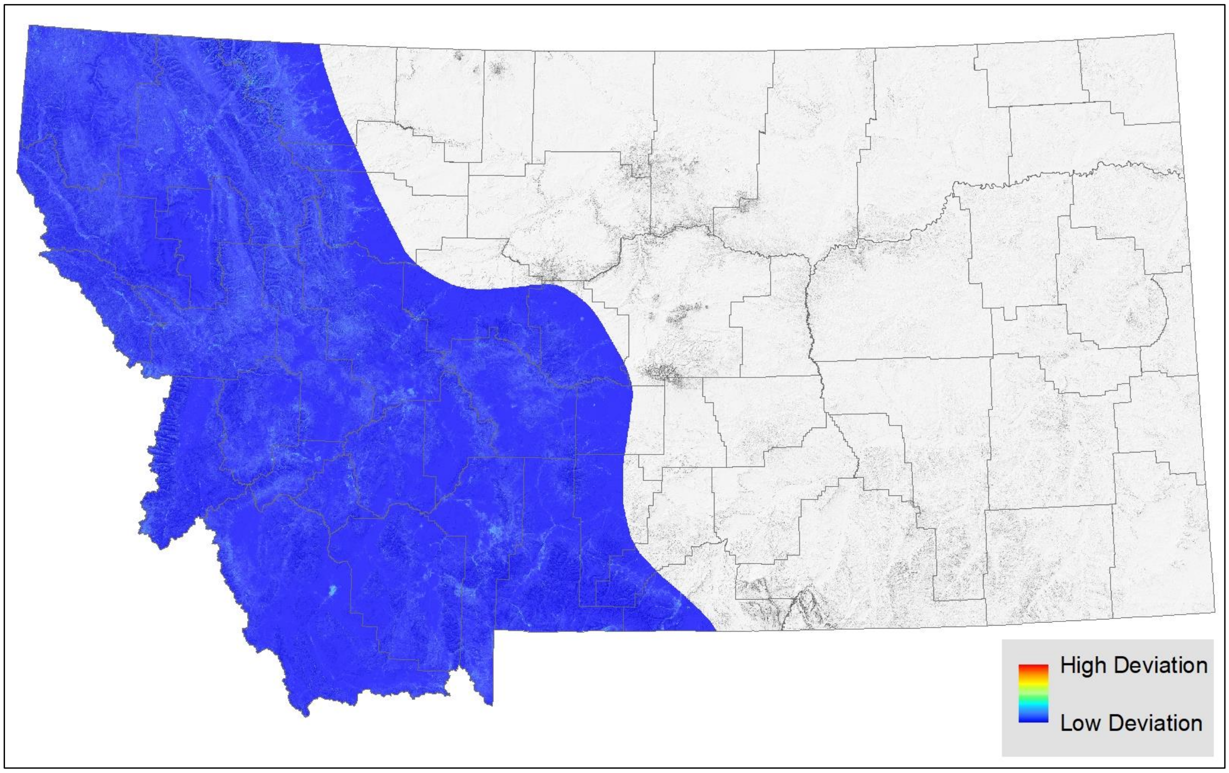


Figure 7. Model output for 90-meter pixels classified into habitat suitability classes.

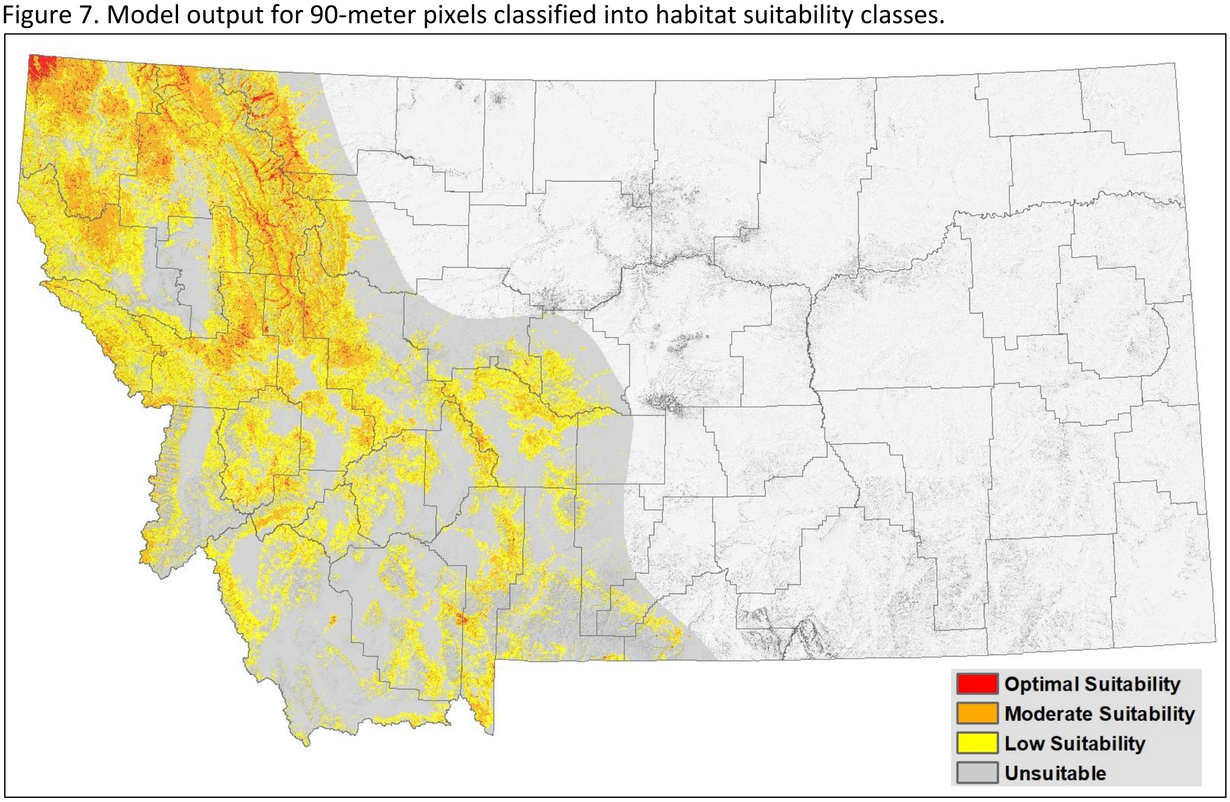


Figure 8. Model output classified into habitat suitability classes and aggregated into hexagons at a scale of 259 hectares per hexagon. This is the finest scale suggested for management decisions and survey planning.

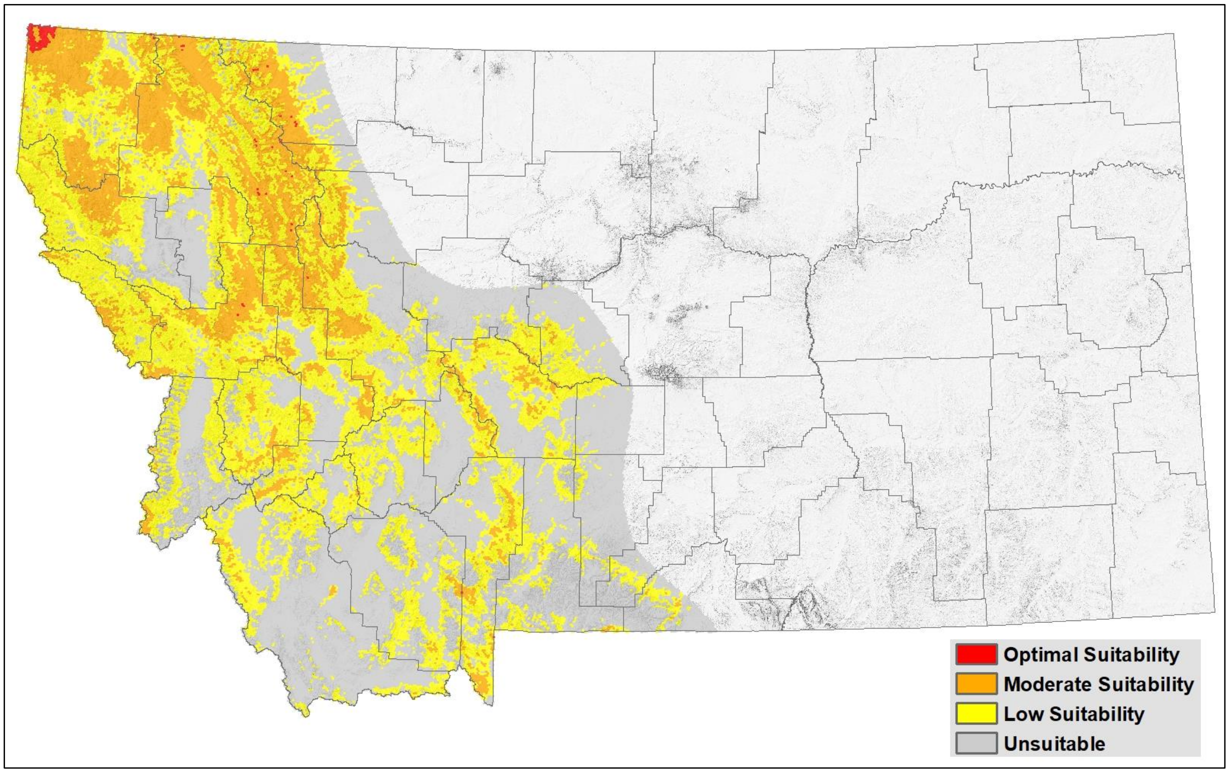
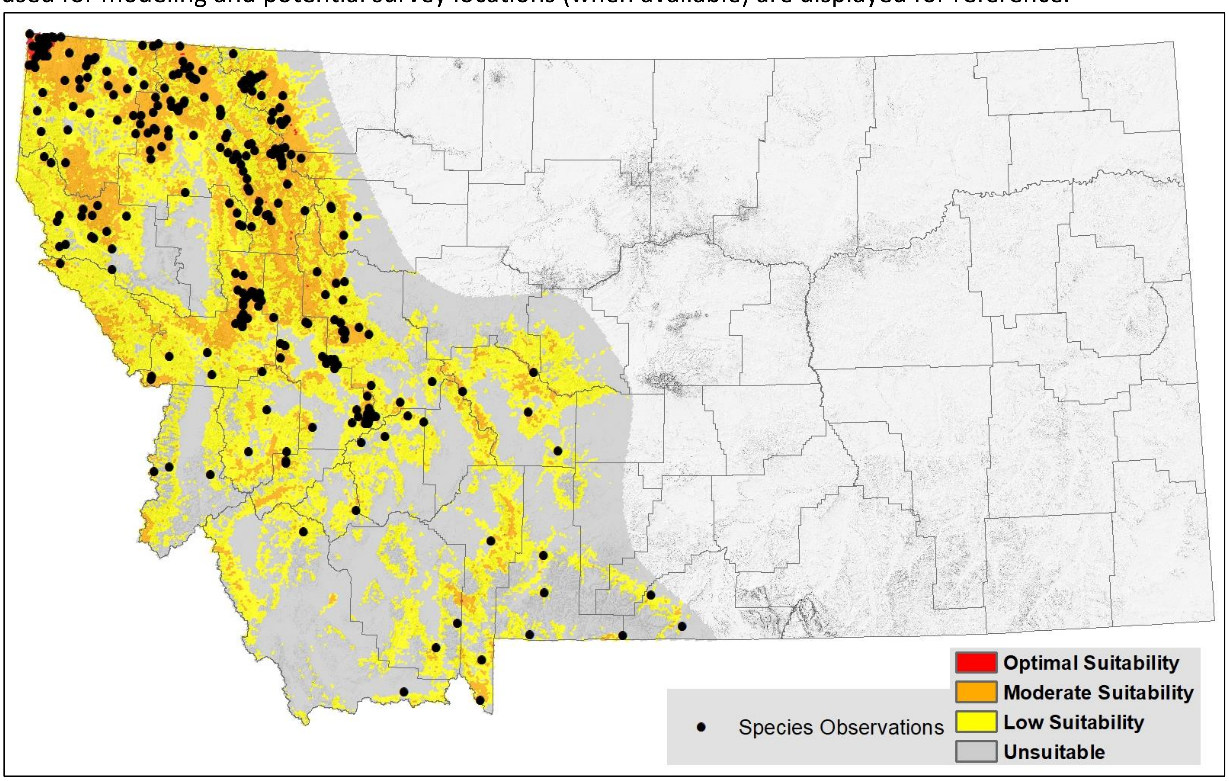


Figure 9. Model output classified into habitat suitability classes and aggregated into hexagons; observations used for modeling and potential survey locations (when available) are displayed for reference.



Deductive Modeling

Model Limitations and Suggested Uses

Species associations with ecological systems should be used to generate lists of potential species that may occupy broader landscapes for the purposes of landscape-level planning. Users of this information should be aware that the land cover data used to generate species associations was only intended to be used at broader landscape scales. Land cover mapping accuracy is particularly problematic when the systems occur as small patches or where the land cover types have been altered over the past decade. Thus, particular caution should be used when using the associations in assessments of smaller areas (e.g. less than one quarter of a public land survey system (PLSS) section, 64 hectares). Model outputs should not be used in place of on-the-ground surveys for species, and wildlife and land management agency biologists should be consulted about the value of using these associations to guide habitat management decisions for regional planning efforts or local projects. See Suggested Contacts for State and Federal Natural Resource Agencies attached to this document. Data used in model evaluation often have locational uncertainties that exceed the 30-meter pixel size of the land cover dataset, potentially intersecting incorrect ecological systems. Additionally, the habitat within a pixel may have been assigned to the wrong ecological system or the habitat may have been modified. As a result, evaluation metrics may be skewed low, especially for species occupying ecotones or patchy ecological systems. Finally, users should note that ecological systems associated with a species are only mapped within the range of that species, although portions of that ecological system may occur elsewhere.

Deductive Model Methods

Modeling Process

This model is based on the 2017 statewide land cover classifications at 30×30-meter raster pixels (Montana Land Use/Land Cover Dataset). Level 3 ecological systems (90) were used for this model and these data were originally mapped at a scale of 1:100,000. In general, species were associated as using an ecological system if structural characteristics of used habitat documented in the literature were present in the ecological system or large numbers of point observations were associated with the ecological system. However, species were not associated with an ecological system if there was no support in the literature for use of structural characteristics in an ecological system, even if point observations were associated with that system. Species were either commonly associated, occasionally associated, or not associated with each ecological system. This assignment was based on the degree to which the structural characteristics of an ecological system matched the preferred structural habitat characteristics for each species in the literature. The percentage of observations associated with each ecological system relative to the percent of Montana covered by each ecological system was also used to guide assignments of habitat quality. Associations are shown in Table 6.

Model Outputs and Evaluation

The model output is a spatial dataset of categorical habitat suitability based on ecological system associations (commonly or occasionally associated) within the species' presumed range (Figure 10) and resulting tabular estimates of the area of commonly and occasionally associated habitat (Table 7). We evaluated this model output based on known or potential distribution and habitat use in Montana and absolute validation indices (AVI) (Hirzel et al. 2006) using presence-only data (Table 8).

Deductive Model Results

Table 6: Ecological Systems Associated with Canada Lynx

Ecological System	Code	Association	Count[a]
Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	4232	Common	28
Rocky Mountain Lodgepole Pine Forest	4237	Common	28
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	4242	Common	24
Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	4243	Common	21
Rocky Mountain Mesic Montane Mixed Conifer Forest	4234	Common	18
Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland	9155	Common	18
Rocky Mountain Montane Douglas-fir Forest and Woodland	4266	Common	9
Rocky Mountain Subalpine Deciduous Shrubland	5326	Common	7
Insect-Killed Forest	8700	Common	4
Harvested forest-tree regeneration	8601	Common	3
Harvested forest-shrub regeneration	8602	Common	3
Rocky Mountain Poor Site Lodgepole Pine Forest	4267	Common	0
Rocky Mountain Subalpine-Montane Riparian Woodland	9171	Common	0
Rocky Mountain Subalpine-Montane Riparian Shrubland	9187	Common	0
Recently burned forest	8501	Occasional	15
Rocky Mountain Ponderosa Pine Woodland and Savanna	4240	Occasional	5
Post-Fire Recovery	8505	Occasional	5
Aspen Forest and Woodland	4104	Occasional	3
Rocky Mountain Montane-Foothill Deciduous Shrubland	5312	Occasional	2
Rocky Mountain Subalpine-Montane Mesic Meadow	7118	Occasional	2
Aspen and Mixed Conifer Forest	4302	Occasional	1
Rocky Mountain Subalpine Woodland and Parkland	4233	Occasional	0
Rocky Mountain Conifer Swamp	9111	Occasional	0
Rocky Mountain Wooded Vernal Pool	9162	Occasional	0

[a] A count of the observation records intersecting each ecological system, based on the 272 observation records used in the inductive model (see Table 1). This may be zero if the number of observations is low or if the ecological system is patchily distributed.

Table 7: Area of Range and Ecological System (ES) Classes

Measure	Value
Area of entire modeled range (percent of Montana)	152,154.5 km2 (40.0%)
Area of Commonly and Occasionally Associated ES	81,898.0 km^2
Area of Commonly Associated ES	62,193.0 km^2
Area of Occasionally Associated ES	19,705.0 km^2

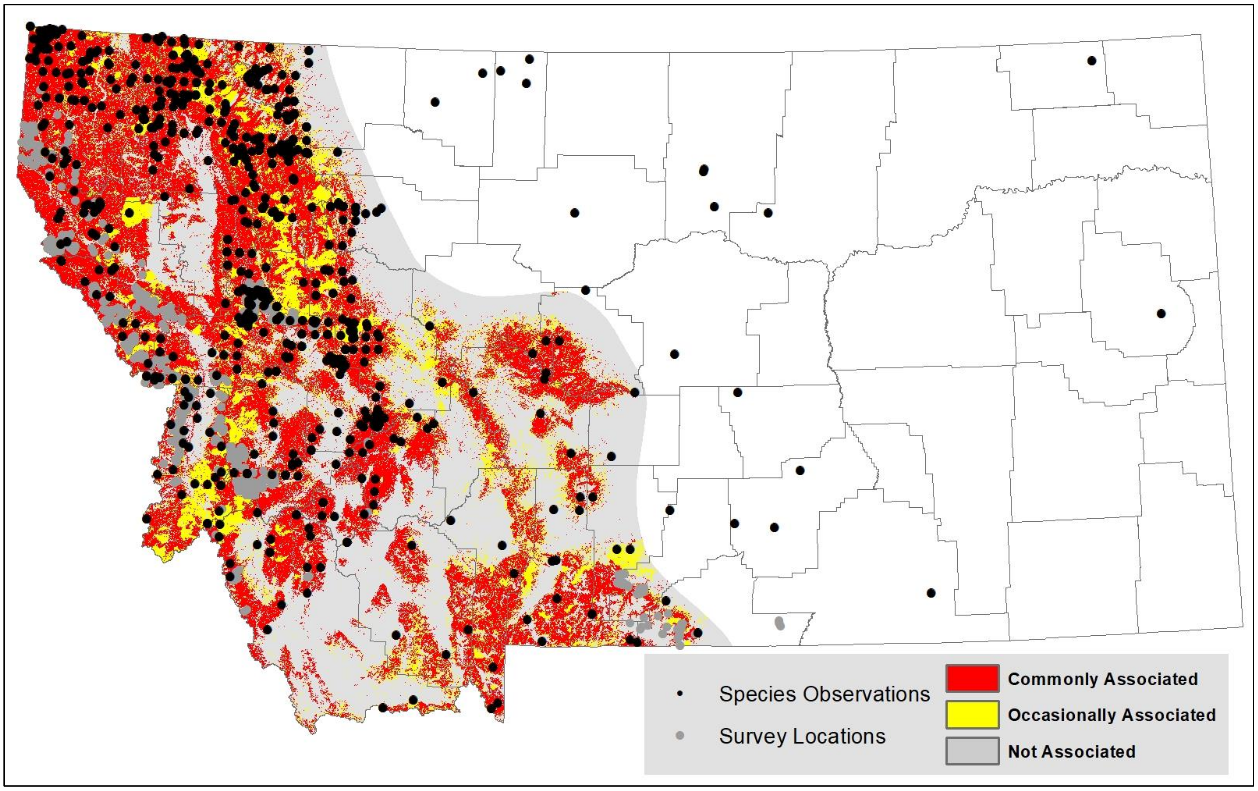
Table 8: Evaluation Metrics

Metric	Value
Commonly and Occasionally Associated ES AVI[a]	72.1%
Commonly Associated ES AVI[a]	59.9%
Occasionally Associated ES AVI[a]	12.1%

[a] Absolute Validation Index: The proportion of test locations that fall within the class(es).

Deductive Model Map Output

Figure 10. Deductive model output classified into habitat associations.



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Appendix

Table A. Detailed Descriptions of Environmental Layers

Layer Name	Class	Variable	Original Scale	Description
LC_AgDry_97	Landcover	Developed - Dry Agriculture	30m	Proportion (0-1) of cells classed as Agriculture without Irrigation within a 97-cell neighborhood (~150m radius).
LC_AgIrr_97	Landcover	Developed - Irrigated Lands	30m	Proportion (0-1) of cells classed as Agriculture with Irrigation within a 97-cell neighborhood (~150m radius).
LC_Alpine_97	Landcover	Alpine	30m	Proportion (0-1) of cells classed as Alpine cover types within a 97-cell neighborhood (~150m radius).
LC_Barren_97	Landcover	Sparse and Barren	30m	Proportion (0-1) of cells classed as Sparse or Barren within a 97-cell neighborhood (~150m radius).
LC_Developed_97	Landcover	Developed - All Other	30m	Proportion (0-1) of cells classed as Developed (e.g. towns, roads, mines) within a 97-cell neighborhood (~150m radius).
LC_ForestBurn_97	Landcover	Forest - Burned	30m	Proportion (0-1) of cells classed as Burned Forest within a 97-cell neighborhood (~150m radius).
LC_ForestConif_97	Landcover	Forest - Conifer	30m	Proportion (0-1) of cells classed as Conifer Forest within a 97-cell neighborhood (~150m radius).
LC_ForestDecid_97	Landcover	Forest - Deciduous	30m	Proportion (0-1) of cells classed as Deciduous Forest within a 97-cell neighborhood (~150m radius).
LC_ForestHarv_97	Landcover	Forest - Harvested	30m	Proportion (0-1) of cells classed as Harvest Forest within a 97-cell neighborhood (~150m radius).
LC_ForestInsct_97	Landcover	Forest - Insect Killed	30m	Proportion (0-1) of cells classed as Insect Killed Forest within a 97-cell neighborhood (~150m radius).
LC_Grassland_97	Landcover	Grasslands	30m	Proportion (0-1) of cells classed as Grassland cover types within a 97-cell neighborhood (~150m radius).
LC_IntroVeg_97	Landcover	Introduced Vegetation	30m	Proportion (0-1) of cells classed as Introduced Vegetation within a 97-cell neighborhood (~150m radius).
LC_ShrubBurn_97	Landcover	Shrublands - Burned	30m	Proportion (0-1) of cells classed as Burned Shrubland within a 97-cell neighborhood (~150m radius).
LC_Shrubland_97	Landcover	Shrublands	30m	Proportion (0-1) of cells classed as Shrubland cover types within a 97-cell neighborhood (~150m radius).
LC_WetRip_97	Landcover	Wetland Riparian	30m	Proportion (0-1) of cells classed as Wetland or Riparian within a 97-cell neighborhood (~150m radius).
LC_Dist2Forest	Landcover	Distance to Forest	30m	Distance in meters to any forest cover type, after consolidating to patches 900m^2.
MCO_DegreeDays	Climate	Degree Days	800m	Average annual total of degree days (°F) above 32°F for 1981-2010.
MCO_MaxSumTemp	Climate	Maximum Summer Temp	800m	Average maximum temperature (°C) in July for 1981-2010.
MCO_MinWinTemp	Climate	Minimum Winter Temp	800m	Average minimum temperature (°C) in January for 1981-2010.
MCO_NDVI	Climate	Normalized Difference Vegetation Index	925m	Normalized Difference Vegetation as a measure of yearly mean greenness from the MODIS Terra satellite, 2000-2014.
MTGeol_Dist2Alluv	Geology	Distance to Alluvium	vector	Distance in meters to alluvial, glacial, or other unconsolidated surface geology types.
MTGeol_Dist2C03	Geology	Distance to Carbonate Rock	vector	Distance in meters to geological units with major components of either limestone or dolostone.

Layer Name	Class	Variable	Original Scale	Description
NED_AspectEW	Landform	Aspect (East-West)	≈10m	Aspect of slopes, ranging from 1 (east) to -1 (west).
NED_AspectNS	Landform	Aspect (North-South)	≈10m	Aspect of slopes, ranging from 1 (north) to -1 (south).
NED_Elevation	Landform	Elevation	≈10m	Elevation in meters above mean sea level.
NED_Ruggedness	Landform	Ruggedness	≈10m	Vector ruggedness measure from 0 (flat) to 1 (rugged), based on 5-cell neighborhood.
NED_Slope	Landform	Slope	≈10m	Percent slope (x100) of landscape.
NED_SRISummer	Landform	Summer Solar Radiation	≈10m	Solar radiation (WH/m^2) for the day of the summer solstice.
NED_SRIWinter	Landform	Winter Solar Radiation	≈10m	Solar radiation (WH/m^2) for the day of the winter solstice.
NED_TPI	Landform	Topographic Position Index	≈10m	Relative topographic position, based on a 5- to 10-cell radius envelope; positive values represent ridges, negative values are valleys/drainages.
NHD_Dist2WaterEdge	Hydrography	Distance to Water Edge	vector	Distance in meters to edges of lakes, reservoirs, streams, or rivers, as mapped in high resolution NHD.
NHP_AnthroInfl	Human	Anthropogenic Influence	vector	An index of human impact on landscape, based on structure density and road use.
NRCS_FrostFreeDays	Climate	Frost Free Days	30m	Estimated number of days without frost: daily minimum temperature 0°C based on a 5 in 10 year probability.
NRCS_REAP	Climate	Relative Effective Annual Precipitation	10m	REAP, an adjusted annual precipitation estimate enhanced with DEM attributes (cm) over 30 years.
PRISM_Precipitation	Climate	Annual Precipitation	≈800m	Average annual precipitation (mm) for 1981-2010.
PRISM_WinPrecip	Climate	Percent Winter Precipitation	≈800m	Average percent (0 to 1) of the total annual precipitation that occurs during winter (Nov-Apr) for 1981-2010.
SoilGrid_BD	Soils	Bulk Density	100m	Bulk density (inversely related to pore space), g/cm^3 (0-5cm depth).
SoilGrid_Clay	Soils	Percent Clay	100m	Percent Clay in soil (0-5cm depth).
SoilGrid_EC	Soils	Electric Conductivity	100m	Electric conductivity (measure of salinity) of soil, dS/m (x100) (0-5cm depth).
SoilGrid_OrgC	Soils	Organic Carbon	100m	Soil organic carbon, % weight (x1000) (0-5cm depth).
SoilGrid_pH	Soils	Soil pH	100m	Soil pH (0-5cm depth).
SoilGrid_Sand	Soils	Percent Sand	100m	Percent Sand in soil (0-5cm depth).
SoilGrid_Silt	Soils	Percent Silt	100m	Percent Silt in soil (0-5cm depth); derived, based on Sand and Clay percentages.
SoilGrid_TotN	Soils	Total Nitrogen	100m	Total nitrogen in soil, % weight (x1000) (0-5cm depth).

Data Sources/Environmental Layer Name Prefix Key

LC - Montana Land Use/Land Cover Dataset (MSDI)

MCO - Montana Climate Office (MSDI)

MTGeol - Montana Bureau of Mines Geology (MSDI)

NED - National Elevation Dataset (MSDI)

NHD - National Hydrological Dataset (MSDI)

NHP - NHP Data (unpublished)

NRCS - Natural Resources Conservation Service (MSDI)

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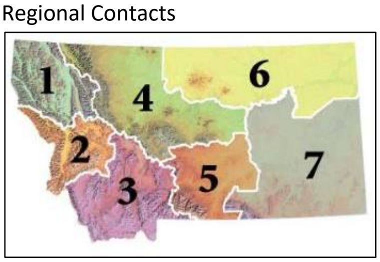
For your convenience, we have compiled a list of relevant agency contacts and links below; check our website for updates.

Montana Fish, Wildlife, and Parks

Fish Species	Zachary Shattuck zshattuck@mt.gov (406) 444-1231 or Eric Roberts eroberts@mt.gov (406) 444-5334
American Bison Black-footed Ferret Black-tailed Prairie Dog Bald Eagle Golden Eagle Common Loon Least Tern Piping Plover Whooping Crane	Kristina Smucker ksmucker@mt.gov (406) 444-5209
Grizzly Bear Greater Sage Grouse Trumpeter Swan Big Game Upland Game Birds Furbearers	Brian Wakeling Brian.Wakeling@mt.gov (406) 444-3940
Managed Terrestrial Game and Nongame Animal Data	Smith Wells – MFWP Data Analyst smith.wells@mt.gov (406) 444-3759
Fisheries Data	Ryan Alger – MFWP Data Analyst ryan.alger@mt.gov (406) 444-5365
Wildlife and Fisheries Scientific Collector's Permits	https://fwp.mt.gov/buyandapply/commercialwildlifeandscientificpermits/scientific Kammi McClain for Wildlife Kammi.McClain@mt.gov (406) 444-2612 Kim Wedde for Fisheries kim.wedde@mt.gov (406) 444-5594
Fish and Wildlife Recommendations for Subdivision Development	Charlie Sperry CSperry@mt.gov (406) 444-3888 See also: https://fwp.mt.gov/conservation/living-with-wildlife/subdivision-recommendations
Regional Contacts 	Region 1 - Kalispell (406) 752-5501 fwprg12@mt.gov Region 2 - Missoula (406) 542-5500 fwprg22@mt.gov Region 3 - Bozeman (406) 577-7900 fwprg3@mt.gov Region 4 - Great Falls (406) 454-5840 fwprg42@mt.gov Region 5 - Billings (406) 247-2940 fwprg52@mt.gov Region 6 - Glasgow (406) 228-3700 fwprg62@mt.gov Region 7 - Miles City (406) 234-0900 fwprg72@mt.gov

Montana Department of Agriculture

General Contact Information: https://agr.mt.gov/About/Office-Locations/Office-Locations-and-Field-Offices
Noxious Weeds: https://agr.mt.gov/Noxious-Weeds

Montana Department of Environmental Quality

Permitting and Operator Assistance for all Environmental Permits: https://deq.mt.gov/Permitting

Montana Department of Natural Resources and Conservation

Overview of, and contacts for, licenses and permits for state lands, water, and forested lands: http://dnrc.mt.gov/licenses-and-permits

Stream Permitting (310 permits) and an overview of various water and stream related permits (e.g., Stream Protection Act 124, Federal Clean Water Act 404, Federal Rivers and Harbors Act Section 10, Short-term Water Quality Standard for Turbidity 318 Authorization, etc.). http://dnrc.mt.gov/divisions/cardd/conservation-districts/the-310-law

Flood and Fire Resources: http://dnrc.mt.gov/flood-and-fire

Bureau of Land Management

Montana Field Office Contacts:

Billings	(406) 896-5013
Butte	(406) 533-7600
Dillon	(406) 683-8000
Glasgow	(406) 228-3750
Havre	(406) 262-2820
Lewistown	(406) 538-1900
Malta	(406) 654-5100
Miles City	(406) 233-2800
Missoula	(406) 329-3914

United States Army Corps of Engineers

Montana Regulatory Office for federal permits related to construction in water and wetlands
(406) 441-1375 https://www.nwo.usace.army.mil/Missions/Regulatory-Program/Montana/

United States Environmental Protection Agency

Environmental information, notices, permitting, and contacts https://www.epa.gov/mt
Gateway to state resource locators https://www.envcap.org/srl/index.php

United States Fish and Wildlife Service

Information Planning and Conservation (IPAC) website: https://ecos.fws.gov/ipac/
Montana Ecological Services Field Office (406) 449-5225 https://www.fws.gov/montanafieldoffice/

United States Forest Service

Regional Office Contacts – Missoula			
Wildlife Program Leader	Tammy Fletcher	tammy.fletcher2@usda.gov	(406) 329-3086
Wildlife Ecologist	Cara Staab	cara.staab@usda.gov	(406) 329-3677
Fish Program Leader	Scott Spaulding	scott.spaulding@usda.gov	(406) 329-3287
Fish Ecologist	Cameron Thomas	cameron.thomas@usda.gov	(406) 329-3087
TES Program	Lydia Allen	lydia.allen@usda.gov	(406) 329-3558
Interagency Grizzly Bear Coordinator	Scott Jackson	scott.jackson@usda.gov	(406) 329-3664
Acting Regional Botanist	Amanda Hendrix	amanda.hendrix@usda.gov	(651) 447-3016
Regional Vegetation Ecologist	Mary Manning	marry.manning@usda.gov	(406) 329-3304
Invasive Species Program Manager	Michelle Cox	michelle.cox2@usda.gov	(406) 329-3669

Tribal Nations

Assiniboine Gros Ventre Tribes – Fort Belknap Reservation
Assiniboine Sioux Tribes – Fort Peck Reservation
Blackfeet Tribe - Blackfeet Reservation
Chippewa Creek Tribe - Rocky Boy's Reservation
Crow Tribe – Crow Reservation
Little Shell Chippewa Tribe
Northern Cheyenne Tribe – Northern Cheyenne Reservation
Salish Kootenai Tribes - Flathead Reservation

Natural Heritage Programs and Conservation Data Centres in Surrounding States and Provinces

Alberta Conservation Information Management System
British Columbia Conservation Data Centre
Idaho Natural Heritage Program
North Dakota Natural Heritage Program
Saskatchewan Conservation Data Centre
South Dakota Natural Heritage Program
Wyoming Natural Diversity Database

Invasive Species Management Contacts and Information

Aquatic Invasive Species

Montana Fish, Wildlife, and Parks Aquatic Invasive Species staff
Montana Department of Natural Resources and Conservation's Aquatic Invasive Species Grant Program
Montana Invasive Species Council (MISC)
Upper Columbia Conservation Commission (UC3)

Noxious Weeds

Montana Weed Control Association Contacts Webpage
Montana Biological Weed Control Coordination Project
Montana Department of Agriculture - Noxious Weeds
Montana Weed Control Association
Montana Fish, Wildlife, and Parks - Noxious Weeds
Montana State University Integrated Pest Management Extension
Integrated Noxious Weed Management after Wildfires
Fire Management and Invasive Plants

Attachment 2

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ORIGINAL RESEARCH

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Improved prediction of Canada lynx distribution through regional model transferability and data efficiency

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Abstract

The application of species distribution models (SDMs) to areas outside of where a model was created allows informed decisions across large spatial scales, yet transferability remains a challenge in ecological modeling. We examined how regional variation in animal-environment relationships influenced model transferability for Canada lynx (*Lynx canadensis*), with an additional conservation aim of modeling lynx habitat across the northwestern United States. Simultaneously, we explored the effect of sample size from GPS data on SDM model performance and transferability. We used data from three geographically distinct Canada lynx populations in Washington ($n = 17$ individuals), Montana ($n = 66$), and Wyoming ($n = 10$) from 1996 to 2015. We assessed regional variation in lynx-environment relationships between these three populations using principal components analysis (PCA). We used ensemble modeling to develop SDMs for each population and all populations combined and assessed model prediction and transferability for each model scenario using withheld data and an extensive independent dataset ($n = 650$). Finally, we examined GPS data efficiency by testing models created with sample sizes of 5%–100% of the original datasets. PCA results indicated some differences in environmental characteristics between populations; models created from individual populations showed differential transferability based on the populations' similarity in PCA space. Despite population differences, a single model created from all populations performed as well, or better, than each individual population. Model performance was mostly insensitive to GPS sample size, with a plateau in predictive ability reached at ~30% of the total GPS dataset when initial sample size was large. Based on these results, we generated well-validated spatial predictions of Canada lynx distribution across a large portion of the species' southern range, with precipitation and temperature the primary environmental predictors in the model. We also demonstrated substantial redundancy in

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our large GPS dataset, with predictive performance insensitive to sample sizes above 30% of the original.

KEYWORDS
Canada lynx, generalizability, GPS telemetry data, local adaptation, *Lynx canadensis*, niche similarity, regional variation, sample size, species distribution model, transferability

1 | INTRODUCTION

Species distribution models (SDMs), which compare environmental conditions at presence and background locations and calculate a relative probability of habitat suitability (Elith & Leathwick, 2009), are a useful tool to better understand the distribution of a species' habitat across landscapes (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). These models can provide both an understanding of the specific environmental components that might define a species' habitat as well as generate spatial predictions of distribution at a landscape scale (Elith & Leathwick, 2009). Species distribution models have been used extensively to create maps of predicted habitat (Derville et al., 2018; Gantchoff et al., 2019), evaluate threats from climate change or increased anthropogenic disturbance (Diniz-Filho et al., 2009; Requena-Mullor et al., 2019), or consider habitat corridors and connectivity (Zeller et al., 2018). Accurate SDMs are particularly important for landscape-scale conservation planning given the large-scale changes associated with climate (Park Williams et al., 2013), anthropogenic alterations (Curtis et al., 2018), habitat loss and fragmentation (Sala et al., 2000), wildfire (Hansen et al., 2010), and insect outbreaks (Kurz et al., 2008). However, one of the limitations faced by SDMs, and indeed all ecological models, is uncertainty about their transferability when applied to novel conditions (Lonergan, 2014; Yates et al., 2018).

When SDMs are implemented across a species' range, they assume a uniform response to the variety of environmental conditions encountered. However, SDMs often encompass multiple, geographically distinct populations which may vary in their responses to local conditions (Barbosa et al., 2009; Habibzadeh et al., 2019; Valladares et al., 2014). Differentiation between individual populations may generate poor model performance outside the model training area, producing erroneous conclusions if that model is applied to other areas. The importance that regional variability plays in SDMs has been demonstrated frequently in plants (O'Neill et al., 2008; Valladares et al., 2014), amphibians (Davies et al., 2019), birds (Habibzadeh et al., 2019), and mammals (Barbosa et al., 2009). Regional variation in intraspecific habitat relationships has been attributed to multiple biological processes, including local adaptation through genetic differentiation (Peterson et al., 2019), biotic interactions (Wisz et al., 2013), or functional responses to differences in habitat availability (Vanreusel et al., 2007). By understanding differences in environmental relationships associated with individual populations, we can improve the development of SDMs, generating improved model predictability and transferability (O'Neill et al., 2008; Vanreusel et al., 2007).

Additionally, SDMs may not generalize geographically because of model over-fitting, whereby model predictive ability is high in areas where data were collected, but low in areas outside those conditions (Wenger & Olden, 2012). Complex models with excessive environmental covariates, for instance, may result in models which are less generalizable to novel areas (Yates et al., 2018). Similarly, models with large amounts of localized data may not generalize to other landscapes because of the specificity of the species-environment relationships characterized (Boria & Blois, 2018; Wenger & Olden, 2012). While the impact of sample size on SDMs has been extensively considered, the general concern has been with too little data, rather than too much (Hernandez et al., 2006; Stockwell & Peterson, 2002). However, the recent availability of extensive Global Positioning System (GPS) datasets presents a novel challenge to conventional SDMs as there is little consensus regarding how to treat the large volume of animal relocations (Gantchoff et al., 2019; Li et al., 2017; Magg et al., 2016; Maiorano et al., 2015; Rice et al., 2013; Shoemaker et al., 2018) which may create redundant or spatially correlated nonindependent information with respect to species distributions, particularly if few animals are sampled. Yet, GPS data provide high spatial accuracy, reduced sampling bias, and less species misidentification; all these issues plague the opportunistic sampling schemes common in SDM literature (Aubry et al., 2017; Newbold, 2010). The challenge of modeling distributions of species with large GPS datasets has received little attention (but see Boria & Blois, 2018), but given the availability and benefits of extensive GPS data, an evaluation of the trade-offs between sampling efficiency and SDM performance is needed.

Our study goals are twofold: (a) evaluate SDM generalizability to model the distribution of Canada lynx (*Lynx canadensis*; hereafter lynx), a federally listed specialist forest carnivore in the contiguous United States, and (b) develop a process to assess GPS data efficiency with respect to SDM predictability and transferability. Lynx rely almost entirely on snowshoe hares (*Lepus americanus*) as a food source (Aubry et al., 2000; Squires & Ruggiero, 2007), and thus are closely tied to boreal forests with high horizontal vegetation cover (Holbrook et al., 2017; Squires et al., 2010). Lynx are an excellent species to assess geographic generalizability of SDMs across populations, because we expect habitat specificity and selection for a narrow range of environmental conditions to result in less intraspecific variation and more habitat generalizability compared to generalist species (Bonthoux et al., 2017; Yates et al., 2018). We used data from three geographically distinct populations at the species' southern range periphery in Washington, Montana, and Wyoming, USA. Our conservation aim was to model the distribution of habitat capable of supporting lynx across the northwestern United States, including areas outside known populations. To inform predictions of SDM generalizability among lynx populations, we first evaluated regional variation in lynx-environment relationships between populations. We hypothesized that, if regional variation was present, models built on individual populations would perform best for the training population but be less transferable outside that population. We suspected a combined model (using all populations) might perform more poorly on any single population but have higher overall performance across the entire region. We assessed model performance using withheld data as well as an independently collected dataset. To evaluate the efficiency of GPS data in SDMs, we compared model performance and transferability across a range of sample sizes to determine optimal sample size for SDMs when using GPS datasets.

2 | METHODS

2.1 | Study areas

Our study area covered a large region in the northwestern United States, including parts of Washington (WA), Idaho (ID), Montana (MT), and Wyoming (WY), as well as the area directly to the north, including parts of British Columbia and Alberta, Canada (Figure 1). We bounded the study area using the level II ecoregion "western cordillera," which is primarily forested mountains with limited grasslands or other open areas (Omernik & Griffith, 2014). Within our study area were three monitored lynx populations: one in north-central Washington and into Canada, one in western Montana, and one in northwest Wyoming (Figure 1). These populations are discrete and, though genetic data indicates that north-south movement renders the contiguous United States and Canada populations panmictic (Schwartz et al., 2002), telemetry data from marked individuals exhibit no east-west dispersal between populations. Pairwise distances between population centroids were approximately 400 km, 600 km, and 1,000 km for Washington and Montana, Montana and Wyoming, and Wyoming and Washington, respectively. General environmental conditions averaged at lynx locations within each geographic area are given in Table 1; we calculated elevation from a digital elevation model (DEM; U.S. Geological Survey, National Elevation Dataset), and mean annual precipitation, mean annual temperature, and mean snow depth on April 1 from Wang et al. (2016).

2.2 | Occurrence data

We used GPS data from radio-collared lynx. Data consisted of 17 individuals (n = 21,518 locations) monitored from 2007 to 2013 in Washington, 66 individuals (n = 164,612 locations) monitored from 2004 to 2015 in Montana, and 10 individuals monitored from 1996 to 2010 in Wyoming (n = 539 GPS locations, n = 218 Argos locations). Because of fewer marked lynx in Wyoming, we included both individuals with GPS collars (n = 2) and individuals with Argos satellite collars (n = 8). We used only Argos locations with spatial accuracy ≤500 m, which was sufficient for our scale of inference. Since the grain of the environmental covariates we used was large (250 m) compared to the resolution of the GPS data, resulting in multiple GPS locations per grid cell, we converted all GPS or Argos locations within a single 250 m cell into a single observation and used this dataset (WA n = 7,476, MT n = 22,510, WY n = 670) as the starting point for all analyses.

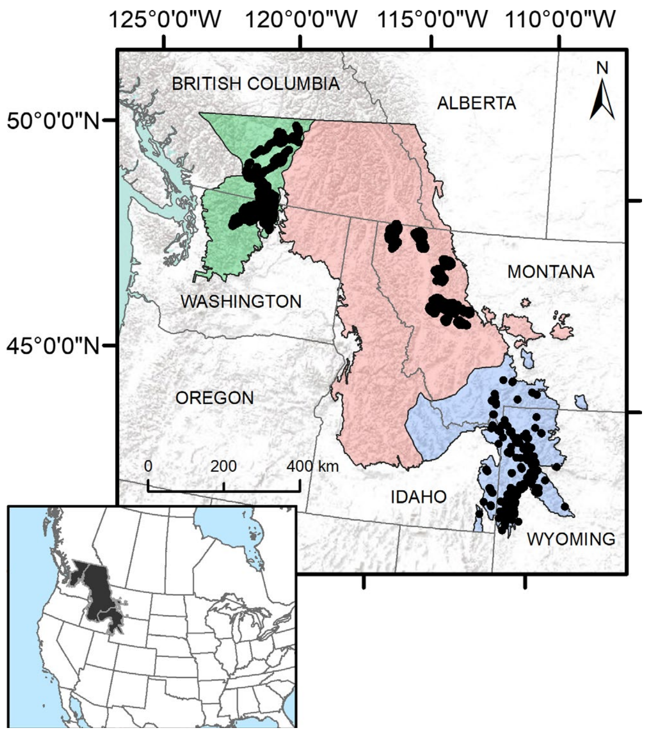

FIGURE 1 Species distribution modeling extent for Canada lynx covering portions of Washington, Idaho, Montana, and Wyoming, USA, and British Columbia and Alberta, Canada. Black dots indicate lynx GPS locations; color shading indicates the background extent used for each population-level model (green = Washington, red = Montana, blue = Wyoming). Inset shows location of modeling extent in North America. Background image sources ESRI, USGS, NOAA

2.3 | Environmental predictors

Environmental predictors were initially selected based on previous knowledge of Canada lynx natural history and ecological relationships (Holbrook et al., 2017; Ivan & Shenk, 2016; Koehler et al., 2008; Maletzke et al., 2008; Squires et al., 2010). We selected 16 climate, topographic, anthropogenic, and vegetative covariates that we expected to be related to Canada lynx distribution (see Appendix A: Table A1 for information on variable selection). To accommodate the temporal period over which our data were collected (1996–2015), we used covariates averaged over the same timeframe whenever possible. Climate variables included mean temperature of the coldest month, winter (December to February)

	Elevation (m)	Annual precipitation (cm)	Annual temperature (°C)	Snow depth (m)
Washington	1,634 (453–2,452)	76 (60–261)	2.9 (−0.7 to 7.9)	1.3 (0–4.0)
Montana	1,680 (737–2,499)	98 (43–180)	3.4 (0.4–7.0)	1.3 (0–2.8)
Wyoming	2,572 (1,568–3,405)	70 (38–175)	1.3 (−1.1 to 5.9)	1.5 (0–2.8)

TABLE 1 Mean and range of environmental conditions averaged across Canada lynx locations at each of the three distinct populations used to make species distribution models across the northwestern United States

precipitation, summer (Jun to Aug) precipitation, and mean annual relative humidity generated from the ClimateNA v5.10 software package over a period of 1980–2010 with a native resolution of 1 km (AdaptWest Project, 2015; Wang et al., 2016). Heat load (an index of temperature considering aspect and slope), compound topographic index (a steady-state wetness index), and integrated moisture index (an estimate of soil moisture based on topographic heterogeneity), were created using a 250 m digital elevation model and the Geomorphometric and Gradient Metrics Toolbox (Evans et al., 2014) in ArcMap (Environmental Systems Research Institute, ArcGIS Desktop: Release 10.5.1. Redlands, CA). Snow water equivalent (SWE) and snow depth at 1 km resolution were downloaded from 2003 to 2017 from the National Weather Service's Snow Data Assimilation program (National Operational Hydrologic Remote Sensing Center, 2004) and averaged across years. Minimum snow density was created by dividing snow depth by snow water equivalent (Natural Resources Conservation Service Oregon; United States Department of Agriculture, 2020).

Topographic variables included surface area, an index of topographic ruggedness (Jenness, 2013b), and topographic position index, a measure of the concavity or convexity of a landscape (Jenness, 2013a), created from a 250 m digital elevation model. Vegetation covariates included normalized difference vegetation index (NDVI) from Landsat 5 and 8 imagery averaged during the growing season (1 July to 30 September) from 2000 to 2015, which characterized long-term vegetation presence and productivity with a 30 m native resolution (Pettorelli et al., 2005). We also calculated standard deviation of percentage of tree cover (Hansen et al., 2013) in a 1 km neighborhood as an index of forest heterogeneity. We considered soil pH, since the wetter conditions of boreal forests would be expected to have lower pH (Hengl et al., 2017), as well as anthropogenic influences of road density (highway, local, and open forest roads) within a 1 km neighborhood (OpenStreetMap Foundation, 2017) and night light intensity, an index of anthropogenic presence compiled from nighttime lights visible from cities and towns from 1996 to 2011 (National Oceanic & Atmospheric Administration, 2014). We resampled all predictors to a 250 m resolution and reprojected to the Albers Equal Area projection. Pairwise correlations between predictors are given in Appendix B; all covariates were correlated $r \leq |0.7|$.

2.4 | GPS data efficiency

To explore the impact of sample size on model performance and determine the optimum sample size of GPS locations for model calibration, we performed a sensitivity analysis of predictive performance across varying sample sizes. From the original dataset (WA $n = 7,476$, MT $n = 22,510$, WY $n = 670$), we randomly sampled a percentage of each population (MT, WA, or WY) from 5% to 100% of the original sample size in increments of 5%. For each sample size, we selected an equal number of background locations within the extent of each population and fit the same ensemble model including 11 topographic and climate variables and six modeling algorithms, and evaluated models using withheld and independent datasets (see below for full modeling and validation details). We compared model performance using AUC (Marmion et al., 2009) to assess model predictive ability as well as transferability across sample sizes. We used the outcome from the sample size simulation to determine optimum trade-off between model performance and data parsimony, with the assumption that the sample size reached before a drop in performance had little to no data redundancy or spatial correlation, and adopted this sample size (WA $n = 2,243$, MT $n = 6,753$, WY $n = 540$) for each GPS dataset for the remainder of our analyses.

2.5 | Regional variation between populations

To explore the hypothesis that regional variation was present between populations, we performed a principal component analysis (PCA; Hällfors et al., 2016). If regional variation was present, we expected to observe distinct clustering of the three populations within the PCA dimensions. We used all 16 covariates from our models and ran the PCA on the lynx locations from the dataset used in the SDM modeling process using the "PCA" function from the R package "FactoMineR" (Lê et al., 2008). We plotted lynx locations with 95% confidence intervals of clustering on the first two dimensions of the PCA to visualize grouping of the populations. We used the correlation between individual covariates and the first two principal components to inform which covariates were contributing most to each component. This allowed us to identify the environmental gestalt associated with each population. We hypothesized that populations similar in principal component space would be more transferable to each other than populations farther away, regardless of geographic distance, because of environmental similarity.

2.6 | SDM modeling approach

2.6.1 | SDM development

We constructed separate SDMs for each individual population and a regional model with all combined populations. Since one of our modeling goals was to explore the effects of data efficiency given the use of large GPS datasets, we considered three sample size scenarios for models from the entire region: unequal sample sizes from each region ("Unequal," based on initial size of each population dataset; WA n = 2,243, MT n = 6,753, WY n = 540), equal sample size where possible based on Washington ("WA Equal," MT and WA n = 2,243, WY n = 540), and equal sample size based on Wyoming ("WY Equal," all sample sizes reduced to equal WY sample size n = 540; Figure 2). Presence locations for reduced datasets were chosen randomly from the initial population dataset. Since SDMs are often sensitive to the extent and locations chosen as randomly distributed background data (Iturbide et al., 2018), we also considered two scenarios to explore the effect of background extent of individual population models on model prediction and transferability: background data from either the entire region or an area associated with only the local population (Figures 1 and 2). We split our combined regional study area into three population areas subjectively based on landscape features such as large rivers and nonforested spaces that we hypothesized would be difficult for lynx to cross (Figure 1). This resulted in a total of 9 modeling scenarios (Figure 2).

Background locations were initially sampled at approximately 1 point per 1.5 km^2 across the study area to ensure adequate coverage. We then subsampled from these points to create a background sample equal to the number of lynx GPS locations per population, depending on which scenario was being modeled. We used the "biomod2" package (Thuiller et al., 2009) in program R v. 3.6.0 (R Core Team, 2019) for all distribution modeling, and six modeling algorithms were selected to include a range of regression (Boosted Regression Trees, Multiple Adaptive Regression Splines, Generalized Linear Models, and Generalized Additive Models) and machine-learning methods (Random Forest, Maxent) commonly used in an SDM context. To decrease variability resulting from a random sampling of background locations, we ran each model 10 times with a different random sample of background replicates each time (Barbet-Massin et al., 2012). This resulted in 60 models per scenario, which were combined into a weighted average based on area under the curve (AUC) of the receiver operating characteristic (ROC), so that better-performing models contributed more to the final ensemble, with the threshold for inclusion greater or equal to the median AUC calculated from all 60 models. Ensemble modeling has demonstrated equal or superior predictive performance relative to single models (Hao et al., 2020; Marmion et al., 2009).

2.6.2 | SDM validation

We assessed model predictive performance using AUC (Fielding & Bell, 1997), the continuous Boyce index (Hirzel et al., 2006), and the minimal predicted area (MPA; Engler et al., 2004). The AUC considers model discriminatory ability at all possible thresholds; we used the partial-area ROC (Peterson et al., 2008), which uses the proportion of background area predicted as present, rather than absence locations, as the x-axis metric. This variation makes the AUC metric more applicable to SDMs, since the models are based on presence and background (rather than presence and absence) data. For background data, we again randomly sampled the entire study area at a density of 1 point per 10 km^2 to provide a spatially well-distributed sample. The continuous Boyce index quantifies the delineation of capable habitat using a Spearman rank correlation between the ratio of predicted to expected number of presence locations and mean habitat capability grouped into equal-area bins (Boyce et al., 2002; Hirzel et al., 2006). MPA uses a chosen threshold (in our case 90% of presence locations) applied to the prediction surface to determine extent of the area above this threshold; this evaluation provides a metric of model efficiency, illustrating the trade-off between correctly identifying presence locations while doing so with a minimum of predicted area. We used the R package "pROC" (Robin et al., 2011) to calculate AUC and "ecospat" (Di Cola et al., 2017) to calculate the Boyce index.

We used two datasets for model validation: a withheld dataset consisting of GPS data that were not used in model calibration (WA n = 5,233, MT n = 15,757, WY n = 130) and an independent dataset

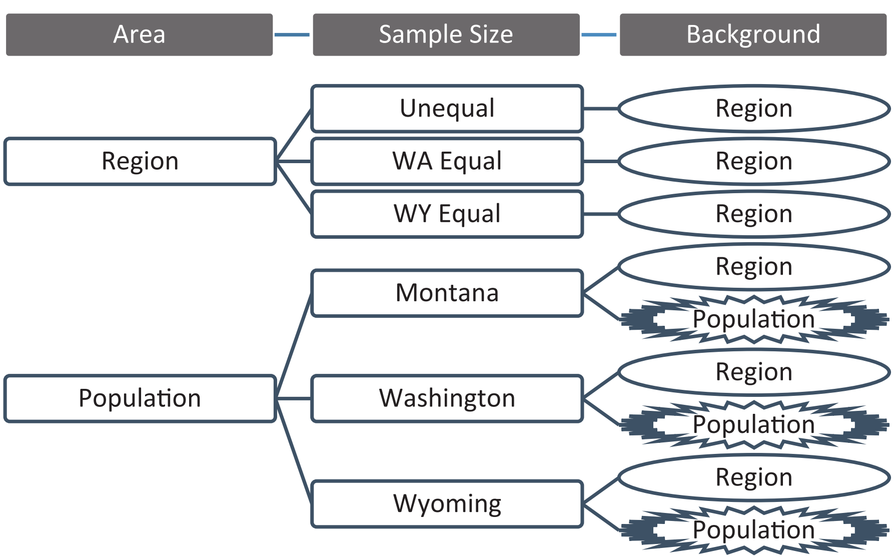

FIGURE 2 Schematic showing the number of species distribution modeling scenarios performed for the study; models were performed on either populations or the entire region, with varying sample sizes, and different extents for the selection of background locations

compiled from diverse data sources (WA n = 52, MT n = 445, WY n = 23, ID n = 103, Canada n = 27), including noninvasive genetic sampling (n = 375), camera traps (n = 71), den locations (n = 80), incidental sightings and mortalities (n = 31), other Argos locations (n = 62), and two GPS collared individuals that were outside of the three main populations of interest and thus included only as validation data (n = 27). We assessed model performance for each SDM within the population on which it was calibrated, the geographically separate populations to determine model transferability, and the entire region (all three populations combined). Additionally, for only the best-performing (most predictive) model, we also assessed relative contribution of each environmental covariate to better understand what factors were contributing to modeled lynx distribution (Hällfors et al., 2016). We evaluated the importance of covariates by permuting a single variable, generating model predictions, and calculating the correlation between these permuted predictions and the original model predictions; if a variable was important, model predictions would be altered, and correlation between predictions would be low when the variable was permuted (Thuiller et al., 2009). Since we used an ensemble of six modeling techniques, each variable was given six measures of importance, which we combined in a single boxplot for illustrative purposes.

2.6.3 | SDM mapping

To identify key conservation areas for sensitive species, like lynx, that occupy extensive ranges, we generated predictions from the top-performing SDM in both continuous and categorical formats. Continuous predictions provide a detailed look at the relative habitat suitability of lynx across the study area, while a categorical map provides simplified predictions that may be more useful to managers responsible for conservation planning (Freeman & Moisen, 2008). For example, an important application for the lynx SDM developed here is to generate habitat predictions in areas between the three main populations. Therefore, we applied a threshold to our top-performing model chosen to include 90% of lynx GPS locations (composed of reproductive populations on home ranges) as "high" probability lynx habitat and a threshold chosen to include 85% of independent data as "medium" probability lynx habitat. The independent location data for lynx included incidental sightings of animals outside the range of core populations and therefore may represent a larger array of behaviors and thus of habitat use. We chose the 90% and 85% cutoff for high and medium lynx data, respectively, to maintain a high conservation standard with low acceptable error (here 15% or less) and using values consistent with data cut-offs for home-range delineation and various habitat thresholds in the literature (Börger et al., 2006; Freeman & Moisen, 2008). However, to acknowledge a range of potential thresholds for different conservation goals, we also considered two thresholds that bracketed these criteria, one of 95% lynx locations and 90% independent data, and a second of 85% lynx locations and 80% independent data.

3 | RESULTS

3.1 | GPS data efficiency

We found model performance to be mostly insensitive to sample size. Models trained on 100% of GPS location data were less than 0.05 AUC (<5% gain) better than those trained on only 5% when tested on withheld data (MT: 5% AUC = 0.938, 100% AUC = 0.959; WA: 5% AUC = 0.916, 100% AUC = 0.959; WY: 5% AUC = 0.914, 100% AUC = 0.958; Figure 3). Independent data validation showed even less difference, with a gain of 0.03 AUC (<4% gain) or less (MT: 5% AUC = 0.840, 100% AUC = 0.855; WA: 5% AUC = 0.822, 100% AUC = 0.858; WY: 5% AUC = 0.800, 100% AUC = 0.803). Despite large differences in sample size between populations, we did not find pronounced differences in AUC between populations at similar sample size percentages (Figure 4). For instance, at 5% of the data, Wyoming's model contained n = 34 locations and had an AUC of 0.800 with independent data, while Washington had n = 374 and an AUC of 0.822, and Montana had n = 1,126 and AUC of 0.840. Taken together, these results indicate that model performance within the calibration area was robust to small sample size and relatively unaffected by up to 33-fold differences in absolute number of presences. Additionally, while model performance plateaued above ~30% data, we did not detect any drop in model performance up to the maximum sample size of n = 22,510 in Montana. While differences in AUC between sample sizes were small, the biggest gain in AUC appeared between 5% and 30% before reaching a plateau (Figure 4). Thus, for further modeling, we considered a sample size of 30% of the data (WA: n = 2,243, MT: n = 6,753), to be the appropriate balance between model performance and data redundancy. However, we found the Wyoming population increased in model performance until approximately 80% of the dataset was included. We assumed this was a function of the limited data that defined lynx in Wyoming compared to other populations, so we used 80% of the Wyoming data (WY: n = 540) in subsequent analyses to maximize model predictive performance for the Wyoming population (Figure 4).

The percent of data used had little effect on model transferability across populations (Figure 3), but with some differences between individual populations. The model created with data from only the Washington population had the highest predictive performance in the other two populations, with a mean AUC of 0.811 on withheld data in Montana (5% = 0.772, 100% = 0.815) and 0.678 in Wyoming (5% = 0.718, 100% = 0.637). The models built from the Montana population were less transferable but more stable in performance across the gradient of sample size, most likely due to the large absolute sample size of Montana. Montana models performed well in Washington (mean AUC = 0.772, 5% AUC = 0.753, 100% AUC = 0.777) but poorly in Wyoming (mean AUC = 0.473, 5% AUC = 0.458, 100% AUC = 0.476; Figure 3). Models built in Wyoming were inconsistent in transferability across sample sizes (Figure 3); transferability of Wyoming models was similarly poor in Montana (mean AUC = 0.601, 5% AUC = 0.430, 100% AUC = 0.561) and Washington (mean AUC = 0.618, 5% AUC = 0.490, 100% AUC = 0.466).

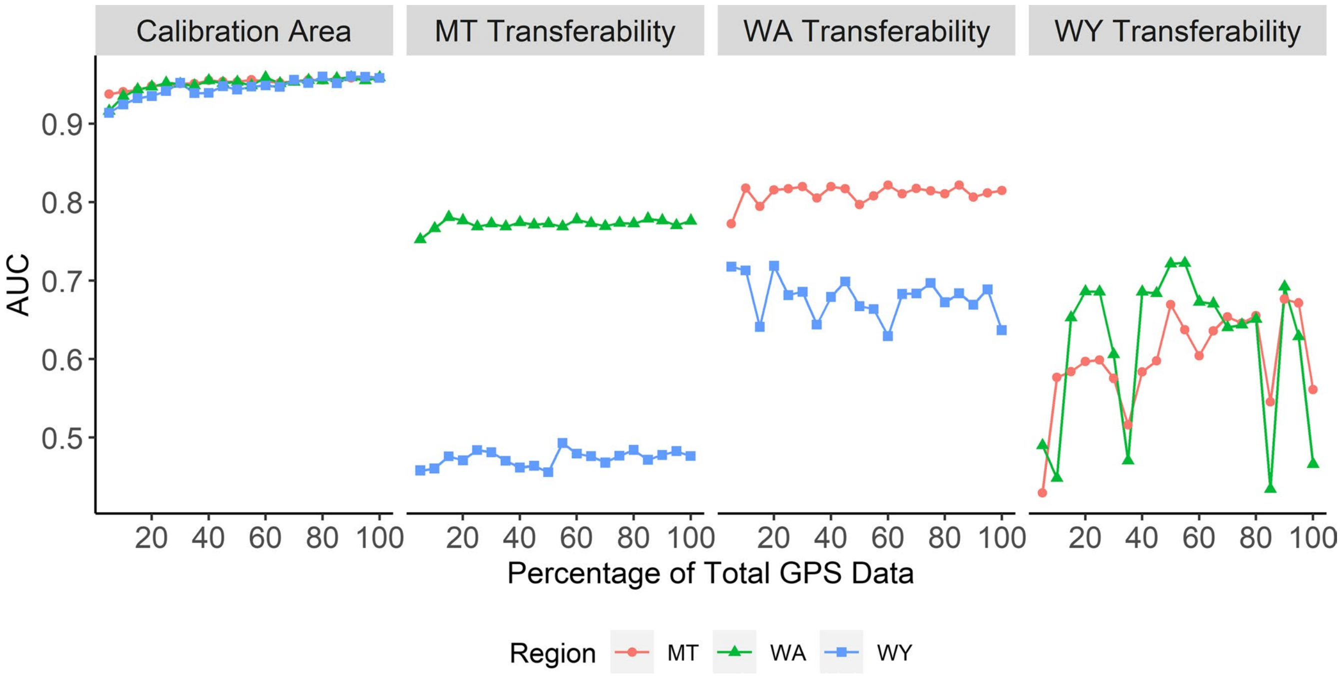

FIGURE 3 Performance of species distribution models, as measured by the area under the curve (AUC), for a range of sample sizes from 5% to 100% of the original Canada lynx GPS dataset. The first panel shows model performance when evaluated on data within the area that the model was trained on (Calibration Area). The second through fourth panels show the performance of models trained on a given population ("MT" = Montana, "WA" = Washington, "WY" = Wyoming) when transferred to the remaining populations. For example, "WA Transferability" shows models calibrated in Washington but tested on data from Montana and Wyoming

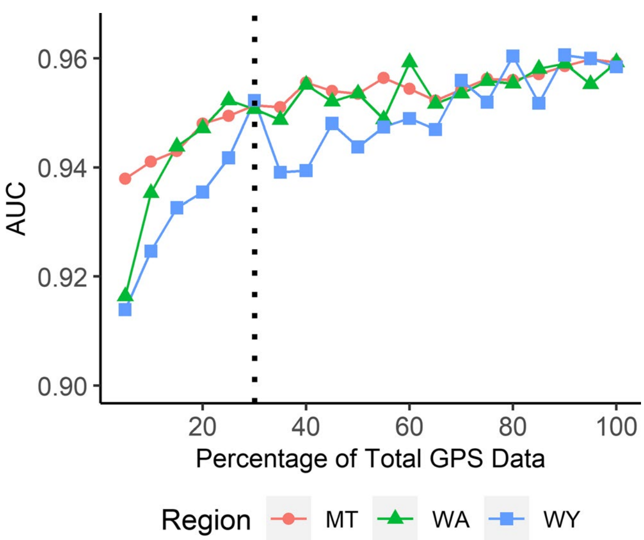

FIGURE 4 Performance of species distribution models, as measured by area under the curve (AUC), for a range of sample sizes from 5% to 100% of the original Canada lynx GPS dataset. This figure shows a close-up of the first panel from Figure 3, of model performance when evaluated on data within the area that the model was calibrated on. Model performance for each region ("MT" = Montana, "WA" = Washington, "WY" = Wyoming) improves steeply from 5% to approximately 30%, but plateaus thereafter

3.2 | Regional variation between populations

Counter to our expectations for a specialist species, some regional variation was present across the three populations of lynx as demonstrated through clustering in PCA space. Wyoming and Montana populations were the most differentiated, while Washington exhibited a combination of characteristics between Wyoming and Montana (Figure 5). The PCA explained 33% of the variation in the first two axes, with PC1 dominated by precipitation-related covariates (summer and winter precipitation, relative humidity, and soil pH) and PC2 dominated by vegetation-related covariates (long-term NDVI, forest heterogeneity, and road density; Appendix C: Tables C1 and C2). The Wyoming population was grouped on the PCA axes based on less moisture, lower long-term NDVI, and more forest heterogeneity than the Montana population. Interestingly, Washington fell in between Montana and Wyoming along these axes, despite its relative isolation in geographic space (Figure 1).

3.3 | Lynx SDM performance

Consistent with the PCA results, individual lynx population models performed well in the area from which they were developed and were less transferable to other populations (Table 2). Based on

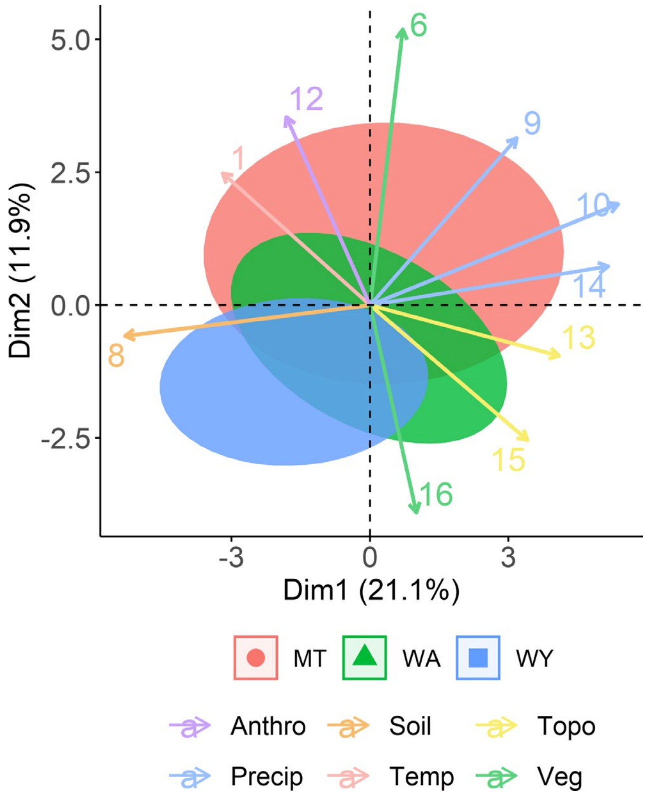

FIGURE 5 The results of a principal components analysis across the three Canada lynx populations using the 16 climate, topographic, vegetation, and anthropogenic covariates included in species distribution models. The red ellipse represents the 95% confidence interval around the Montana population, green Washington, and blue Wyoming. Arrows represent correlation between each covariate to the principal component axes; arrows are colored by type of covariate (Anthropogenic, Soil, Topography, Precipitation, Temperature, Vegetation), and only the top 10 contributing covariates are shown. The direction of the arrow indicates to which dimension the covariate contributes most. Covariate arrows are labeled by number for readability: 1 = Compound Topographic Index, 6 = NDVI, 8 = Soil pH, 9 = Summer Precipitation, 10 = Winter Precipitation, 12 = Road Density, 13 = Surface Area, 14 = Snow Water Equivalent, 15 = Topographic Position Index, 16 = Forest Heterogeneity. Percentage by axes show how much variation is explained by the first (Dim1) and second (Dim2) dimension in the principal components

model performance assessed on both withheld and independent data, the regional model that used 30% of Washington data and a Montana sample size to match ("WA Equal," Table 2) was the most predictive of lynx use locations across each population and the entire region combined (see Appendix D for validation results for continuous Boyce Index and MPA). Individual population models made from 30% of the data from each population were slightly more predictive for Montana (AUC = 0.981) and Washington (AUC = 0.959) than the regional model (MT AUC = 0.974, WA AUC = 0.954), but the "WA Equal" regional model performed best in the Wyoming population and across all three populations together (Table 2). Regional models from the three combined populations were consistent in performance when tested separately on each population and exhibited good predictive performance of withheld data (AUC > 0.90) in each population and good predictive performance of independent data (AUC > 0.80) in each population (Table 2). Spatial predictions from the "WA Equal" model matched well with our expectations of lynx habitat and demonstrated areas of high habitat probability in the areas with known reproductive lynx populations as well as smaller islands of probable habitat in areas between populations (Figure 6). Covariates of greatest relative importance were primarily related to snow and precipitation, with mean temperature in the coldest month contributing the most to model predictions, and lesser contributions from snow water equivalent, precipitation in summer and winter, and long-term NDVI (Figure 7). For population-specific models, background extent (population versus region) had very little effect on model performance within the calibration area, but model transferability was better for models made with population-level backgrounds (Table 2).

3.4 | SDM mapping

Our best-performing SDM generated predictions consistent with known lynx habitat use (Mckelvey, 2000), with Canada lynx patchily distributed in mountainous areas throughout the Pacific Northwest and the Greater Yellowstone Area (see Figure 8 for details). Categorical predictions created by 90% and 85% threshold values when applied to the "WA Equal" model delineated the location of habitat most likely to be selected by lynx in a reproductive population ("high" probability habitat) and habitat that was less favorable but potentially still used by lynx ("moderate" probability habitat), particularly for connectivity or as part of a matrix with "high" and "low" probability habitat (Figure 8). We delineated 34,930 km^2 of "high" probability habitat and 125,580 km^2 of "moderate" probability habitat across the study area. By state, Montana had the largest area of "high" habitat, with 11,961 km^2, followed by Washington (4,411 km^2), Idaho (2,497 km^2), and Wyoming (2,424 km^2). Differences in amount of area in each category were more pronounced with changes in the threshold generated from independent data, since this dataset included more variation in habitat use (Appendix E: Figures E1 and E2).

4 | DISCUSSION

Accurate representations of species distributions are increasingly important given the many challenges facing wildlife today. Habitat loss or fragmentation (Hornseth et al., 2014), a changing climate (Zielinski et al., 2017), and negative wildlife-human interactions (Reilly et al., 2017) all serve to increase the need for conservation of important habitat. Yet the delineation of important habitat is still sometimes unknown, causing conservation actions to be misdirected and wasting the limited resources available. Here, we used data from multiple Canada lynx populations across the northwestern United States and southern Canada, considered

TABLE 2 Model validation, as measured with AUC, for all species distribution models generated for Canada lynx in the northwestern United States

Validation data source	Data location	Model being tested	Background	Performance in MT	WA	WY	Region
Withheld	Region	Unequal	Region	0.977[b]	0.937	0.927	0.939
		WA equal	Region	0.974	0.954[b]	0.973[a]	0.969[a]
		WY equal	Region	0.951	0.929	0.945	0.950[b]
	Population	MT	Region	0.970	0.790	0.540	0.722
		MT	Population	0.981[a]	0.792	0.580	0.781
		WA	Region	0.701	0.946	0.664	0.684
		WA	Population	0.786	0.959[a]	0.781	0.862
		WY	Region	0.535	0.785	0.952	0.692
		WY	Population	0.641	0.469	0.960[b]	0.764
				MT	WA	WY	Region
Independent	Region	Unequal	Region	0.833	0.880	0.912[b]	0.865
		WA equal	Region	0.834	0.884[b]	0.922[a]	0.883[a]
		WY equal	Region	0.821	0.854	0.910	0.868[b]
	Population	MT	Region	0.857[a]	0.766	0.832	0.768
		MT	Population	0.851[b]	0.771	0.824	0.799
		WA	Region	0.652	0.889[a]	0.693	0.683
		WA	Population	0.699	0.863	0.868	0.788
		WY	Region	0.524	0.710	0.791	0.624
		WY	Population	0.624	0.610	0.819	0.734

Note: Values in each column marked with a superscript "a" indicate best model performance in that population, superscript "b" indicate second best.

niche differentiation and model transferability, and created a highly predictive model of lynx habitat, validated using withheld and independent data. This model provides a refined depiction of lynx habitat that will facilitate the application of conservation management to areas most relevant to Canada lynx.

We expected generalizability between individual lynx population models given the known habitat specificity of lynx but found that, while lynx exhibit narrow habitat selection (Holbrook et al., 2017; Squires et al., 2010), there was enough variation in local animal-environment relationships to limit transferability of any single population model to our entire inference area. Regional models built using data from all populations combined, however, performed strongly across the entire study area, generated predictions for areas that were outside the three main populations and thus lacked data, and performed comparably to individual population models. Our use of principal components analysis (PCA) to examine regional variation between populations revealed differences and similarities between populations, and thus provided informed predictions of model transferability. The use of GPS data in our work resulted in models with very high predictive accuracy, which was maintained above 0.90 AUC even when data were reduced to approximately 5% of their original sample size.

SDMs are often constructed with opportunistic data collected across large spatial extents or with intensive data collection across smaller extents (Aubry et al., 2017; Thuiller et al., 2006). Few studies have the resources required for extensive data collection at multiple locations across a large area (Bonthoux et al., 2017). However, we combined GPS data from multiple collaborators to directly assess regional differences in habitat selection across populations within a large spatial area. We believe that large-scale species distribution modeling will increasingly benefit from similar collaborative approaches for creating accurate, regional-scale suitability models for other species and regions, given the widespread prevalence of GPS monitoring of a range of species by academic, government, and non-profit institutions.

We found that individual population models performed well for a given population but were less predictive when generalized across the region, consistent with the presence of regional variation in animal-environment relationships. This result is in line with other studies testing variation in habitat selection across regions or populations. For instance, Torres et al. (2015) demonstrated strong predictive performance of SDMs within individual islands of gray petrels (*Procellaria cinerea*) but weak performance across islands, while McAlpine et al. (2008) found that multiscale models of koala (*Phascolarctos cinereus*) habitat performed more poorly cross-regionally than within the region of model training. A potential explanation for this is differences in small-scale habitat availability (Habibzadeh et al., 2019; McAlpine et al., 2008; Torres et al., 2015) that manifest as slightly different realized niches between populations (Soberón & Nakamura, 2009; Torres et al., 2015). Our PCA results demonstrated

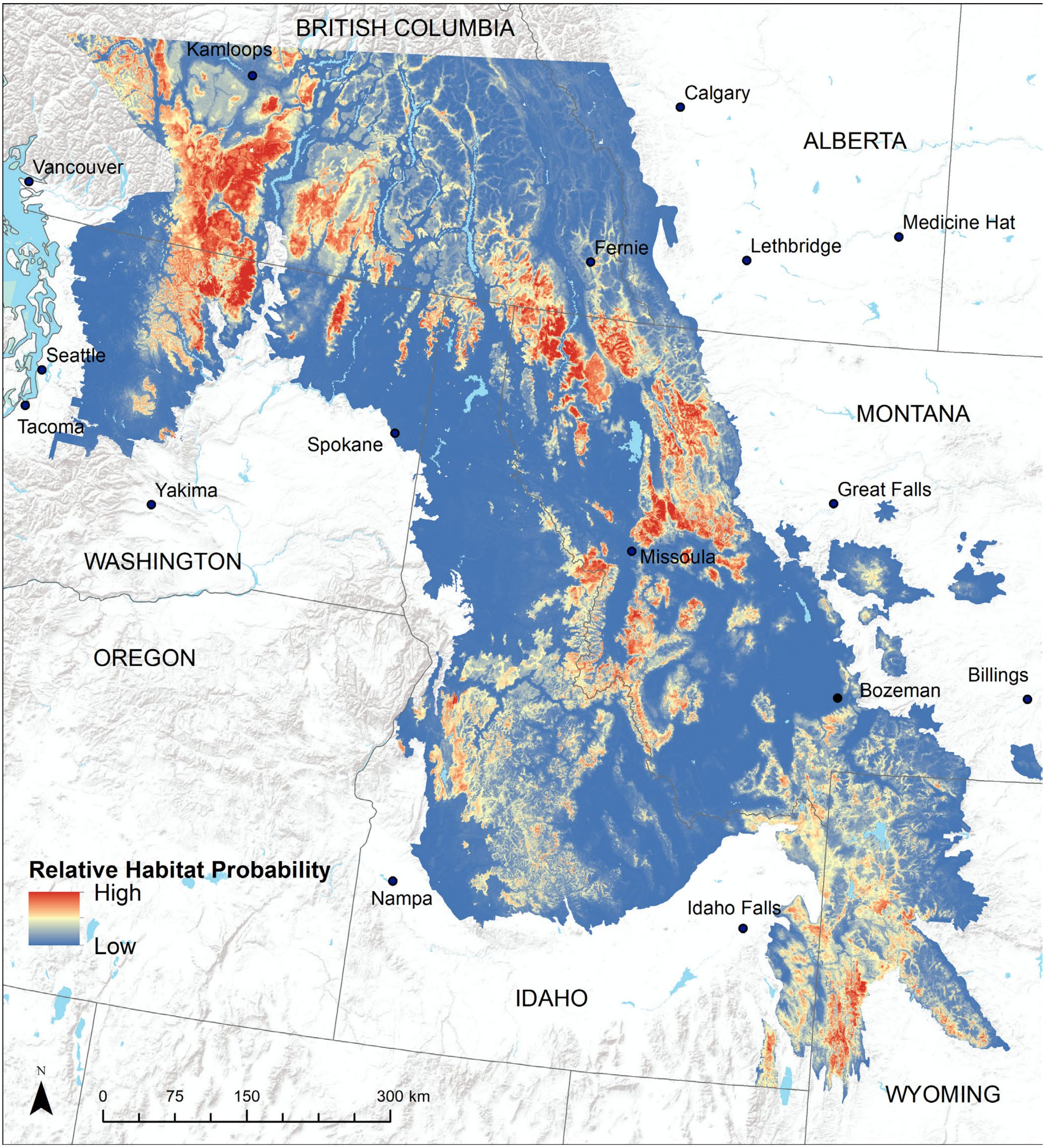

FIGURE 6 Spatial predictions of Canada lynx relative habitat probability across the study region in the northwest United States, as predicted by the top-performing species distribution model. Background image sources ESRI, USGS, NOAA

differences in the environmental conditions used by lynx in each of the three populations, with the degree of difference reflected in their transferability to one another. For instance, the Washington population was located between Montana and Wyoming in PCA space, and this overlap in environmental similarity was reflected in the greater transferability of this model to the Wyoming and Montana populations.

Generalizability of SDMs is also predicted to be related to specificity in diet or habitat selection (Bonthoux et al., 2017; Yates et al., 2018), although this pattern appears to be born out in some species and not others. A similar lack of transferability in habitat selection was observed in koalas (McAlpine et al., 2008), a specialist on eucalyptus leaves, while the opposite pattern was found in several species of European birds living in mixed agricultural land,

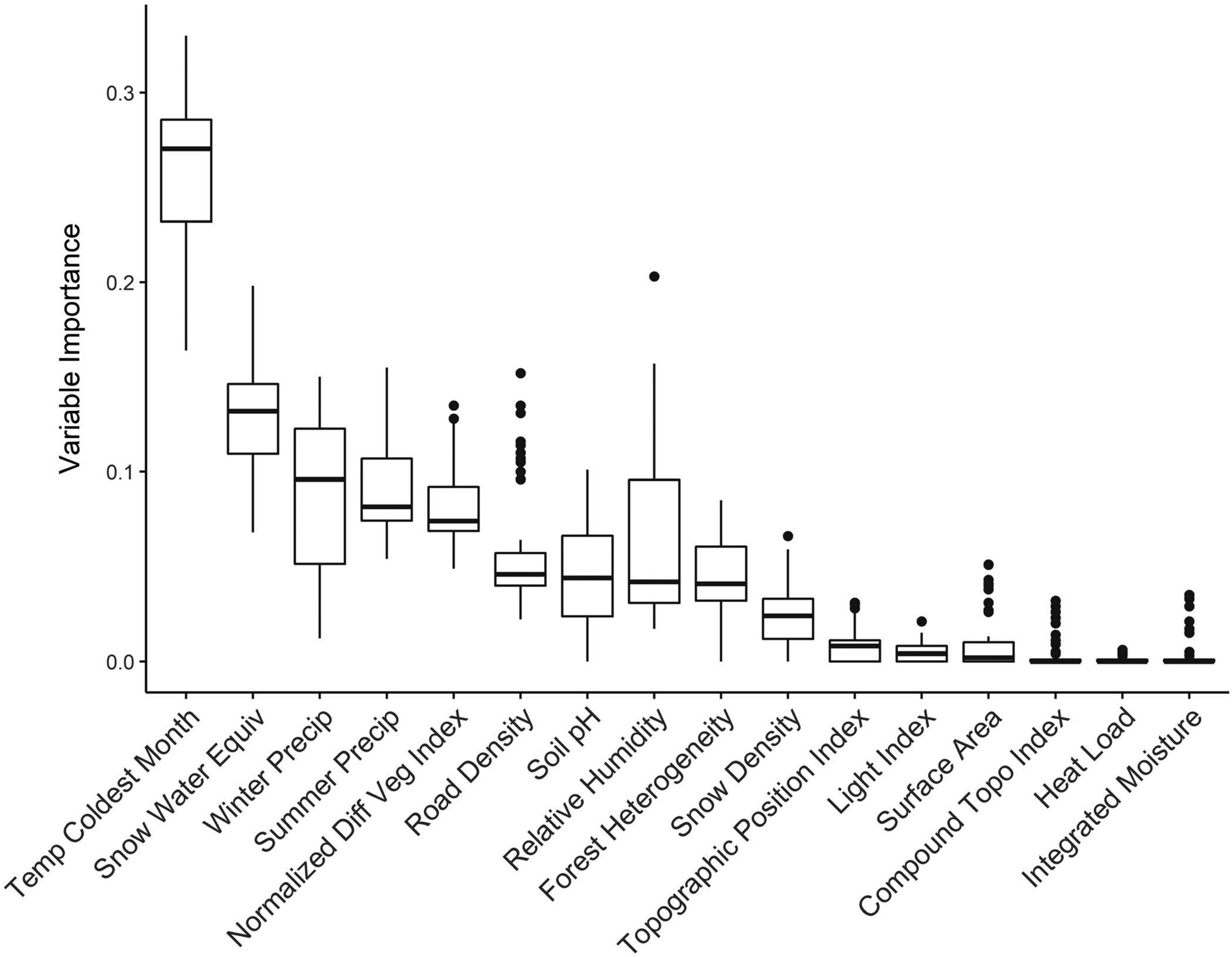

FIGURE 7 Estimated variable importance of each covariate to the best-performing species distribution model. Variable importance was estimated by permuting each covariate in turn, generating predictions, and comparing predictions to those from the original, unpermuted model. If a covariate was important, predictions would be changed and the correlation between sets of predictions would be lower

which demonstrated increased model transferability with habitat specialization (Bonthoux et al., 2017). Specialists are generally predicted to select a narrower range of environmental conditions (Kassen, 2002; Peers et al., 2012), and thus are predicted to favor homogenous environments with resource use similar and transferable across populations. Canada lynx reliance on snowshoe hares as prey make them similarly reliant on the environmental conditions that favor hares (Ivan & Shenk, 2016; Squires et al., 2010). Previous works show that lynx select boreal forest environments with deep snow and high horizontal cover (Holbrook et al., 2017; Mowat et al., 2000; Squires et al., 2010), leading to predicted transferability of SDMs. Instead, models from each individual population had marginal fit when applied to geographic areas outside their training location. One possible explanation is that lynx may use alternate prey when necessary; while their dependence on hares is well known, when hare abundance is low they may turn to alternative prey such as blue grouse (*Dendragapus obscurus*) or red squirrels (*Tamiasciurus hudsonicus*) (Ivan & Shenk, 2016), and thus differ somewhat in habitat use. Alternatively, while the populations sampled may vary in some environmental characteristics, they may be similar enough in features important to hares, such as high horizontal cover in mature forests (Squires et al., 2010), that lynx can find adequate food while still exhibiting habitat differentiation. The lynx population in Wyoming, for instance, is located in habitat that appears strikingly similar in forest structure and horizontal cover to lynx habitat in Montana (J. Squires, pers. com.). Additionally, the lynx in Wyoming that were monitored with Argos collars were partly comprised of individuals originally reintroduced from Canada to Colorado and had exhibited long-distance post-reintroduction movements (Devineau et al., 2010). These animals might therefore have been exhibiting atypical habitat selection, which may have included a less specialized pattern of selection, possibly also contributing to the low transferability of the Wyoming model.

Interestingly, despite differences in animal-environment relationships between populations, the regional model which included data from all populations performed well across the entire study area. Given the lack of generalizability demonstrated by the individual population models, we might expect that a SDM

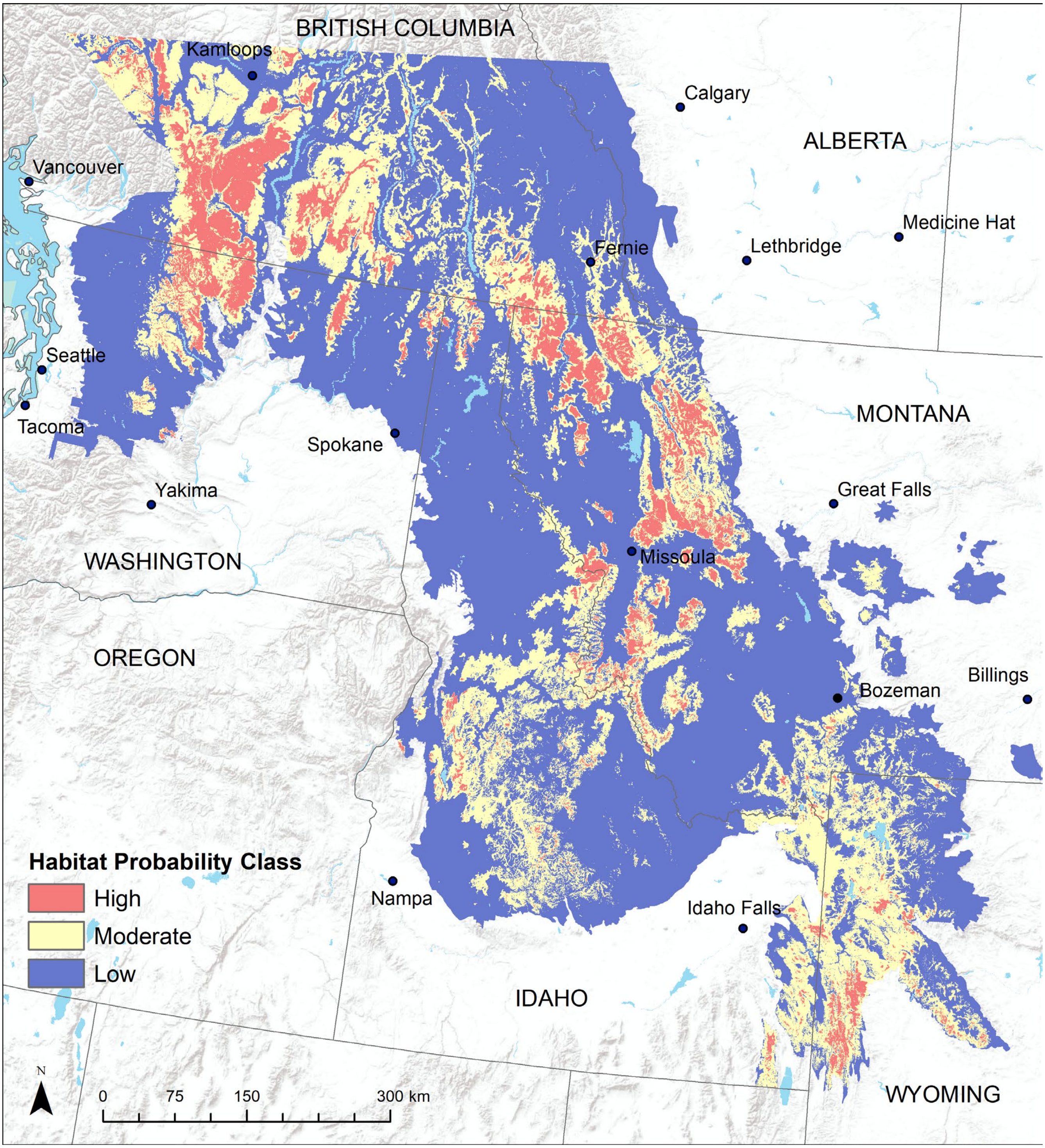

FIGURE 8 Categorical spatial predictions of Canada lynx relative habitat probability across the study region in the northwest United States, as generated by the top-performing species distribution model. Model thresholds are based on correctly assigning 90% of Canada lynx withheld GPS locations for the "High" category and 85% of independent lynx locations for the "Moderate" category. Background image sources ESRI, USGS, NOAA

created from all populations would perform more poorly in any given population than a model created only on those data (Torres et al., 2015). Instead, the regional model performed better than the individual population model for Wyoming and was nearly indistinguishable in performance from population-level models for Washington and Montana. The strong performance of the regional model might be explained by the larger geographic range that it sampled. Sampling a larger portion of the range is more likely to encompass the fundamental niche of lynx, thus increasing the predictive performance of the model across the study area. In other words, while any one population is unlikely to represent the totality of a species' geographic distribution, a sufficient sample of multiple populations throughout a larger portion of its range is capable of describing individual populations quite well. Qiao et al. (2018) showed that SDMs were more transferable when more of the fundamental niche was used for model training, resulting in less extrapolation between calibration and transfer regions. Here, the covariates that had the most effect on lynx habitat capability were primarily temperature and moisture related, with the top four variables all related to snow, precipitation, or cold temperatures, as well as NDVI, a measure of long-term forest presence or productivity. These results have conservation implications for the species' future at the southern range periphery under a changing climate, as temperature is likely to increase and snow to decrease if anthropogenic climate change continues unabated. Previous work has shown that warming trends are more severe in areas with mean annual temperatures in the range of 0°C to 5°C, due to a snow-ice feedback loop where loss of snow causes lowered surface albedo, which in turn further speeds warming (Pepin & Lundquist, 2008). Our study area had a mean annual temperature ranging from −1°C to 12°C (Table A1), suggesting that snow-ice feedback might influence warming patterns in lynx habitat, resulting in faster warming and decreased habitat suitability. King et al. (2020) found a similar susceptibility to changes in temperature and snow pack for the persistence of Canada lynx at their range periphery in Washington.

We found the amount of data provided by most GPS studies may greatly exceed what is necessary for peak SDM model performance and may be deleterious to model generalizability at some sizes, possibly reflected in the decreased transferability of our large dataset from the Montana population, as compared to the smaller dataset of Washington. Boria and Blois (2018) found that an SDM using approximately 13,000 occurrences from deer mice (*Peromyscus maniculatus*) decreased in predictive ability at large sample sizes, and that models with 10%–20% of the presence locations performed as well as those with greater percentages. Our results were similar, in that models with approximately 30% or more of our ~22,000 occurrences performed similarly. This number may be influenced by the number of individuals or sample size, however, as Wyoming, which had the fewest individuals and smallest sample, required closer to 70%–80% of the dataset to reach peak predictive performance. While the sample size of our Wyoming population was small compared to other datasets in our study, the number of presences was large ($n = 670$) compared to what is often recommended as the minimum sample size necessary for species distribution modeling ($n \approx 25$, Hernandez et al., 2006; $50 < n < 100$, Stockwell & Peterson, 2002). The Wyoming model performed well when assessed within the model training area, but exhibited poor transferability, which reinforces the need for caution in extrapolating even models that validate highly to novel areas. An aspect of GPS data collection that we acknowledge we were unable to address here was the effect of fix rate on GPS data efficiency. The fix rate, which determines the number of GPS locations taken during a given time period, was similar for GPS data from all three study populations, with one fix per hour in Montana, one fix per four hours in Washington, and one fix per three hours in Wyoming. Previous work has shown that autocorrelation increases with increased fix rate (Fieberg et al., 2010); thus, when applying methods used here, a reduction to 30% of the data should be considered when fix rates are similar, while a further reduction in data will likely be necessary for datasets with faster fix rates and less reduction when fix rate is slower.

Sensitive carnivores require large-scale monitoring to evaluate population status (Golding et al., 2018). These efforts are aided by SDMs that spatially map the likelihood of species presence or habitat suitability so ecologists and managers can evaluate management actions such as recreation or timber production (Rowland & Vojta, 2013). Our work here provides the most comprehensive evaluation of lynx habitat at the species' southern range periphery in the northwestern United States. In addition, we used an extensive sample of known lynx locations across the study area to evaluate model performance. As such, this SDM for lynx will be central to conservation planning across the northwestern United States. The map we generated provides users with consistent predictions across multiple jurisdictions, allowing land management decisions to be made and applied consistently over a broad area. The model delineated large areas of high-quality contiguous lynx habitat in parts of the Rocky Mountains in western Montana and the Cascade Range in Washington and British Columbia. With the use of our regional model, we also predicted the probability and spatial distribution of habitat that lacked detailed GPS data. These smaller but still potentially suitable habitat patches were in areas outside of the three main populations, including portions of northern Idaho, the Kettle Mountains in Washington, and scattered areas in the Bitterroot and Pioneer Mountains in Montana. Although some habitat patches may be too small to support long-term occupancy and reproduction, they may provide valuable areas of refuge or connectivity to maintain population persistence at the species' southern range periphery (Walpole et al., 2012). The delineation of habitat patches in Canada also provides important conservation information, since these areas often act as "source" populations for the lynx populations in the northwestern United States (Schwartz et al., 2002). The methods we used here should provide managers and conservationists with a more refined depiction of "high" probability habitat, allowing conservation actions, which are limited by time and resources, to be focused on areas which will be the most beneficial to lynx.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.13383023.

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APPENDIX A

TABLE A1 Table of 41 environmental predictors initially screened for use in species distribution models. The type of predictor (climate, soil, topography, vegetation, anthropogenic) is given in the "Category" column, as well as a description of the covariates, the units (if not unitless) and range of covariate values, the original source of the data, and whether the variable was used in the final covariate set

Category	Covariate description	Units; range	Source	Used
Climate	Degree days below 18°C	2,462–9,232	1	
Climate	Frost-free period	days; 15–198	1	
Climate	Heat load	0.42–0.92	2	X
Climate	Integrated moisture index	60–6,055	2	X
Climate	Maximum snow density	0–0.45	3	
Climate	Mean annual precipitation	mm; 255–4,837	1	
Climate	Mean annual relative humidity	%; 44–75	1	X
Climate	Mean annual temperature	°C; −1 to 12	1	
Climate	Mean snow density	0–0.28	3	
Climate	Mean summer (May to Sep) precipitation	mm; 111–596	1	
Climate	Mean temperature in coldest month	°C; −9 to 2	1	X
Climate	Mean temperature in warmest month	°C; 9 to 24	1	
Climate	Minimum snow density	0–0.19	3	X
Climate	Number of frost-free days	days; 28–277	1	
Climate	Precipitation as snow	mm; 7–1,463	1	
Climate	Snow density difference	0–0.29	3	
Climate	Snow depth	m; 0–3	3	
Climate	Snow water equivalent	m; 0–1.2	3	X
Climate	Summer heat moisture index (Mean Temp Warmest Mo/(Mean Summer Precip/1,000))	22–216	1	
Climate	Summer mean temperature (Jun to Aug)	°C; 8–23	1	
Climate	Summer precipitation (Jun to Aug)	mm; 56–305	1	X
Climate	Variation in snow density	0–0.05	3	
Climate	Winter mean temperature (Dec to Feb)	°C; −9 to 2.7	1	
Climate	Winter precipitation (Dec to Feb)	mm; 34–846	1	X

(Continues)

TABLE A1 (Continued)

Category	Covariate description	Units; range	Source	Used
Soil	Soil bulk density at 5 cm (The lighter the bulk density then potentially more organic matter and better water holding capacity)	(kg/m^3) 200–2,870	4	
Soil	Soil organic carbon at 5 cm	‰ (g/kg) 0–450	4	
Soil	Soil pH (The wetter the habitat in a general sense then the lower the ph. Alpine fir and that climatic zone would be expected to have a low pH from litter, high precipitation and cold temps)	pH × 10 20–110	4	X
Topography	Elevation	m, 0–5,089	5	
Topography	Roughness	unitless, 0–82,216	2	
Topography	Slope	degrees, 0–81	6	
Topography	Surface area	unitless, 1–5.5	7	X
Topography	3-D surface area	square m; 62,500–346,263	7	
Topography	TPI (1k, 5k, 10k)	unitless, 10k: −1,000 to 1,100, 5k: −806 to 891, 1k: −350 to 430	8	X
Topography	Compound Topographic Index	2.3–23.7	2	X
Veg	Enhanced vegetation index	−1 to 1	5, 9	
Veg	Normalized burn ratio	−1 to 1	5, 9	
Veg	Normalized difference vegetation index	−1 to 1	5, 9	X
Veg	Forest heterogeneity (Standard deviation of forest presence or absence at 1k, 5k, 10k scales)	unitless; 1k: 0–47, 5k: 0–43, 10k: 0–43	6	X
Veg	Percent forest cover	%, 0–100	5, 10	
Anthro	Lights from cities, towns, and other sites with persistent lighting, including gas flares, as a proxy for human disturbance	unitless; 0–1,106	5	X
Anthro	Road density	km/km^2; 0–50	11	X

Note: Data Sources:

1: Wang, T. et al. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS One 11: e0156720.

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Initially, we considered 41 environmental predictors: 24 related to climate, 3 related to soil conditions, 7 related to topography, 5 related to vegetation, and 2 depicting anthropogenic factors (Table A1). Since many of these covariates were highly correlated with each other, we initially ran a single global model with all covariates using only machine-learning modeling methods (global boosted models, random forest, and multiple adaptive regression splines) since these are known to be robust to correlation among covariates (Li & Wang, 2013). We used the "biomod2" package to run models, and included a measure of variable importance, created by randomizing a single variable, making new model predictions, and comparing these predictions to predictions from the entire model. Predictions that were very similar indicate little importance of the randomized variable, whereas very different predictions indicate that the variable was an important contributor. We ran 10 model repetitions using different sets of pseudoabsences each time, ranked the variables by their importance at each repetition, and calculated the median rank for each variable across all 3 models and 10 repetitions. We then eliminated covariates with pairwise correlations of |*r*| > 0.7, keeping the higher-ranked covariate in the pair. This resulted in a final covariate set of 12 topographic and climatic variables, 2 vegetation and 2 anthropogenic covariates.

APPENDIX B

Pairwise correlations between each of the 16 covariates used in the final species distribution model. Covariate pairs correlated at *r* > |0.6| are shown in bold.

	Heat Load	Int Moist	Temp Cold Mo	Snow Den	NDVI	Lights	Soil pH	Sum Prec	Win Prec	Rel Hum	Road Den	Surf Area	Snow Water Eq	TPI	Forest Het
Comp Topo Index	−0.07	0.34	0.08	−0.20	0.02	0.10	0.26	−0.20	−0.20	−0.23	0.19	−0.42	−0.21	−0.36	−0.17
Heat Load	1.00	−0.01	0.01	0.02	0.05	−0.01	−0.03	0.02	0.03	0.01	−0.01	0.07	0.02	0.02	0.03
Int Moisture		1.00	0.01	−0.04	0.00	0.01	0.08	−0.04	−0.04	−0.05	0.03	−0.05	−0.03	−0.10	−0.05
Temp Cold Mo			1.00	−0.15	0.32	0.13	0.13	−0.39	0.22	0.12	0.33	−0.15	−0.33	−0.23	−0.28
Snow Density				1.00	0.33	−0.10	**−0.72**	0.31	0.57	0.51	−0.17	0.31	**0.68**	0.12	0.25
NDVI					1.00	−0.05	−0.46	0.10	0.31	0.32	0.09	−0.09	0.11	−0.15	0.02
Lights						1.00	0.14	−0.09	−0.08	0.00	0.53	−0.09	−0.12	−0.06	−0.06
Soil pH							1.00	−0.51	**−0.65**	−0.59	0.22	−0.31	**−0.66**	−0.30	−0.36
Summer Precip								1.00	0.38	0.45	−0.24	0.39	0.41	0.25	0.21
Winter Precip									1.00	0.51	−0.09	0.37	**0.61**	0.19	0.10
Relative Humid										1.00	−0.11	0.35	0.38	0.27	0.16
Road Density											1.00	−0.26	−0.29	−0.21	−0.15
Surface Area												1.00	0.37	0.17	0.28
Snow Water Eq													1.00	0.22	0.27
TPI														1.00	0.08
Forest Het															1.00

Abbreviations: Comp Topo Index, Compound Topographic Index; Forest Het, Forest Heterogeneity; Int Moisture, Integrated Moisture; Lights, Night Lights; NDVI, Normalized Difference Vegetation Index; Rel Hum, Relative Humidity; Road Den, Road Density; Snow Den, Snow Density; Snow Water Eq, Snow Water Equivalent; Sum Prec, Summer Precipitation; Surf Area, Surface Area; Temp Cold Mo, Mean Temperature in the Coldest Month; TPI, Topographic Position Index; Win Prec, Winter Precipitation.

APPENDIX C

TABLE C1 The eigenvalue, a measure of the amount of variation retained by each principal component, percent variance contribution, and cumulative percent variance contribution of each dimension in the principal components analysis (PCA)

	Eigenvalue	Percent variance	Cumulative percent variance
Dim.1	3.37	21.06	21.06
Dim.2	1.90	11.85	32.92
Dim.3	1.56	9.75	42.67
Dim.4	1.52	9.51	52.18
Dim.5	1.33	8.31	60.48
Dim.6	0.99	6.22	66.70
Dim.7	0.96	6.02	72.72
Dim.8	0.93	5.82	78.54
Dim.9	0.77	4.79	83.33
Dim.10	0.64	4.03	87.35
Dim.11	0.60	3.72	91.08
Dim.12	0.46	2.88	93.96
Dim.13	0.32	2.01	95.97
Dim.14	0.30	1.85	97.82
Dim.15	0.20	1.27	99.09
Dim.16	0.15	0.91	100.00

Note: The first two PCA axes explain 32.92% of the variance in the covariates.

TABLE C2 The percent contribution of each covariate to the first five principal component dimensions

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5
Compound Topographic Index	6.11	6.56	12.91	14.69	0.24
Heat Load	1.55	0.01	1.86	2.83	1.55
Integrated Moisture	2.07	4.17	16.43	11.30	0.79
Mean Temp in Coldest Month	0.46	7.28	2.34	2.74	39.24
Snow Density	5.00	0.34	0.61	24.69	5.67
Normalized Difference Veg Index	0.30	28.65	2.15	2.39	2.80
Night Lights	0.65	0.31	0.68	3.50	0.56
Soil pH	16.89	0.36	0.14	7.78	5.50
Summer Precipitation	6.05	10.51	0.05	2.16	23.51
Winter Precipitation	17.32	3.84	6.69	1.40	1.86
Relative Humidity	8.08	0.00	10.28	15.53	3.68
Road Density	1.97	13.34	1.69	0.43	8.83
Surface Area	10.05	0.97	2.89	9.24	2.74
Snow Water Equivalent	15.94	0.56	15.55	0.21	0.00
Topographic Position Index	6.96	6.87	12.69	0.92	0.27
Forest Heterogeneity	0.61	16.20	13.03	0.20	2.78

Note: Dimension 1 is dominated by moisture-related covariates including summer and winter precipitation, soil pH, and relative humidity, while dimension 2 is dominated by forest-related covariates including long-term NDVI, forest heterogeneity, and road density.

APPENDIX D

TABLE D1 Model validation, as measured with continuous Boyce Index, for all species distribution models generated for Canada lynx in the northwestern United States

Validation data source	Data location	Model being tested	Background	Performance in MT	WA	WY	Region
Withheld	Region	Unequal	Region	1.000[a]	1.000[a]	0.996[a]	0.998[a]
		WA equal	Region	1.000[a]	0.985	0.992[b]	0.992[b]
		WY equal	Region	1.000[a]	0.943	0.985	0.985
	Population	MT	Region	1.000[a]	−0.811	0.220	0.481
		MT	Population	1.000[a]	−0.258	−0.201	0.468
		WA	Region	0.919[b]	0.998	0.561	0.774
		WA	Population	0.697	0.999[b]	0.953	0.998[a]
		WY	Region	−0.808	0.897	0.954	0.498
		WY	Population	−0.182	0.138	0.973	0.897
				MT	**WA**	**WY**	**Region**
Independent	Region	Unequal	Region	0.8670	0.9190[b]	0.9020	0.9600[b]
		WA equal	Region	0.9860[b]	0.8870	0.9070[b]	0.9450
		WY equal	Region	0.9880[a]	0.9200[a]	0.9610[a]	0.9660[a]
	Population	MT	Region	0.9240	0.6270	0.5690	0.8130
		MT	Population	0.8710	0.6390	0.8140	0.6210
		WA	Region	0.3250	0.9020	0.3580	0.7600
		WA	Population	0.6520	0.8940	0.8870	0.9560
		WY	Region	0.0150	0.7680	0.4960	0.4500
		WY	Population	−0.3240	0.3920	0.7160	0.8030

Note: Values in each column marked with a superscript “a” indicate best model performance in that population, superscript “b” indicate second best.

TABLE D2 Model validation, as measured with minimum predicted area at 90% threshold, for all species distribution models generated for Canada lynx in the northwestern United States

Validation data source	Data location	Model being tested	Background	Performance in MT	WA	WY	Region
Withheld	Region	Unequal	Region	17,290[b]	13,092	21,042	83,267
		WA equal	Region	20,647	8,570[b]	8,463[a]	40,790[a]
		WY equal	Region	39,667	13,816	17,585	64,957[b]
	Population	MT	Region	22,411	25,538	64,727	297,087
		MT	Population	14,112[a]	26,188	63,155	235,920
		WA	Region	182,116	11,178	50,266	327,534
		WA	Population	132,787	7,962[a]	43,122	159,878
		WY	Region	212,295	30,605	12,224	307,298
		WY	Population	203,309	58,771	11,395[b]	280,977
				MT	WA	WY	Region
Independent	Region	Unequal	Region	210,714	22,954	22,331[a]	203,419[b]
		WA equal	Region	205,783	21,802[b]	24,842	213,308
		WY equal	Region	207,134	25,685	24,388[b]	199,545[a]
	Population	MT	Region	150,449[a]	30,488	44,899	254,118
		MT	Population	181,272[b]	27,512	47,534	228,531
		WA	Region	217,707	17,961[a]	50,266	348,497
		WA	Population	213,574	24,580	24,877	263,568
		WY	Region	254,859	36,697	52,116	346,885
		WY	Population	243,840	48,045	39,358	283,051

Note: Values are given in km^2, indicating the minimum area required to correctly identify 90% of Canada lynx locations present in a presence/absence categorical map. Lower values indicate greater model efficiency (less area for the same amount of error). Values in each column marked with a superscript "a" indicate best model performance in that population, superscript "b" indicate second best.

APPENDIX E

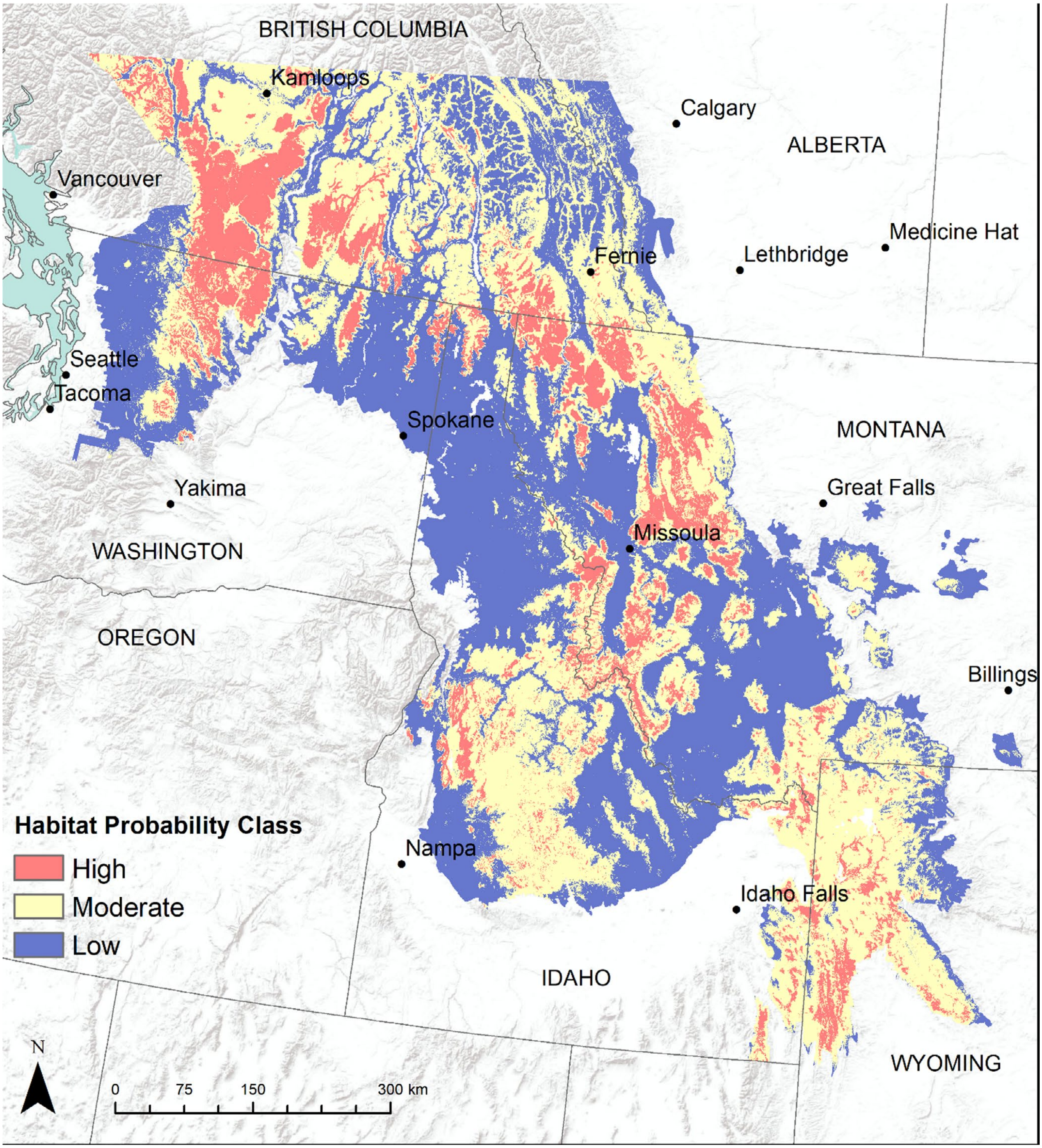

FIGURE E1 Categorical spatial predictions of Canada lynx relative habitat capability across the study region in the northwest United States, as generated by the top-performing species distribution model. Model thresholds are based on correctly assigning 95% of Canada lynx withheld GPS locations for the "High" category and 90% of independent lynx locations for the "Moderate" category. These thresholds provide a more liberal delineation of lynx habitat than the 90%/85% thresholds provided in the main paper

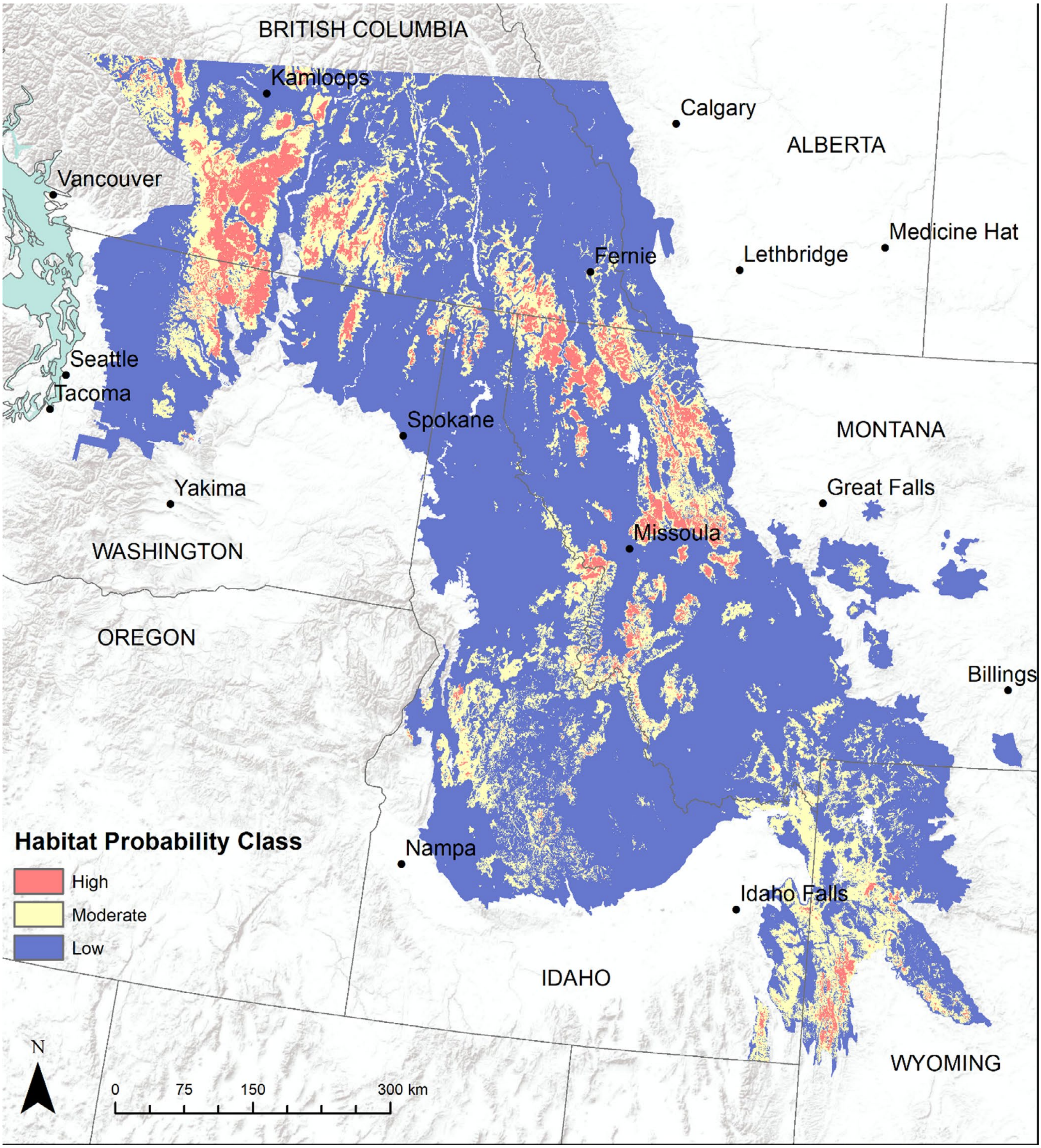

FIGURE E2 Categorical spatial predictions of Canada lynx relative habitat capability across the study region in the northwest United States, as generated by the top-performing species distribution model. Model thresholds are based on correctly assigning 85% of Canada lynx withheld GPS locations for the "High" category and 80% of independent lynx locations for the "Moderate" category. These thresholds provide a more conservative delineation of lynx habitat than the 90%/85% thresholds provided in the main paper