

Habitat use as indicator of adaptive capacity to climate change

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Abstract

Aim: Populations of cold-adapted species at the trailing edges of geographic ranges are particularly vulnerable to the negative effects of climate change from the combination of exposure to warm temperatures and high sensitivity to heat. Many of these species are predicted to decline under future climate scenarios, but they could persist if they can adapt to warming climates either physiologically or behaviourally. We aim to understand local variation in contemporary habitat use and use this information to identify signs of adaptive capacity. We focus on moose (*Alces alces*), a charismatic species of conservation and public interest.

Location: The northeastern United States, along the trailing edge of the moose geographic range in North America.

Methods: We compiled data on occurrences and habitat use of moose from remote cameras and GPS collars across the northeastern United States. We use these data to build habitat suitability models at local and regional spatial scales and then to predict future habitat suitability under climate change. We also use fine-scale GPS data to model relationships between habitat use and temperature on a daily temporal scale and to predict future habitat use.

Results: We find that habitat suitability for moose will decline under a range of climate change scenarios. However, moose across the region differ in their use of climatic and habitat space, indicating that they could exhibit adaptive capacity. We also find evidence for behavioural responses to weather, where moose increase their use of forested wetland habitats in warmer places and/or times.

Main conclusions: Our results suggest that there will be significant shifts in moose distribution due to climate change. However, if there is spatial variation in thermal tolerance, trailing-edge populations could adapt to climate change. We highlight that prioritizing certain habitats for conservation (i.e., thermal refuges) could be crucial for this adaptation.

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Funding information

CST was funded by an NSF Graduate Research Fellowship and the NSF Graduate Research Internship Program. Funding was also provided to APKS by a T-2-3R grant for Nongame Species Monitoring and Management through the New Hampshire Fish and Game Department, and a E-1-25 grant for Investigations and Population Recovery through the Vermont Fish and Wildlife Department.

Editor: Luigi Maiorano

KEYWORDS

adaptive capacity, climate change, habitat suitability, moose (*Alces alces*), range shifts, species distribution model, thermoregulation

1 | INTRODUCTION

Rapid changes to the environment, including those to climate and land cover, threaten the persistence of plant and animal populations globally. Predicting how species will respond to global change is important for developing conservation and management strategies to prevent population declines. Even within species, these responses vary among populations, with populations at the low-elevation or low-latitude edges of a species' range often more sensitive and exposed to climate change than those in the interior or at the leading edge of the range (Morelli et al., 2012). In the absence of climate change refugia, range shifts or adaptation (Hampe & Petit, 2005; Morelli et al., 2012, 2017), these trailing-edge populations will be particularly vulnerable to extirpation from warming climates and declining habitat suitability along the range edge.

Adaptations to increasing temperatures could allow populations to persist as climate warms (Williams et al., 2008). In particular, spatial variation in physiology, morphology and behaviour can allow species to adjust to shifting thermal conditions. For example, sock-eye salmon (*Oncorhynchus nerka*) populations across the Fraser River (British Columbia, Canada) exhibited 2–3°C differences in thermal optima, suggesting that there is potential for salmonid adaptation for greater thermal tolerance (Eliason et al., 2011). Also, American pikas (*Ochotona princeps*) in warmer portions of their range reduce their activity and forage less during the daytime compared to those at higher elevations and latitudes (MacArthur & Wang, 1974; Smith et al., 2016). This example of behavioural plasticity in the face of heat stress is one form of adaptive capacity (Beever et al., 2017). Adaptive capacity is the ability of a species or population to cope with climatic changes and is characterized by three fundamental components: phenotypic plasticity, dispersal ability and genetic diversity (Beever et al., 2016). When the potential for evolutionary adaptation is limited by species generation times, behavioural plasticity (e.g., use of thermal refuges, shifts in activity patterns) is important for species to respond to changing thermal conditions (Beever et al., 2017). Therefore, identifying spatial variation in behaviour can help predict how species' distributions will be affected as the climate warms.

Moose (*Alces alces*) are a cold-adapted ungulate with a geographic range covering much of the forests of northern North America and Eurasia (Hundertmark, 2016). Moose have been expanding northward at the northern edge of their geographic range,

possibly due to increased food availability linked to higher temperatures (Tape et al., 2016). The northeastern United States (hereafter the Northeast) represents part of the southern, trailing edge of the moose geographic range. Moose populations in the Northeast have grown and recolonized southwards despite warming temperatures over the last century (Kunkel et al., 2013; Musante et al., 2010; Wattles & Destefano, 2011). This expansion was enabled by legal protection for populations, changes in forestry practices that improved habitat conditions, and reduced predation (Musante et al., 2010), but moose in the Northeast currently face threats from epizootics of winter ticks exacerbated by warmer winters (Martin et al., 2007). As the region's climate warms, moose may also experience direct thermal stress. In fact, estimates of thermal tolerance for moose suggest that much of the Northeast is unlikely to be optimal for moose even at the present time (McCann et al., 2013; Renecker & Hudson, 1986).

The capacity to adapt to warmer temperatures could allow moose to survive and persist in the Northeast currently and into the future. Prior estimates of thermal thresholds for moose were derived from a small number of captive individuals from cooler regions (McCann et al., 2013; Renecker & Hudson, 1986), so these estimates could prove inaccurate in the Northeast if moose are adapted to regional temperatures (Borowik et al., 2020; McCann et al., 2013). Geographic differences in coat characteristics or body size could alter thermal tolerances (Herfindal et al., 2014; Hoy et al., 2018). For example, moose grow and shed seasonal coats, resulting in a substantial difference in upper critical temperatures between winter (~0°C) and summer (~14°C, McCann et al., 2013; Renecker & Hudson, 1986). Smaller body sizes are associated with warmer temperatures in moose, both over time (Hoy et al., 2018) and across space (e.g., Sand, 1996). Identifying variation in thermal niches across the moose range can help understand whether moose are locally adapted and, by extension, whether this variation might enable future persistence (Peterson et al., 2019; Valladares et al., 2014).

Moose in the Northeast could also tolerate warm temperatures by behaviourally thermoregulating. Moose move to thermal refuges such as forested wetlands and high-shade forests on warm days or during the warmest hours (Street et al., 2015; Wattles et al., 2018a) and increase nocturnal activity on warm days (Dussault et al., 2004). However, this behaviour presents a trade-off between thermoregulation and foraging in early successional forests, which are

optimal for foraging but tend to be less shaded and warmer (van Beest et al., 2012). Moving between thermal refuges and foraging habitat can also increase energy expenditure and mortality risk (e.g., in Alpine ibex: Brivio et al., 2019; Mason et al., 2017), such as road crossing (Wattles et al., 2018b). Further, future temperatures could exceed moose thermal optima even within thermal refuges, because the differences in temperature between habitat types can be relatively small (Lowe et al., 2010). Thus, moose could become more physiologically stressed as temperatures increase due to climate change (Weiskopf et al., 2019). Though many of these mechanisms of behavioural thermoregulation are well established (Ditmer et al., 2018; Montgomery et al., 2019; Street et al., 2015; van Beest et al., 2012; Wattles et al., 2018a), few studies have integrated climate change projections to understand the degree to which variation in habitat use could facilitate future persistence.

Here, we identified characteristics of current moose habitat across the Northeast and used these results to predict the locations of suitable moose habitat in the Northeast in the future under two climate change scenarios. We predicted that moose would select for low temperatures, forested areas, and wetlands (Herfindal et al., 2009; Wattles et al., 2018a). Given this hypothesis, we expected that areas of high habitat suitability for moose would shrink and shift northward under climate change. We also expected that moose populations across the region would occupy different habitat types. Specifically, we predicted that moose in the southernmost portion of the region, where climates are warmer, would use more thermal refuge habitats than those in northern areas, even after accounting for differences in available habitat. We then analysed whether moose habitat use depends on daily temperature and humidity. In this case, we predicted that moose would respond

behaviourally to temperature by using thermal refuges such as forested wetlands on warmer and more humid days.

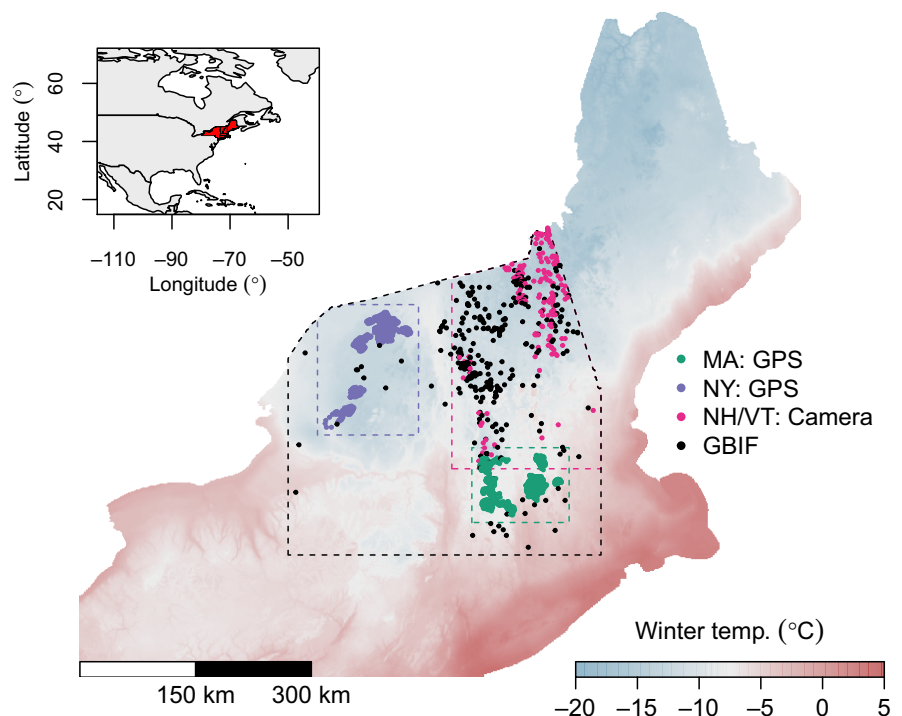
2 | METHODS

2.1 | Study system and moose occurrence data

The study area contains three main ecological subregions: Northeastern Mixed Forest, Adirondack-New England Mixed Forest and Eastern Broadleaf Forest (McNab et al., 2007). Winters are colder and are longer and snowier in northern, inland, and high-elevation areas. Vegetation generally consists of boreal forest (spruce/fir) in the north and at high elevations and broadleaf deciduous forest (maple/beech/birch or oak/hickory) in the south and at low elevations (Janowiak et al., 2018; McNab et al., 2007). Approximately 65% of the region is forest, and an additional 10% is composed of wetlands, which are interspersed within forests (Janowiak et al., 2018).

We used moose occurrence data from three field studies covering four US states: Massachusetts (MA), New Hampshire (NH), New York (NY) and Vermont (VT) (Figure 1). One dataset was obtained from 257 camera traps across Vermont and New Hampshire active between 2014 and 2019. Pictures of moose were taken at 188 of these 257 camera locations (Figure S1). The mean distance between these 188 cameras was 87 km (*SD*: 77 km), and they captured a total of 61,096 photographs of moose, with an average of 638 photographs of moose per camera (range: 72–3,447); given this large number of photographs and the distances between cameras, each camera probably represents multiple individuals. A second dataset covered the Adirondacks region of New York and consisted of GPS

FIGURE 1 Study area and moose locations from the four datasets. The study area is shown in red in the inset map. Each dataset is shown in a different colour: Massachusetts GPS collar data (green), New York GPS collar data (purple), New Hampshire and Vermont camera trap data (pink) and GBIF observations (black). The background is shaded by winter temperature (mean of the daily minimum temperatures from December 1 to February 28). The study area on which background points were randomly placed is shown in the black dashed box. Coloured dashed boxes show the background area for the restricted background set and each of the three local-scale models: Massachusetts only, New Hampshire and Vermont only and New York only



tracking data for 26 adult moose (23 females, three males) over the years 2015–2019. GPS collars obtained one fix every 2 hr for an average of 2 years per individual. The third dataset included 20 GPS-tracked adult moose in Massachusetts (five females, 15 males) with variable fix rates (45–135 min), monitored from 2006 to 2009.

We supplemented these data with an independent dataset, which consisted of all research-grade moose locations in the study area available from the Global Biodiversity Information Facility (GBIF, www.gbif.org) on 6 September 2019. GBIF is an online portal that collates records of species occurrences globally from multiple sources, including institutions and individuals. We used this dataset because it includes different sampling biases than our tracking data. For example, records from online databases like GBIF tend to be closer to human development (Mair & Ruete, 2016) and are more evenly distributed within the study area relative to our GPS and camera trap data (Figure 1). We did not include GBIF data from Maine except as an independent validation dataset (see “Habitat suitability models” section below) because we did not have enough data to represent Maine's moose population, which is the largest in the Northeast (Jones et al., 2019; Wattles & Destefano, 2011).

2.2 | Environmental data

We obtained land cover and climate covariates from the Designing Sustainable Landscapes (DSL) dataset (McGarigal et al., 2017). This dataset provides ecosystem and climate information across the Northeast at 30-m resolution. To map climate, we used mean minimum winter temperature (i.e., mean of the daily minimum temperatures from December 1 to February 28, hereafter “winter temperature”) and mean maximum summer temperature (i.e., mean of the daily maximum temperatures from June 1 to August 31, hereafter “summer temperature”). Mean annual temperature is highly correlated with the other temperature variables ($r > .9$), so we did not include it in our models. To map other habitat variables, we used the DSL's land cover classification at the “ecosystem” level, which provides 153 land cover classes, or at the coarser “formation” level, which provides 20 land cover classes. We also used the DSL's estimated forest biomass (in Mg/ha) as a proxy for both stand age, which is an important determinant of canopy cover and forage availability (Wattles & Destefano, 2011). All DSL variables are estimates for the year 2010, which approximates the temporal extent of our camera trap and GPS location data (2006–2019).

2.3 | Habitat suitability models

To understand the current distribution of moose in relation to land cover and climate, we built a regional habitat suitability model (also called a species distribution model or an ecological niche model; Hirzel & Le Lay, 2008) for the Northeast. Here, “habitat” encompasses both climate and land cover. This model was designed to understand broad-scale patterns in moose distribution, and because

moose in the Northeast are nonmigratory (Healy et al., 2018) and variation in climate is much larger across the landscape than within a single moose home range, we did not model seasonal distributions separately.

We used a presence-background design, which models habitat suitability by comparing habitat at known occurrences to available habitat. We placed background (i.e., pseudo-absence) points randomly in the study area. We restricted this background area to the extent (i.e., minimum bounding rectangle) of our occurrences plus 10 km on all sides, as long as these points fell within the bounds of the DSL dataset (the United States, Figure 1). Different background sets can influence model performance (Barbet-Massin et al., 2012), so we used two background set sizes: either 10,000 background points or the same number of background points as presence points (720, see below).

We also subsampled moose occurrence and background data to reduce overfitting and sampling bias and to account for the differences in sampling rates between our datasets. We resampled all data (presence points, background points and covariates) to an 800-m resolution. We selected this resolution because it minimized differences in sampling intensity between our presence datasets while still maintaining adequate sample sizes and spatial resolution. For example, subsampling to this resolution reduced the number of points from Massachusetts GPS collars from 128,843 to 1,523, but only reduced the sample size for camera traps from 188 to 180. This 800-m resolution has also been effectively used in previous habitat suitability models that study climate change (Franklin et al., 2013; Morelli et al., 2012). We subsampled our data to have at most one presence or background point per 800-m pixel and extracted values for all covariates (described above) for these subsampled pixels. For continuous covariates, we used the mean value within each pixel. For land cover, we used the modal value to identify the dominant land cover class in each pixel.

Next, we separated our data into training data (for fitting the habitat suitability model) and test data (for evaluating the model). To reduce overfitting to different datasets (e.g., GPS data had higher-frequency data collection and thus more occurrences), we stratified sampling for our training data to include an equal number of points from each data source. Because the camera trap data included the fewest occurrences ($n = 180$), the training dataset included 180 randomly selected points from each dataset, for a total of 720 occurrences (Figure S1). The test dataset included the remaining 3,036 subsampled occurrences.

We used the boosted regression tree method (BRT), which fits many decision trees and combines them to produce one best model. We chose this method because it can handle missing values by taking advantage of correlations in the data (Elith et al., 2008; Tierney et al., 2015); biomass values were missing in a small number of cases (1.7%) where the pixel was composed entirely of non-forested land cover classes. In addition, BRTs perform better than linear models or additive models when using a large number of predictors and interactions (De'ath, 2007), which is important because of the large number of land cover classes

included in this study. These models fit nonlinear relationships between predictor and response variables because they estimate the data model from patterns in the data rather than assuming an *a priori* (e.g., linear) relationship across the range of a predictor variable (Elith et al., 2008). We built BRT models predicting presence/background (a binary variable) from winter temperature, summer temperature, biomass and land cover (at either the coarse “formation” or granular “ecosystem” level). The unit of analysis was an 800×800 m pixel, which could represent multiple individuals or GPS fixes, or multiple randomly placed background points.

Using BRTs requires optimizing three parameters: learning rate (the contribution of each tree to the final model), tree complexity (the number of variables in interactions) and bag fraction (the proportion of training data used at each step; Elith et al., 2008). We fit models using 24 combinations of these parameters and selected the parameter set that produced the lowest predictive deviance while still fitting at least 1,000 trees. We repeated this process separately for each background set size (i.e., 10,000 vs. 720 points) and each land cover variable (i.e., “formation” vs. “ecosystem” level). We then simplified these models by removing any predictors that did not decrease the predictive deviance of the full model (Elith et al., 2008); however, this process ultimately did not remove any predictors.

We assessed the precision and accuracy of these four regional models using our test data. We also included in our test data all research-grade moose locations from GBIF in Maine ($N = 73$) and randomly-placed background points in Maine. This independent dataset allowed us to evaluate the ability of our model to predict moose occurrences outside the study area. Next, we evaluated model accuracy using multiple model evaluation metrics: the area under the receiver operating characteristic curve (AUC; Allouche et al., 2006; Fielding & Bell, 1997), the Boyce Index (Boyce et al., 2002; Hirzel et al., 2006), sensitivity (i.e., true positive rate) and specificity (i.e., true negative rate) of the model for thresholds of 0–1, and the true skill statistic (TSS), which is defined as sensitivity + specificity – 1 (Allouche et al., 2006). We selected the model with the background set and land cover variable that maximized the mean of AUC, TSS and Boyce Index as our final regional model. This was the model that used the full set of background points and the coarse “formation” level land cover variable.

We also built separate local models for each of our three tracking datasets (i.e., MA GPS, NY GPS and NH/VT camera data) using the same process as for the full region (i.e., BRTs, parameter optimization). For these models, we used the corresponding background set for each dataset (Figure 1) and the “formation” level land cover classification. Each model included 5,000 background points. Using these separate models, we compared the relative importance of the different predictors for moose in each subregion of the Northeast.

All analyses were performed in R version 3.5.1 (R Core Team, 2018) with packages “raster” (Hijmans, 2019) and “sp” (Pebesma & Bivand, 2005) for manipulating spatial data, “dismo” (Hijmans et al., 2017) for habitat suitability modelling and “ecospat” for calculating the Boyce Index (Di Cola et al., 2017).

2.4 | Projecting future moose habitat suitability

We used the regional habitat suitability model to project future habitat suitability in 2080 under two emissions scenarios: Representative Concentration Pathway (RCP) 4.5 and RCP 8.5. These scenarios represent a peak in greenhouse gas emissions in the mid-21st century and continuing increases in emissions through the 21st century, respectively. DSL provides the same climate variables as used in the final regional model (i.e., winter and summer temperatures) for each of these scenarios in 2080 based on an ensemble average of 14 General Circulation Models (McGarigal et al., 2017). The increase in mean annual temperature from 2010–2080 in a grid cell ranges from 1.60–2.13°C under RCP 4.5 and 3.33–4.40°C under RCP 8.5; increases are larger for winter temperatures. We used our model parameters to predict current and future habitat suitability across the region and at known moose occurrence locations. We did not have future projections for land cover and biomass, so we used values from 2010 to make predictions for 2080. Although land cover and biomass will inevitably change by 2080, forest cover (a particularly relevant class for moose) in New England is projected to decrease only slightly in the near future (4% by 2060, Duveneck & Thompson, 2019). Forest biomass depends more on timber harvest than on land-use change, and harvesting often occurs at a finer spatial scale than the 800-m pixels we model here (Duveneck & Thompson, 2019). Further, previous work shows that including static variables in models improves projections, even if it requires assuming that these characteristics do not change into the future (Stanton et al., 2012). We also calculated the mean suitability within current protected areas using the Protected Areas Database (PADUS; U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2018).

2.5 | Habitat use in response to weather

We gathered hourly temperature and humidity data from the ERA5 and Daymet climate-reanalysis datasets, which are gridded “best estimates” of past conditions (Copernicus Climate Change Service, 2017; Thornton et al., 2018). ERA5 has a spatial resolution of approximately 30 km and a temporal resolution of 1 hr, while Daymet's resolutions are 1 km and 1 day, respectively. We interpolated values spatially and temporally to estimate temperature at the time and location of each of the GPS points. We produced the best estimate of temperature at each moose occurrence by linearly interpolating from neighbouring ERA5 grid points at the closest hour, adjusting the result by the weighted difference of the daily maxima and minima of Daymet and ERA5 at the closest grid point available. This procedure maximizes accuracy by combining the spatial resolution of Daymet with the temporal resolution of ERA5. We quantified uncertainty for this estimate by comparing against two alternative estimates, one using ERA5 only and the other using Daymet only. In the former case, the spatial interpolation is necessarily coarse; in the latter case, an hourly value is derived by assuming a sinusoidal temperature curve connecting the daily maximum and minimum values. Temperature and humidity were then used

to calculate wet-bulb temperature (i.e., air temperature adjusted for humidity) at each moose occurrence point using the Davies-Jones formula (Davies-Jones, 2008).

To analyse the relationship between daily temperature and habitat use by moose, we examined the proportion of moose occurrences in each land cover class under different temperature conditions. We used the occurrence from each GPS-collared individual that was closest to 3:00 p.m. local time on each day to focus on the warmest time of day, reduce potential effects of pseudoreplication, and control for differences in sampling frequency between the two GPS datasets. For this analysis, we used the 30-m DSL data and the “formation” level of land cover classification as in the regional habitat suitability model. However, we also distinguished between forested and open wetlands using the “ecosystem” classification and NatureServe descriptions of the habitats (NatureServe explorer: explorer.natureserve.org; Table S1). We collapsed uncommon land cover classes (agriculture; cliff & rock; developed; grassland & shrubland; lentic; and stream) into an “other” class. The final classes used were as follows: boreal upland forest; Northeastern upland forest; forested wetland; open wetland; and other. We classified occurrences into seasons based on the month (winter: December–March, spring: April–May, summer: June–September, fall: October–November, Lenarz et al., 2009) and binned temperatures every 2°C. Next, we grouped occurrences (using the resampled 3:00 p.m. data) by temperature bin, season and data source (i.e., NY vs. MA GPS data) across all individuals and calculated the proportion of occurrences within each of these groups that fell in each land cover class.

We used a generalized linear model with a quasibinomial (logit) link to model the proportion of occurrences as a function of land cover class, temperature, season and their two-way and three-way interactions. We also included a three-way interaction between land cover type, data source and temperature to account for differences in available habitat across the region and potential differences in responses between populations. Each data point was weighted by the number of relocations in that temperature/season/data source combination, so that combinations that were more common would receive greater weight in the model. We used the MuMIn package to perform model selection on all subsets of the model to simplify our model (Barton, 2015), but ultimately selected the full model (Table S2). We performed this analysis separately for both air and wet-bulb temperatures; we present the results for wet-bulb temperatures in an appendix.

We used this model to predict moose habitat use under a future climate scenario. For this analysis, we used the projected daily maximum air temperatures in 2080 from three Earth system models (CANESM5, MRI-ESM2-0 and BCC-ESM2-MR) from the Coupled Model Intercomparison Project Phase 6 (CMIP6), run under the SSP3-7.0 emissions scenario (Earth System Grid Federation, 2020; Eyring et al., 2016). This scenario results in approximately 2.9–6.3°C of global mean warming by 2,100, roughly comparable to the RCP 8.5 scenario used by the DSL landscape projections described above. We resampled these modelled temperature data to a common grid (1.12×1.12 degrees, the largest common grid size of the Earth

TABLE 1 Variable importance for local and regional models

	MA only	NH/VT only	NY only	Regional
Land cover	6.8	6.8	3.8	7.2
Summer temperature	34.0	68.1	23.9	30.1
Winter temperature	53.5	14.6	63.5	38.1
Biomass	5.7	10.4	8.8	24.6

Note: Values indicate the percentage of total variance explained by each variable.

system models) and calculated the mean and standard deviation of projections for each pixel across the three models. Using these projected air temperatures, we recalculated the number of points that would fall in each temperature bin during the hottest and/or most humid part of the day in 2080 and used our habitat use model to predict the proportion of time moose would spend in each habitat type in 2080 (compared to the present).

3 | RESULTS

3.1 | Habitat suitability models

In our regional habitat suitability model, land cover, winter temperature, forest biomass, and summer temperature all increased the predictive ability of the model and were important predictors of moose presence (Table 1). Of these variables, winter and summer temperature were the most important predictors. Moose were more likely to occur in areas with low temperatures and high biomass relative to background points (Figure 2). There was also an interaction between summer temperature and biomass, where suitability increased most strongly with biomass in areas where summer temperature was highest (Figure S2). Among land cover classes, moose showed the strongest positive relationship with wetlands and upland forests, and the strongest negative relationship with human development, agriculture and coastal land cover classes. The regional model fit well to the test dataset (Boyce Index = 0.963, AUC = 0.871, TSS = 0.484).

The relative importance of each variable differed slightly among our local habitat suitability models. Temperature variables were slightly more important in the New York and Massachusetts models than in New Hampshire/Vermont (Table 1), and biomass and land cover were more important in the regional model than in any local model. The shapes of partial response curves also differed between local models. For instance, low temperatures were more important for habitat suitability in the northern portions of the region (i.e., NY and NH/VT) than in Massachusetts (Figures S3 and S4).

3.2 | Projecting future moose habitat suitability

Under both scenarios (RCP 4.5 and 8.5), our models predicted that the area of suitable habitat for moose will shrink and move by 2080,

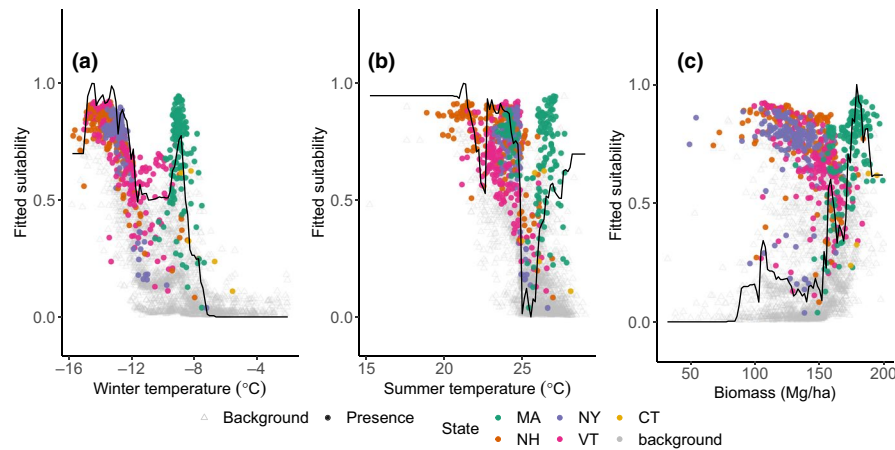


FIGURE 2 Partial dependence plots for moose habitat suitability. Higher values indicate a higher probability of moose presence. Lines are fitted response functions from the regional habitat suitability model. Solid coloured points show fitted values for known occurrences; background points are grey and partially transparent. State abbreviations are: MA (Massachusetts), NH (New Hampshire), NY (New York), VT (Vermont) and CT (Connecticut). Moose tend to occur in low to moderate winter temperatures (a), low to moderate summer temperatures (b), and high-biomass forest (c), relative to what is available in the study area. Local peaks and troughs in fitted response functions (e.g., between -12 and -9°C in panel a) are an effect of using the BRT method (Elith et al., 2008). These dips are probably an effect of sparse sampling in these areas of the data space and do not represent mechanistic relationships between temperature and occurrence

generally retreating northward (Figure 3). Using a threshold of 0.5 for suitable habitat (the optimal TSS threshold value), the expected area of moose presence would decrease 71% under RCP 4.5 and 99% under RCP 8.5. The suitability at known occurrence points under RCP 4.5 would decline most for moose at low latitudes and for all populations under RCP 8.5 (Figure S5). Protected areas were generally more suitable than the overall landscape, but still declined in suitability under future climate projections. For example, the mean suitability of protected areas was 0.48 for current climate versus 0.32 for the entire study area. Under RCP 8.5, these values were 0.11 and 0.07, respectively. This decline in suitability occurred even though protected areas tend to be at northern latitudes within the study area (Figure S6).

3.3 | Habitat use in response to weather

Moose in Massachusetts and New York (the study areas for the habitat use analysis) occurred most often in Northeastern upland forest (70% of GPS points), followed by forested wetlands (13%), and then other categories (8% in boreal upland forest, 4% in open wetlands, and 4% in other). Air and wet-bulb temperatures often exceeded previously published thermal thresholds for moose (e.g., 41% of winter temperatures were $>0^{\circ}\text{C}$ and 70% of summer temperatures were $>20^{\circ}\text{C}$ at 3:00 p.m.). In our linear models, there were significant relationships between moose habitat use, temperature, and season (Figure 4, Table S3). Use of forested wetlands grew as temperatures increased (i.e., significant positive interaction between forested wetland

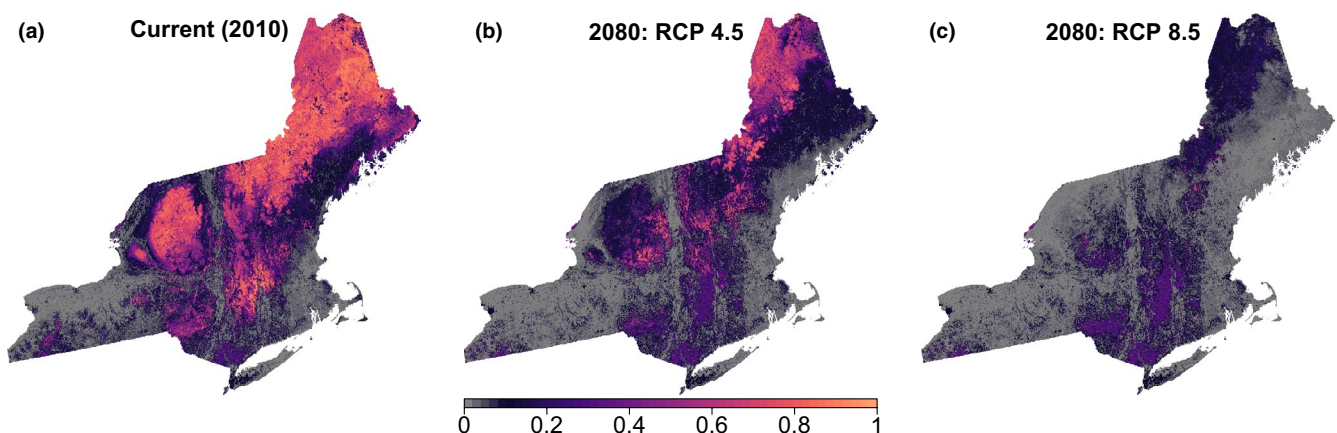


FIGURE 3 Model predictions of moose habitat suitability for the region in 2010 (a) and 2080 under RCP 4.5 (b) and RCP 8.5 (c). Suitability values below 0.1 are shown in grey to increase contrast. Habitat suitability scales from 0 to 1, with increasing values indicating higher probability of moose presence

and temperature, Table S3). For example, the model predicted that, in the spring in Massachusetts, forested wetlands would comprise 4% of moose occurrences on the coolest days (-3°C) and 19% of occurrences on the warmest days (32°C). Accordingly, use of forest habitats decreased with increasing air temperature, though the type of forest that was most affected (boreal or Northeastern upland) depended on the location and season (Figure 4, Figure S7). These results were similar for wet-bulb temperature (i.e., temperature accounting for humidity, Figure S8). Relationships between temperature and land cover were strongest in spring and summer, but were weak in winter (Figure 4, Figure S7). At any given temperature, moose in Massachusetts were more likely to use forests than those in New York.

We predicted small but consistent increases in moose use of wetlands in 2080 under CMIP6 climate projections roughly equivalent to RCP 8.5 projections above. The CMIP6 models predict a mean increase of 5.1°C ($SD: 2.1^{\circ}\text{C}$) across all seasons and the entire study area in 2080. Based on these projected temperatures at each location and date, our habitat use model predicted a 1.1% increase in the proportion of occurrences in forested wetlands in 2080 and a corresponding 1.5% decrease in the proportion of occurrences in Northeastern upland forests (Table S4).

4 | DISCUSSION

Moose in the contiguous United States are considered highly vulnerable to climate change. Their cold-adapted morphology and physiology make them sensitive to increasing temperatures, and they experience particularly high exposure to warm temperatures at the southern edge of their range (Lenarz et al., 2009; Ruprecht et al., 2016; Weiskopf et al., 2019). Our habitat suitability models indicated that moose occurred in locally cooler areas within the Northeast, confirming that they select for cooler areas, even at this

regional scale. Moreover, in many of these areas, at least 50% of days were warmer than previously-identified thresholds at which moose respiration rates begin to increase (McCann et al., 2013; Renecker & Hudson, 1986). That moose persist in warmer climates suggests that these physiological temperature thresholds established on captive animals do not define the limit of the moose geographic range, either because of differences in physiology between captive and wild animals or because exceeding these thresholds causes thermal stress but not to the extent of extirpating a population (see also Montgomery et al., 2019; Murray et al., 2012). Our habitat suitability models also predicted a substantial reduction in the area of suitable moose habitat in 2080 based on changes in temperature alone. These reductions were more severe in the high-emissions scenario (RCP 8.5) than under low emissions (RCP 4.5). However, these predictions do not take into account the potential adaptive capacity of moose, which could be crucial for their persistence in the region.

Our habitat suitability and habitat use models showed that the habitats occupied by moose differ across the Northeast and that moose moved to thermal refuges at relatively fine spatial and temporal scales. These models suggested that moose in southern portions of the region occupied warmer areas than those in the north, even after accounting for warmer average temperatures in the south (Figures S3 and S4). This pattern could stem from differences in morphology, including coat thickness and body size, or from differences in habitat selection. For example, moose in Massachusetts occurred in higher-biomass forests compared to moose in other states. Similarly, our analysis of habitat use indicated that as temperatures increased at the daily scale, moose used a higher proportion of forested wetlands, which provide both shade and evaporative cooling (Wattles et al., 2018a). This relationship between temperature and use of forested wetlands by moose was slightly stronger in Massachusetts than in the Adirondacks Region. This difference in effect size could stem from higher average temperatures in Massachusetts,

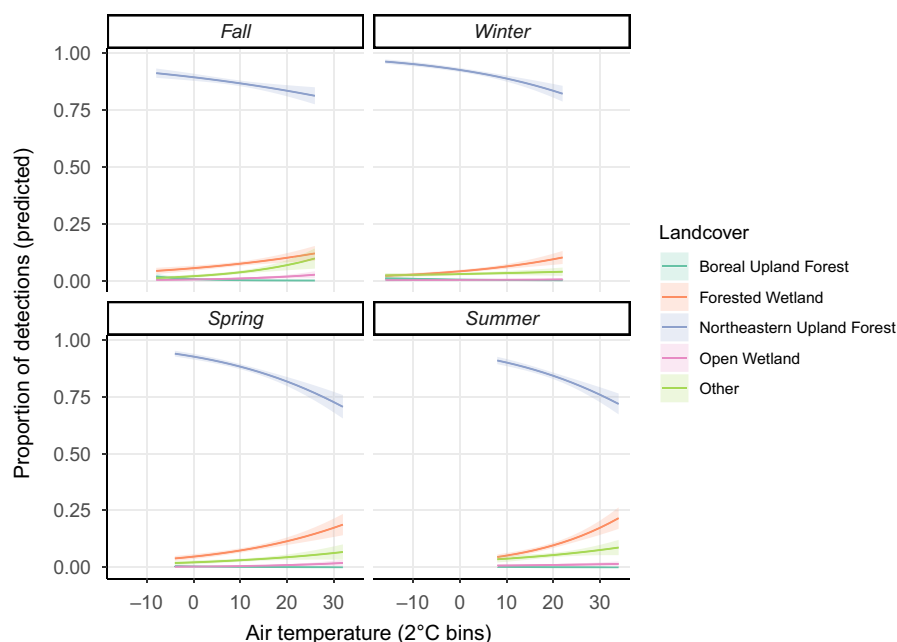


FIGURE 4 Model results predicting moose habitat use according to temperature and season. Lines show means and shaded areas show confidence intervals of predicted proportion of locations in each habitat type. In general, higher temperatures are associated with a lower proportion of locations in forest habitats and a higher proportion of locations in forested wetlands. Lines extend only within the range of temperatures actually observed in each season. Only MA results are shown for clarity of visualization, but NY results were similar; see Figure S7 for both MA and NY results

differences in habitat availability in the two states, or differences in sex ratios of the GPS-collared moose in the two datasets (i.e., female bias in Adirondacks, male bias in Massachusetts; Ofstad et al., 2019). This temperature-dependent habitat selection could be beneficial by reducing energy expenditure for thermoregulation and is consistent with observations of moose habitat selection for forested wetlands in the Northeast (Wattles et al., 2018a) and selection for dense-canopy forests as thermal refuges in Europe (Borowik et al., 2020; Melin et al., 2014; van Beest & Milner, 2013).

Our results show that temperature is associated with changes in habitat suitability and habitat use at multiple scales; however, it is not clear from our study whether these patterns are true adaptations (i.e., that they confer a fitness benefit). Our models are based on occurrence data and thus do not consider the effects of behaviour on other population-level differences, such as population density and reproductive rates (Hoy et al., 2018). High-biomass, late-successional forests are more common in the southern, warmer portion of the region because of forest management practices (Zheng et al., 2010). These habitats can provide thermal refuges, but are generally considered low-quality foraging habitat for moose (Healy et al., 2018; Thompson et al., 1995). At the same time, moose populations in Massachusetts are stable (Massachusetts Department of Conservation and Recreation, *unpublished data*), indicating that moose are able to persist even when they spend more time in high-biomass forests and that the trade-off between foraging and thermoregulation could be weaker than previously assumed (Bjørneraas et al., 2011; Mysterud & Østbye, 1999; van Beest et al., 2012). Smaller body sizes are beneficial in warmer climates, but are also associated with lower reproductive rates in moose (Hoy et al., 2018; Pekins, 2020; Sand, 1996). Similarly, moving to thermal refuges might require crossing roads (Wattles et al., 2018b), which poses a significant mortality risk for moose (Musante et al., 2010). Accordingly, as temperatures increase with climate change, moose may be able to adapt in multiple ways, but this plasticity could also constrain their population sizes or vital rates. Future studies that link morphological and behavioural traits directly to fitness proxies (e.g., Hoy et al., 2018; van Beest & Milner, 2013) could verify our predictions about moose persistence under climate change.

The importance of temperature for moose habitat use suggests that individuals should increase their use of thermal refuges with future climate warming (see above; van Beest et al., 2012; Wattles et al., 2018a). However, our behavioural models predicted relatively little change in use of cover types in 2080 under projected climate change. This small change in habitat use could indicate that moose are constrained by other behavioural requirements or conversely that even small changes in habitat preference could be effective for thermoregulation. It is also possible that our models underpredict changes in moose behaviour over time, since they are based solely on changes in temperature, not on other environmental factors such as land cover and biotic interactions. Similarly, land cover change and indirect effects of temperature could limit the efficacy of this behavioural plasticity; for example, higher site fidelity to thermal refuges during warmer winters could increase winter tick loads (Healy

et al., 2018; Weiskopf et al., 2019), resulting in lower reproductive success (Jones et al., 2017; Pekins, 2020). Tick epizootics are most common in high-density moose populations (Samuel, 2007), so limiting population densities could be important for preventing outbreaks (Ellingwood et al., 2020). Moose might be more strongly constrained by these indirect effects of climate than by direct thermal stress, as suggested by their southward range expansion even as temperatures have increased over the last century (Murray et al., 2012) and by theory that predicts that interactions between abiotic and biotic factors define species' range edges (Sexton et al., 2009; Sirén & Morelli, 2019).

Land cover, forest biomass, temperature, and their interaction were all important for predicting moose habitat suitability, but at different scales. Temperature variables were more important in local models than in the regional model, indicating that local populations are temperature-constrained, but that availability of suitable habitat is important for moose occurrence at a larger spatial scale. This cross-scale variation in variable importance is not uncommon. For example, topography can be important at small but not large scales (Rahbek & Graves, 2001) because small-scale topographical thermal refugia are masked by larger-scale variation in temperature and habitat (Austin & Van Niel, 2011). Local differences in variable importance could also stem partially from differences in data types across our study area (Broman et al., 2014), because camera traps and GBIF data predominated in the northern, colder areas and GPS data predominated in warmer areas. We also observed a weaker behavioural response of moose to temperature in winter, which could be because of alternative thermoregulatory behaviour (e.g., bedding in snow: Sarmiento et al., 2019; van Beest et al., 2012), physiological adaptations (e.g., reduced metabolic rate: Olson et al., 2014), or because temperatures exceeded thermal thresholds less often in winter. Our results complement those from previous studies, which used step-selection methods to show that moose use temperature-dependent habitat selection at the hourly scale (van Beest et al., 2012; Wattles et al., 2018a). Using a similar step-selection approach across the Northeast could further clarify what trade-offs exist in this thermoregulatory behaviour. By building models at multiple spatial and temporal scales, we were able to highlight the potential importance of interactions between climate and habitat in determining moose distribution and behaviour.

This study only covered a portion of the moose's broad, Northern Hemisphere range, but its focus on the relatively small trailing edge area shows its importance to conservation. Trailing range edges contain populations adapted to warmer temperatures that could be critical for safeguarding future populations as climate continues to warm (Zimova et al., 2016). This study suggests that adaptive capacity might enable even sensitive species to persist in the face of rapid climate change. Our results highlight opportunities for decreasing moose vulnerability to climate change in the Northeast (e.g., through restoring and protecting thermal refuges such as closed-canopy forests or forested wetlands in warm areas, Wattles et al., 2018a). Moreover, climate change can induce changes in vegetation (e.g., wetland drying, Sofaer et al., 2016), precipitation patterns (Kunkel et al., 2013; Rodenhouse et al., 2008), and sequences of extreme weather (Kunkel

et al., 2013). These changes, which our models do not consider, could be important for moose forage and parasite transmission (Musante et al., 2010; Weiskopf et al., 2019) and thus could exacerbate or mitigate the direct temperature effects we study here. Next steps include incorporating future changes in land cover and forest biomass, investigating interactions with co-occurring species (e.g., parasites, predators and white-tailed deer, Weiskopf et al., 2019), mapping climate change refugia that can be protected from other stressors to enable persistence of moose, and attempting to identify selective gene regions that have evolved to enable moose to persist in warmer conditions. Our methods, which combine multiple data sources to build regional- and local-scale models under current and projected future conditions, could be applied to other systems to understand species' potential responses to climate change.

ACKNOWLEDGEMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank Agency biologists from the New Hampshire Fish and Game Department, Vermont Fish and Wildlife Department, United States Fish and Wildlife Department and United States Forest Service for assistance with camera trap data. We would specifically like to thank J. Kilborn, R. Patry, R. Cliche, C. Bernier, K. Crumley, T. Smith, L. Rowse, G. Milot, L. Prout and W. Staats. We also thank the many volunteers that assisted with the project, including C. Callahan, K. Courtot, D. Huggins and J. LaRue. We thank H. Kretser and A. D'Amato for early discussions about the project and L. Thompson for reviewing the manuscript. Part of this work was carried out at the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the National Aeronautics and Space Administration.

PERMITS

Massachusetts collar data were collected under permits from the University of Massachusetts Institutional Animal Care and Use Committee (protocol numbers 25-02-15, 28-02-16 and 211-02-01). New York collar data were collected under a permit from the State University of New York—College of Environmental Science and Forestry Institutional Animal Care and Use Committee protocol 140901.

DATA AVAILABILITY STATEMENT

Data and code to reproduce analyses are archived at Dryad Digital Repository (<https://doi.org/10.5061/dryad.6hdr7sqzz>).

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13223>.

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BIOSKETCH

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Author contributions: C.S.T. and T.L.M. designed the study. J.L.F., J.W.H., D.K., K.A.Z., D.W.W. and A.P.K.S. contributed moose location data and advised on its use. C.L., C.R. and E.C. and R.H. advised and contributed climate data. C.S.T. implemented all analyses. C.S.T. and T.L.M. wrote the first draft of the paper, and all authors contributed substantially to revisions and content.

SUPPORTING INFORMATION

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

How to cite this article: Teitelbaum CS, Sirén APK, Coffel E, et al. Habitat use as indicator of adaptive capacity to climate change. *Divers Distrib*. 2021;27:655–667. <https://doi.org/10.1111/ddi.13223>