

Article

Managing Moose from Home: Determining Landscape Carrying Capacity for *Alces alces* Using Remote Sensing

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Abstract: In temperate forests of the northeastern U.S., moose (*Alces alces*) populations are adapted for mixed-age heterogeneous landscapes that provide abundant herbaceous forage in warm months and coniferous forage during winter. Heterogeneity of forest stands is driven by management activities or natural disturbance, resulting in a multi-age forest at a landscape scale. Here, we present a method to estimate landscape carrying capacity of moose by combining remote sensing classification of forest cover class with literature or field-based estimates of class-specific forage abundance. We used Landsat imagery from 1991 to 2013 for the Allegheny National Forest and 2013–2018 for the Adirondack Park, and associated training polygons, to predict based on NDVI and SWI whether a forested landscape fit into one of three cover classes: mature forest, intermediate timber removal, or overstory timber removal. Our three-classes yielded a mean land cover prediction accuracy of 94.3% (Khat = 0.91) and 86.9% (Khat = 0.76) for ANFR and AP, respectively. In the AP, we applied previously calculated summer crude protein values to our predicted cover types, resulting in an estimated average carrying capacity of 760 moose (SD ± 428) across all sampling years, similar in magnitude to a density estimate of 716 moose (95% CI = 566–906) calculated during the same time. Our approach was able to accurately identify forest timber treatments across landscapes at differing spatial and temporal scales and provide an alternative method to estimate landscape-level ungulate carrying capacity. The ability to accurately identify areas of potential conflict from overbrowsing, or to highlight areas in need of land cover treatments can increase the toolset for ungulate management in managed forest landscapes.

Keywords: Adirondacks; *Alces alces*; carrying capacity; LANDSAT; moose; remote sensing



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1. Introduction

Estimating landscape carrying capacity provides a useful tool for the management of ungulates when evaluating the impacts of herbivory on regenerating forest stands [1]. Landscape carrying capacity is the number of ungulates that a landscape can nutritionally support, without individuals experiencing decreases in body condition [2–4]. Although managers have tried to estimate carrying capacity for forested stands in the past for moose [5,6], the estimation process is data intensive, and limited in resolution at large spatial scales. Remote sensing has been used to characterize forested landscapes and moose habitat suitability [7]; however, studies that use forage abundance data to estimate carrying capacity for the landscape have been limited [8]. Estimating landscape-level carrying capacity would allow managers to evaluate potential impacts of land management

decisions on moose populations and assist in managing the complex relationship between forest regeneration and browsing populations.

Over the past twenty-five years, research has highlighted the importance of forest structure on ecosystem services and processes [9,10]. Concurrent advances in remote sensing allow researchers to map and model forest structure using satellite imagery [9,11–13]. Satellite-derived models have been used to estimate aboveground biomass [14,15], land cover type [16], forest structure [11], and successional stage [16–18], and evaluate changes in those metrics over time [19–21]. Satellite-derived data can similarly be utilized to monitor changes in the Normalized Difference Vegetation Index (NDVI), a modified ratio of near infrared to visible red wavelengths, to estimate “greenness” on the landscape [22]. Change in NDVI over time has been used as an index to measure the impacts of drought [23,24], assess forage availability for herbivores [25,26] and estimate agricultural production [27,28]. Most salient to our work, the difference in NDVI over time has been used to identify changes in forest plots due to harvesting activity [16,29].

Moose rely on patches of early successional habitat created by timber harvest for forage and seasonal thermoregulation [30,31]. The vegetation in early successional communities following timber harvest includes species that are preferred forage for moose and are abundant enough to support higher densities of moose compared to mature forests [32,33]. Access to abundant high-quality forage can improve body condition which is vital for species in areas of extreme winter temperatures and snow events [34,35]. However, preference for areas of timber harvest is not without nuance. Moose may avoid recently harvested areas due to continued harvest activity in neighboring stands, lack of vegetation immediately post-harvest, or compositional shifts in the early successional plant community towards non-preferred forage [36,37]. Despite these caveats, early successional habitat is sufficiently important for moose that it is often a primary influence on habitat selection [38]. Therefore, the ability to identify the distribution and quantity of early succession habitat on the landscape is essential for effective population management.

Here we present a method to estimate landscape carrying capacity by combining remote sensing classification of forest cover class with class-specific estimates of forage abundance from the literature. We initially developed the remote sensing method using the northern hardwood ecosystem of the Allegheny National Forest (ANFR) in northwestern Pennsylvania and then applied the method to the mixed temperate/boreal landscape of the Adirondack Park (AP) in northern New York to demonstrate the flexibility of the methodology. We then estimated landscape-level carrying capacity using the remote sensing predictions and data collected by Peterson [39] to demonstrate potential method applications. This relatively rapid and novel approach to estimate landscape-level carrying capacity may be useful for ungulate management where active forestry creates dynamic landscapes that can impact ungulate forage availability.

2. Materials and Methods

2.1. Study Site

2.1.1. Allegheny National Forest, Northwestern Pennsylvania

This study area was within bounds of the Allegheny National Forest Region (ANFR; Figure 1A), in northwestern Pennsylvania (Elk, Forest, McKean, and Warren counties). The ANFR covers 2077 km² in the Allegheny Plateau ecoregion, which is dominated by secondary growth northern hardwood forest [40,41]. The region contains the Allegheny reservoir and is bordered to the west by the Allegheny River, and to the north by the state of New York. The woody overstory is predominately composed of sugar maple (*Acer saccharum*), red maple (*A. rubrum*), black cherry (*Prunus serotina*), and American beech (*Fagus grandifolia*). Areas of development are sparse and typically located at lower elevations across the landscape.

Agricultural production was limited (>7%) in the ANFR and typically occurs as small patches near towns or along roadways. The region has prominent hills and valleys with elevations ranging from 319 to 753 m [42]. The area receives an average of 107 cm of

precipitation a year, including more than 150 cm of snowfall annually, and mean monthly average temperatures range from $-4\text{ }^{\circ}\text{C}$ in winter to $22\text{ }^{\circ}\text{C}$ in summer [41,43,44]. The Allegheny region is well known for production of hardwood timber products [45]. Much of the landscape is subject to periodic timber treatments (e.g., overstory removals and shelterwood cuts; [46]). The distribution of timber treatments are dependent on ownership, stand age, species composition, and the state of neighboring stands, resulting in a dynamic heterogeneous landscape [47].

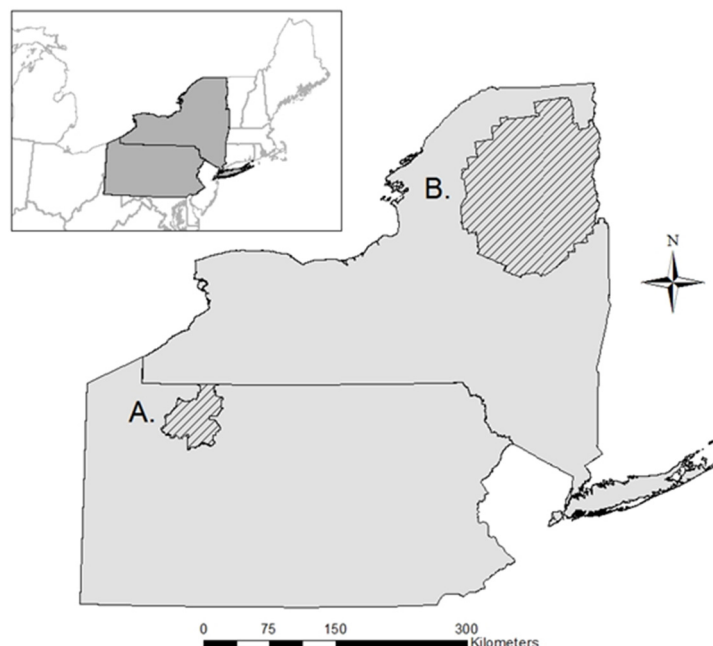


Figure 1. Study site locations of (A) Allegheny National Forest in northwestern Pennsylvania from 1993 to 2013 and (B) Adirondack Park in northern New York from 2015 to 2018.

2.1.2. Adirondack Park, Northern New York

This study area was within the bounds of the Adirondack Park (24,281 km²; Figure 1B), in northern New York. Elevation in the Adirondack Park (AP) ranges from 100 m in low-lying lake shores to over 1600 m in the higher ranges. The park consists of large glacial valleys that gradually rise in elevation to the High Peaks region in the east-central part of the park. Average monthly temperatures range from $-9\text{ }^{\circ}\text{C}$ in winter to $18\text{ }^{\circ}\text{C}$ in summer. The region receives an average of 100 cm of rainfall precipitation a year, with an additional 290 cm of snowfall annually [48].

The AP includes both publicly (61%) and privately owned land (39%), where all publicly owned lands are protected by Article XIV of the New York State Constitution as ‘forever wild forest’ which precludes resource extraction or development. The AP is comprised of a patchwork of the northern boreal ecosystem interspersed with temperate deciduous forests and large peatland complexes. Lower elevations with fertile soils support a diverse array of tree species dominated by American beech, yellow birch (*Betula allegheniensis*), paper birch (*B. papyrifera*), sugar maple and red maple. Higher elevations are more coniferous, dominated by species such as red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*; [33,48]). Because public land acquisition continues within the AP, portions of public land could have been exposed to resource extraction or development immediately prior to acquisition by New York State.

Approximately 25% (13% of all AP land) of the forested private lands within the AP are participants with the New York State Conservation Easement Program. Private properties enrolled in an easement participate in a structured forest management program, which allows for timber harvest and other associated activities. Lands that are subjected to harvest are predominately composed of marketable timber species, such as sugar maple, red maple,

red oak (*Quercus rubra*), white ash (*Fraxinus americana*), black cherry (*Prunus serotina*), and white pine [33]. Timber harvest methods included a combination of shelterwood removal, overstory removal, single tree selection, and salvage thinning.

2.2. Imagery Selection

2.2.1. Allegheny National Forest, Northwestern Pennsylvania

Landsat 5 and 8 satellite imagery (30 m resolution) was acquired from the USGS Global Visualization Viewer for imagery from March to October 1991–2013. We chose one cloudless image (<5% cloud cover) from the acquired Landsat imagery for each year during the focal period, if available. If multiple cloudless images were available within the same year, we selected an image that occurred during peak growing season (July–September) to reduce the seasonal variation associated with spring budding and fall leaf-off to maximize green reflectance. We did not select imagery from consecutive years due to an inability to acquire cloud-free imagery for older imagery at regular intervals. The resulting search yielded images for seven years during 1991–2013: 1991, 1993, 1996, 2000, 2002, 2006, 2009, and 2013 (Appendix A).

2.2.2. Adirondack Park, Northern New York

Landsat 8 satellite imagery (30 m resolution) was acquired annually from the USGS Global Visualization Viewer for imagery from late May to early October 2014–2018. Due to the size of the AP, we used 4 separate Landsat scenes per year (Figure 2). We chose one cloudless image (<5% cloud cover) per scene from the acquired Landsat imagery for each year during the focal period. If multiple cloudless images were available within the same year, we selected an image that occurred during peak growing season (July–September). The resulting data selection process yielded images for each of the five years for two of the four Landsat scenes. For the other two scenes, we only found cloudless images from 2015 to 2018 for one scene and images for 2013 and 2015–2018 for the second. Due to baseline reflectance variation across the four scenes within each year, we analyzed each of the four panels separately through time rather than creating one annual mosaicked landscape to increase prediction accuracy.

2.3. Remote Sensing Classification

We used random forests models [49–51] to classify each of the images across the time series into predictions of forest structure (similar to [16]) for both study sites. Covariates used in the random forests classifiers included NDVI [52,53], two shortwave infrared (SWIR) bands, and the previous predicted map (after 1991) (Table 1). NDVI provides an index of green biomass across a landscape. The use of NDVI helps discern changes in canopy greenness associated with timber harvest.

$$NDVI = \frac{(\text{near} - \text{infrared}) - (\text{red})}{(\text{near} - \text{infrared}) + (\text{red})} \quad (1)$$

Table 1. List of raster variables derived from Landsat satellite imagery used to classify three forest treatment types (i.e., overstory removal, intermediate removal, and mature forest) in northwestern Pennsylvania from 1993 to 2013.

Predictors
NDVI (target scene year)
NDVI (previous scene year)
Difference NDVI (previous target)
Difference in 1.55–1.75 μm Band (previous target)
Difference in 2.09–2.35 μm Band (previous target)
Previous panel prediction (e.g., 2015 landscape for 2016 target scene)

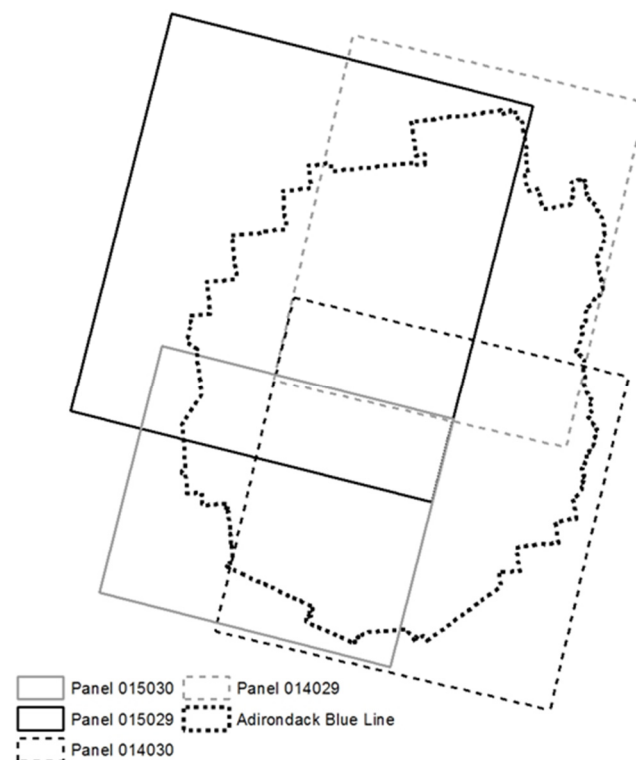


Figure 2. Landsat panels that were required to complete coverage of the Adirondack Park in northern New York from 2015 to 2018.

We also used the two shortwave infrared (SWIR) bands (approximately 1.55–1.75 mm and 2.09–2.35 mm) and took the ratio of each SWIR band divided by the near infrared (NIR) band to reduce the noise from shadows and aerosols. SWIR reflectance can aid in the detection of soil differences following forest harvest activities [54]. We additionally calculated the differences in NDVI and the two SWIR ratios between a given year and the previous time step. Lastly, we included the predicted cover class raster from the previous prediction as a predictor variable in each subsequent model (e.g., cover prediction from 2013 was used in the 2014 model prediction for the AP), using the first panel to create a baseline that would allow for future scenario planning rather than historical evaluations.

The training data for each time period consisted of training polygons derived from landowner data that was provided by two regional timber companies (Lyme Timber Co. and Kane Hardwoods). The data consisted of all timber treatments conducted during and immediately prior to the study. Data for shelterwood and overstory removals were ground-truthed using NAIP Imagery and classified into three forest cover classes: mature (<30% canopy openness, typically no removal), intermediate removal (~30–60% removal), and overstory removal (>60% removal). To ensure adequate representation of the variation within each classification type we used a minimum of 75 polygons representing each of the 3 forest classes. This resulted in 245–270 ($x^- = 260$) training polygons per panel for the ANFR study and 408–1556 ($x^- = 990$) polygons per panel for the AP Study). A mean value was calculated for each training polygon for each predictor raster (NDVI, two SWIR bands, the 3 difference bands, and previous year's prediction, if applicable). The polygon means were aggregated within the respective training polygon classification to create a range of values per classification. For each year, we used a random forest model with 5000 trees, a node size = 2, and proportional sampling of training data where each tree was trained with 70% of the available data for each cover class and the remaining 30% was withheld for out-of-bag testing. After each model was fit, we generated predicted cover classes back out to the landscape as raster values. We measured the accuracy of the model by comparing the value of the training polygon, from each respective sampling year, to the predicted majority

class within each polygon and calculated user's (probability that a polygon is included to an incorrect classification type), producer's (probability that a polygon is excluded from the correct classification type), and overall accuracy (correctly classified polygons/total number of polygons) using a confusion matrix [55]. Lastly, we calculate the Kappa value to evaluate the degree of agreement between our prediction and on the ground training polygons [56].

2.4. Estimation of Landscape-Level Carrying Capacity for Moose

Following the creation of the remote sensed AP map, we incorporated additional land cover layers for non-predicted cover types to create a more accurate depiction of the landscape. First, we removed areas of state-owned public lands acquired ≥ 20 years ago from the prediction raster since those lands were not subject to recent timber treatments. All public forested stands were assumed to be mature given that any lands cut prior to public acquisition have since matured. Additionally, this reduced the amount of model misclassification, since the majority of the high elevation 'high peaks' regions are older public lands. We used NLCD 2016 data for agriculture, developed, conifer, grass, and water classes [57]. We reclassified each of the NLCD datasets into one of seven land cover types to simplify land cover at a large spatial scale (Table 2). In addition to the seven land cover types used in the ANFR, we used a wetland layer developed by the Adirondack Park Agency to ensure that wetlands were adequately identified, given their significance to moose [58].

Table 2. Reclassification of NLCD land cover into one of the seven bins for the Adirondack Park, NY, from 2015 to 2018, used to estimate associated carrying capacity.

NLCD Class	Reclassified
Open water	Water
Developed, open space	Developed
Developed, low intensity	Developed
Developed, medium intensity	Developed
Developed, high intensity	Developed
Rock/clay/sand	Developed
Deciduous forest	Mature Forest
Evergreen forest	Conifer
Mixed forest	Mature Forest
Scrubland	Grass/Scrub
Grassland	Grass/Scrub
Pasture/hay	Agriculture
Cultivated crops	Agriculture
Woody wetlands	Wetlands
Herbaceous wetlands	Grass

We merged the simplified NLCD layer with the AP wetlands layer. The AP wetlands data were higher resolution and derived with more focused methodology, therefore we prioritized the AP wetlands layer; retaining AP wetlands over NLCD data when both were present. We combined the AP wetlands/NLCD layer with four of the non-public lands prediction years (2015–2018) separately into their own annual maps, prioritizing the timber harvest prediction layers over the AP wetlands/NLCD layer in cases where NLCD land cover was classified as deciduous forest, mixed forest, conifer forest and scrubland. Following the merging and classification of the map layers, we then applied known values of animal use days (AUD) for lactating female moose to each cover class [39]. We only derived AUD using summer crude protein nutritional estimate per cover type, as it was determined to be the limiting nutritional value for moose in the Adirondack region of New York (Table 3; [39]). To match the landscape classes of Peterson [39], we used a digital elevation model to differentiate between lowland and upland deciduous and mixed forest at an elevation of 497 m.

Table 3. Land cover class and the estimated number of animal use days (AUD) per kilometer for moose in six different cover types [39] within the Adirondack Park, New York, from 2015 to 2018.

Land Cover Type	Moose/km ²
Conifer forest	0
Upland deciduous forest/mixed forest	0.0028
Lowland deciduous forest/mixed forest	0
Wooded wetland	0
Open wetland	0
Regenerating forest	0.0195

The carrying capacity values for the land cover classes of agriculture, developed/barren, and grassland were not calculated in Peterson [39], and the three cover classes combined accounted for less than five percent of the AP. Additionally, the limited agriculture production in the region focused on hay and corn (1.2% of the landscape), and given other previous works on moose browsing and forage availability [59], we deemed it appropriate to assign those carrying capacity values equal to zero. Lastly, we combined intermediate removal and overstory removal forest cover types to align with the classification of ‘Regenerating Forest’ used in Peterson [39]. We estimated the number of AUD for the Adirondacks for each of the four prediction years by applying the cover capacity estimates to the proportion of each cover type on the landscape and calculated the average AUD value across years. We did not apply a landscape-level moving window because a park-wide estimate of capacity was required, rather than site specific values of capacity. Lastly, we compared our estimates for AUD to moose density estimates calculated using aerial distance sampling during the same time period in the Adirondacks [60].

3. Results

3.1. Allegheny National Forest, Northwestern Pennsylvania

Our three-class prediction (mature forest, intermediate removal and overstory removal) for each of the selected years resulted in overall prediction accuracy of 94.3% across all years (Table 4; Appendix B). The average class producer’s accuracy and user’s accuracy were high across all years (70.6–100%), with intermediate removal cover type having the lowest average user’s accuracy ($x^- = 81.4$) and overstory removal had the lowest producer’s accuracy ($x^- = 88.6$). The majority of the classification confusion occurred between the overstory removal and intermediate removal classes, while mature forest classification had a user’s accuracy of 100% in all but one (2009) of the seven predictive land covers. The average Cohen’s kappa value across all years and panels suggest that the predictions were in agreement (Khat = 0.91) with the reality on the ground. The variable importance plots indicated that NDVI was the most important predictor for land cover in a majority of the predictions ($n = 5$). Following the merging with NLCD spatial layers, the average land cover proportion for mature forest was 70% across all years (Table 5A). The two timber harvest prediction layers, intermediate removal and overstory removal, made up 2.9% and 6.2% of the landscape.

3.2. Adirondack Park, Northern New York

Our predictive land cover for mature forest, intermediate removal and overstory removal in the AP yielded a mean overall accuracy of 86.9% across all years/panels. The average class producer’s accuracy was high across all years and panels, ranging from 80.7 to 91.7%. However, the average user’s accuracy for the three predictive classes of mature forest, intermediate removal and overstory removal were 92.5%, 84.7%, and 62.8% respectively. The average Cohen’s kappa value across all years and panels suggest that the predictions were in ‘substantial’ agreement (Khat = 0.76) with the reality on the ground [56]. The variable importance plots indicated that SWIR bands were the most important predictors for land cover in a majority of the predictions ($n = 15$).

Table 4. The overall prediction accuracy of forest timber treatments (mature forest, intermediate removal or overstory removal) using Landsat 5 and Landsat 8 data for 1993–2013 in northwestern Pennsylvania (A) and for four different Landsat scenes for 2013–2018 in northern New York (B).

A. Study 1: Allegheny National Forest, PA		
Year	Overall Accuracy (%)	Cohen's Kappa
1993	95.5	0.92
1996	93.3	0.89
2000	97.4	0.96
2002	93.7	0.9
2006	94.5	0.92
2009	91.2	0.86
2013	93.1	0.89
B. Study 2: Adirondack Park, New York		
Year	Overall Accuracy (%)	Cohen's Kappa
Panel 014029		
2104	83.9	0.75
2015	88.6	0.8
2016	89.3	0.81
2017	88.9	0.8
2018	89.2	0.81
Panel 014030		
2104	87.8	0.78
2015	84	0.72
2016	83.4	0.7
2017	82.7	0.69
2018	88.6	0.63
Panel 015029		
2015	87.9	0.8
2016	88.6	0.82
2017	86.2	0.77
2018	86	0.74
Panel 015030		
2013	75.8	0.57
2015	91.2	0.84
2016	90.2	0.82
2017	90.6	0.84
2018	87.6	0.79

Table 5. Post remote sensing prediction land cover class landscape proportions after incorporating NLCD data for Allegheny National Forest in northwestern Pennsylvania and after incorporating NLCD data and the Adirondack Park Agency wetlands data for Adirondack Park in northern New York.

Land Cover Class	Year								
Allegheny National Forest	1993	1996	2000	2002	2006	2009	2013	AVG.	STDEV
Mature Forest	75.52	79.24	71.56	72.72	57.06	68.15	63.28	69.65	7.54
Overstory Removal	1.1	2.0	1.0	0.8	13.2	1.0	1.1	2.9	4.6
Intermediate Removal	7.3	2.7	3.8	2.8	6.7	7.8	12.2	6.2	3.4
Conifer	7.3	7.3	6.1	6.1	6.0	6.5	6.0	6.4	0.6
Grass/Scrubland	0.5	0.5	7.0	7.0	6.6	6.1	7.1	5.0	3.1
Water	0.6	0.6	0.8	0.8	0.8	0.8	0.7	0.7	0.1
Developed	1.0	1.0	3.2	3.2	3.2	3.2	3.2	2.6	1.1
Agriculture	6.8	6.8	6.6	6.6	6.6	6.6	6.5	6.6	0.1
Adirondack Park	2015	2016	2017	2018	AVG.	STDEV			
Conifer Forest	16.2	15.5	15.0	15.9	15.7	0.5			
Upland Decid/Mixed Forest	32.3	32.1	32.1	32.0	31.9	0.5			

Table 5. Cont.

Land Cover Class	Year					
Lowland Decid/Mixed Forest	20.3	19.9	18.8	19.5	19.6	0.6
Wooded Wetland	12.4	12.4	12.4	12.4	12.4	0.0
Open Wetland	5.3	5.3	5.3	5.3	5.3	0.0
Regenerating Forest	8.9	10.2	12.9	10.4	10.6	1.7
Ag/Developed/Grass/Scrub	4.6	4.6	4.4	4.5	4.5	0.1

After combining the four spatial layers (prediction, DEC lands, NLCD, and AP Wetlands) and reclassifying to match Peterson [39] cover classes, regenerating forest and upland deciduous/mixed forest accounted for an average 10.6% and 31.9% of the landscape (Table 5B), respectively. The average AUD value across the four years was 759.7 (± 427.8 SD; Figure 3). The AUD estimate was lowest in 2015 (AUD = 679.4) and highest for the 2017 prediction (AUD = 868.6). Additionally, the proportion of predicted regenerating forest was the lowest in 2015 (8.9%) and greatest in 2017 (12.9%). Our estimated moose population in the AP was of similar magnitude as the estimate from aerial distance sampling of 716 (95% CI = 566–906) moose within the Adirondack Park [60].

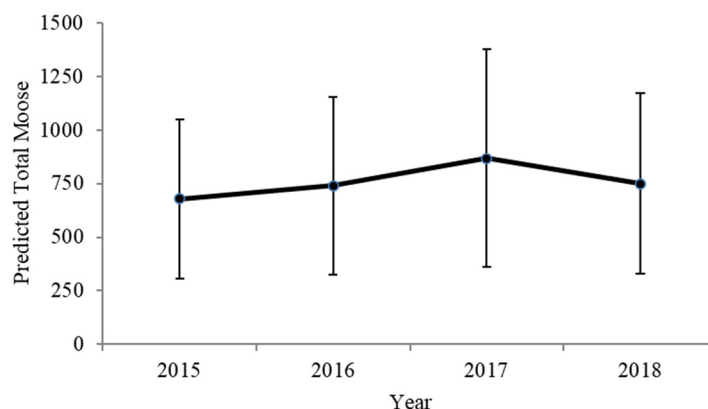


Figure 3. Predicted estimates (mean $\pm$ standard deviation) derived from remote sensing imagery for the total number of moose that can be supported in the Adirondack Park, New York.

4. Discussion

For ungulates that derive the bulk of their necessary forage from only a few land cover types, silvicultural treatments that alter and create those types can inordinately affect forage availability on the landscape. However, assessment of those changes is not possible from general land cover classifications (e.g., NLCD) due to the lack of specific land cover predictions within the national land cover layers [57]. Additionally, compiling silvicultural treatment data at a landscape scale can be difficult due to data variation among multiple stakeholders and the complex public-private nature of timber harvest networks. Here, we show that it is possible to create and update land cover maps that accurately predict the spatial distribution in land cover types in ways that meaningfully relate to moose carrying capacity at large spatial scales. This work highlights the utility of combining multiple forms of remote sensing data and on the ground data collection to (1) refine our understanding of habitat condition by better classifying forest cover into biologically relevant sub-categories; and (2) by incorporating known estimates of forest cover type carrying capacity to estimate landscape-scale carrying capacity. Our method provided a useful tool that can aid in the management of ungulates in dynamic forested landscapes by giving managers the ability to evaluate the current land cover capacity for ungulate populations and to assess long-term impacts by identifying patches of landscape that may transition from one cover class to another (i.e., harvest of a mature stand, significantly increasing capacity, or transitioning from early successional stands into mature forest, significantly decreasing capacity).

Our work emphasizes the role that timber treatments play in influencing landscape-scale carrying capacity for ungulates, and that active engagement with forest management companies and private landowners can produce high-resolution land cover identification. By engaging corporate and private landowners and pooling data across sources, more accurate landscape maps can be developed to help aid in wildlife management and research [37]. Providing managers with the ability to accurately evaluate current land cover composition can help to provide insight on the future trajectory of ungulate populations, thereby helping to determine appropriate actions to meet management objectives. While our work focuses on anthropogenic-driven forest change, the methodology could be applied to blow down, fire or other large-scale forest landscape change and determine how those impacts may influence ungulate populations. Lastly, our method bridges the gap between landowner-driven localized forest management and large-scale population management objectives developed by state agencies.

Our timber harvest modeling approach was applied to two study sites that varied in spatial extent and temporal scale, but yielded predictions that were fairly accurate despite those differences. There was greater prediction variation within the AP, likely because of the AP's land area is ten times greater than the ANFR and contains greater variation in forest types and elevation. The temporal differences between the studies, ranging from annual predictions to up three-year intervals, did not reduce our ability to identify anthropogenic forest change on the landscape or negatively influence prediction accuracy. Despite the greater variation at the larger spatial scale, the demonstrated predictive ability at multiple spatial scales makes our classification approach and associated carrying capacity estimates a viable tool for the management of large ungulates, as large ungulates are managed at multiple spatial scales, from localized impacts to larger scale management units [61]. Additionally, the temporal flexibility allows prediction of the impacts of recent timber harvest on an annual basis or to periodically evaluate landscape changes when setting long-term management objectives [32]. Recent approaches have utilized LiDAR to create more comprehensive forest cover predictions that can identify more subtle variations in stand structure [51,62,63], but LiDAR can be cost prohibitive when predicting forest cover at large spatial scales or at multiple points in time [12].

5. Conclusions

In both of our case studies, only two or three broadly classified land cover types contributed to the carrying capacity for moose at larger spatial scales. While localized forage abundance may impact individual survival and fecundity [64,65], fine-scale variations may be nearly undetectable at the large spatial scales at which large ungulates are managed. It is even possible that a single, potentially rare land cover class (e.g., regenerating forest) can influence carrying capacity on a massive landscape as we identified in the case of moose in the Adirondacks. This can result in substantial shifts in landscape-level carrying capacity in very short-order in dynamic predominately hardwood forests that is controlled by anthropogenic change (i.e., timber harvest regimes). The role of one or two cover classes highlights the need for managers to regularly evaluate the current landscape-level capacity and determine how future cover change can impact large ungulates. Many state agencies tend to regulate ungulates by setting and altering harvest tag allocation, often based on current ungulate browsing impacts. By using remote sensing to predict current forest condition and evaluate potential changes in ungulate carrying capacity, agencies can increase or decrease harvest to reflect anticipated carrying capacity, rather than managing for impacts post-hoc, when landscape change has already been significant and/or animal population size or health have already responded to change.

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Appendix A

List of Landsat 5 and 8 scene images used in a time series regression to estimate forest classes across the Allegheny National Forest, Pennsylvania and the Adirondack Park, New York.

Panel	Year	Date	Scene
<i>Case Study 1: Allegheny National Forest, Pennsylvania</i>			
017031	1991	7-Apr	LT50170311991097XXX03
017031	1993	30-May	LT50170311993150PAC03
017031	1996	26-Aug	LT50170311996239XXX01
017031	2000	6-Sep	LT50170312000250XXX03
017031	2002	12-Sep	LT50170312002255LGS01
017031	2006	9-Oct	LT50170312006282GNC01
017031	2009	23-Mar	LT50170312009082GNC01
017031	2013	26-Sep	LC80170312013269
<i>Case Study 2: Adirondack Park, New York</i>			
014029	2014	8-Sep	LC08_L1TP_014029_20140908_20170303_01_T1
014029	2015	27-Sep	LC08_L1TP_014029_20150927_20170225_01_T1
014029	2016	13-Sep	LC08_L1TP_014029_20160913_20180130_01_T1
014029	2017	30-Jul	LC08_L1TP_014029_20170730_20170811_01_T1
014029	2018	5-Oct	LC08_L1TP_014029_20181005_20181010_01_T1
014030	2014	6-Jul	LC08_L1TP_014030_20140706_20170304_01_T1
014030	2015	27-Sep	LC08_L1TP_014030_20150927_20170225_01_T1
014030	2016	13-Sep	LC08_L1TP_014030_20160913_20180130_01_T1
014030	2017	30-Jul	LC08_L1TP_014030_20170730_20170811_01_T1
014030	2018	5-Oct	LC08_L1TP_014030_20181005_20181010_01_T1
015029	2015	16-Jul	LC08_L1TP_015029_20150716_20170226_01_T1
015029	2016	4-Sep	LC08_L1TP_015029_20160904_20170221_01_T1
015029	2017	23-Sep	LC08_L1TP_015029_20170923_20171013_01_T1
015029	2018	22-Jun	LC08_L1TP_015029_20180622_20180703_01_T1
015030	2013	28-Sep	LC08_L1TP_015030_20130928_20170308_01_T1
015030	2015	16-Jul	LC08_L1TP_015030_20150716_20170226_01_T1
015030	2016	20-Sep	LC08_L1TP_015030_20160920_20170221_01_T1
015030	2017	23-Sep	LC08_L1TP_015030_20170923_20171013_01_T1
015030	2018	21-May	LC08_L1TP_015030_20180521_20180605_01_T1

Classification error matrix for the three-class random forest prediction model for each of the sampling periods in northwestern Pennsylvania from 1993–2013 (A) and for each of the four panels and sampling periods in northern New York from 2013–2018 (B).

A.		Pennsylvania			
Classification		Reference			
	1993	Mature	Overstory Removal	Intermediate Removal	User's Accuracy
	Mature	107	0	0	1.00
	Overstory Removal	0	113	8	0.93
	Intermediate Removal	3	0	19	0.86
	Producer's Accuracy	0.97	1.00	0.71	
	Overall Accuracy (%)	95.5			
	Kappa Index	0.92			
Classification		Reference			
	1996	Mature	Overstory Removal	Intermediate Removal	User's Accuracy
	Mature	100	0	0	1.00
	Overstory Removal	0	113	8	0.93
	Intermediate Removal	5	3	20	0.71
	Producer's Accuracy	0.95	0.97	0.71	
	Overall Accuracy (%)	93.3			
	Kappa Index	0.89			
Classification		Reference			
	2000	Mature	Overstory Removal	Intermediate Removal	User's Accuracy
	Mature	98	0	0	1.00
	Overstory Removal	0	99	5	0.95
	Intermediate Removal	2	0	46	0.97
	Producer's Accuracy	0.98	1.00	0.91	
	Overall Accuracy (%)	97.4			
	Kappa Index	0.96			
Classification		Reference			
	2002	Mature	Overstory Removal	Intermediate Removal	User's Accuracy
	Mature	89	0	0	1.00
	Overstory Removal	2	89	14	0.85
	Intermediate Removal	0	0	57	1.00
	Producer's Accuracy	0.98	1.00	0.80	
	Overall Accuracy (%)	93.7			
	Kappa Index	0.9			
Classification		Reference			
	2006	Mature	Overstory Removal	Intermediate Removal	User's Accuracy
	Mature	94	0	0	1.00
	Overstory Removal	0	83	2	0.98
	Intermediate Removal	8	4	59	0.83
	Producer's Accuracy	0.92	0.95	0.97	
	Overall Accuracy (%)	94.5			
	Kappa Index	0.92			

		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	2009				
	Mature	121	0	1	0.99
	Overstory Removal	1	49	15	0.75
	Intermediate Removal	3	1	58	0.93
	<i>Producer's Accuracy</i>	0.97	0.97	0.78	
	Overall Accuracy (%)	91.2			
	Kappa Index	0.86			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	2013				
	Mature	109	0	0	1.00
	Overstory Removal	0	56	13	0.81
	Intermediate Removal	1	3	68	0.94
	<i>Producer's Accuracy</i>	0.99	0.95	0.84	
	Overall Accuracy (%)	93.1			
	Kappa Index	0.89			
B.	New York				
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 014029—2014				
	Mature	267	2	13	0.95
	Overstory Removal	23	4	138	0.84
	Intermediate Removal	12	142	51	0.69
	<i>Producer's Accuracy</i>	0.88	0.96	0.68	
	Overall Accuracy (%)	83.9			
	Kappa Index	0.75			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 014029—2015				
	Mature	322	0	13	0.96
	Overstory Removal	48	4	422	0.89
	Intermediate Removal	0	57	38	0.6
	<i>Producer's Accuracy</i>	0.87	0.93	0.89	
	Overall Accuracy (%)	88.6			
	Kappa Index	0.8			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 014029—2016				
	Mature	312	0	23	0.93
	Overstory Removal	36	3	435	0.92
	Intermediate Removal	0	60	35	0.63
	<i>Producer's Accuracy</i>	0.9	0.95	0.88	
	Overall Accuracy (%)	89.3			
	Kappa Index	0.81			

		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014029—2017</i>				
	Mature	301	3	31	0.9
	Overstory Removal	30	6	438	0.92
	Intermediate Removal	0	65	30	0.68
	<i>Producer's Accuracy</i>	0.91	0.88	0.88	
	Overall Accuracy (%)	88.9			
	Kappa Index	0.80			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014029—2018</i>				
	Mature	336	3	26	0.92
	Overstory Removal	34	3	397	0.91
	Intermediate Removal	5	73	27	0.7
	<i>Producer's Accuracy</i>	0.9	0.92	0.88	
	Overall Accuracy (%)	89.2			
	Kappa Index	0.81			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014030—2014</i>				
	Mature	335	0	22	0.94
	Overstory Removal	52	4	625	0.92
	Intermediate Removal	0	105	70	0.6
	<i>Producer's Accuracy</i>	0.87	0.96	0.87	
	Overall Accuracy (%)	87.8			
	Kappa Index	0.78			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014030—2015</i>				
	Mature	554	0	32	0.82
	Overstory Removal	77	5	363	0.95
	Intermediate Removal	0	74	75	0.5
	<i>Producer's Accuracy</i>	0.77	0.94	0.88	
	Overall Accuracy (%)	84.0			
	Kappa Index	0.72			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014030—2016</i>				
	Mature	597	0	33	0.95
	Overstory Removal	83	3	336	0.8
	Intermediate Removal	0	51	77	0.4
	<i>Producer's Accuracy</i>	0.88	0.94	0.75	
	Overall Accuracy (%)	83.4			
	Kappa Index	0.70			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014030—2017</i>				
	Mature	586	0	44	0.93
	Overstory Removal	79	2	341	0.81
	Intermediate Removal	0	49	79	0.38
	<i>Producer's Accuracy</i>	0.88	0.96	0.73	
	Overall Accuracy (%)	82.7			
	Kappa Index	0.69			

		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 014030—2018</i>				
	Mature	926	2	12	0.99
	Overstory Removal	73	17	57	0.39
	Intermediate Removal	5	62	26	0.67
	<i>Producer's Accuracy</i>	0.92	0.77	0.6	
	Overall Accuracy (%)	88.6			
	Kappa Index	0.63			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 015029—2015</i>				
	Mature	684	0	37	0.95
	Overstory Removal	63	14	467	0.86
	Intermediate Removal	1	216	74	0.74
	<i>Producer's Accuracy</i>	0.91	0.96	0.81	
	Overall Accuracy (%)	87.9			
	Kappa Index	0.80			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 015029—2016</i>				
	Mature	680	0	41	0.94
	Overstory Removal	49	13	482	0.89
	Intermediate Removal	1	216	74	0.74
	<i>Producer's Accuracy</i>	0.93	0.94	0.81	
	Overall Accuracy (%)	88.6			
	Kappa Index	0.82			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 015029—2017</i>				
	Mature	754	0	47	0.94
	Overstory Removal	61	26	379	0.81
	Intermediate Removal	5	208	76	0.72
	<i>Producer's Accuracy</i>	0.92	0.89	0.75	
	Overall Accuracy (%)	86.2			
	Kappa Index	0.77			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 015029—2018</i>				
	Mature	896	4	52	0.94
	Overstory Removal	68	23	252	0.73
	Intermediate Removal	15	190	56	0.73
	<i>Producer's Accuracy</i>	0.92	0.88	0.7	
	Overall Accuracy (%)	86.0			
	Kappa Index	0.74			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	<i>Panel 015030—2013</i>				
	Mature	111	0	27	0.8
	Overstory Removal	19	4	192	0.89
	Intermediate Removal	0	14	51	0.25
	<i>Producer's Accuracy</i>	0.85	0.78	0.74	
	Overall Accuracy (%)	75.8			
	Kappa Index	0.57			

		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 015030—2015				
	Mature	153	0	18	0.89
	Overstory Removal	12	2	265	0.95
	Intermediate Removal	0	29	11	0.72
	<i>Producer's Accuracy</i>	0.93	0.94	0.9	
	Overall Accuracy (%)	91.2			
	Kappa Index	0.84			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 015030—2016				
	Mature	244	0	13	0.95
	Overstory Removal	20	4	169	0.88
	Intermediate Removal	0	29	11	0.72
	<i>Producer's Accuracy</i>	0.92	0.88	0.88	
	Overall Accuracy (%)	90.2			
	Kappa Index	0.82			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 015030—2017				
	Mature	215	0	16	0.93
	Overstory Removal	12	4	195	0.92
	Intermediate Removal	0	34	14	0.71
	<i>Producer's Accuracy</i>	0.95	0.89	0.87	
	Overall Accuracy (%)	90.6			
	Kappa Index	0.84			
		Reference			
		Mature	Overstory Removal	Intermediate Removal	User's Accuracy
Classification	Panel 015030—2018				
	Mature	238	0	13	0.95
	Overstory Removal	23	8	141	0.82
	Intermediate Removal	1	50	16	0.75
	<i>Producer's Accuracy</i>	0.91	0.86	0.83	
	Overall Accuracy (%)	87.6			
	Kappa Index	0.79			

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