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Modelling moose–forest interactions under different predation scenarios at Isle Royale National Park, USA

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Abstract. Loss of top predators may contribute to high ungulate population densities and chronic over-browsing of forest ecosystems. However, spatial and temporal variability in the strength of interactions between predators and ungulates occurs over scales that are much shorter than the scales over which forest communities change, making it difficult to characterize trophic cascades in forest ecosystems. We applied the LANDIS-II forest succession model and a recently developed ungulate browsing extension to model how the moose population could interact with the forest ecosystem of Isle Royale National Park, USA, under three different wolf predation scenarios. We contrasted a 100-yr future without wolves (no predation) with two predation scenarios (weak, long-term average predation rates and strong, higher than average rates). Increasing predation rates led to lower peak moose population densities, lower biomass removal rates, and higher estimates of forage availability and landscape carrying capacity, especially during the first 40 yr of simulations. Thereafter, moose population density was similar for all predation scenarios, but available forage biomass and the carrying capacity of the landscape continued to diverge among predation scenarios. Changes in total aboveground live biomass and species composition were most pronounced in the no predation and weak predation scenarios. Consistent with smaller-scale studies, high browsing rates led to reductions in the biomass of heavily browsed *Populus tremuloides, Betula papyrifera*, and *Abies balsamea*, and increases in the biomass of unbrowsed *Picea glauca* and *Picea mariana*, especially after the simulation year 2050, when existing boreal hardwood stands at Isle Royale are projected to senesce. As a consequence, lower predation rates corresponded with a landscape that progressively shifted toward dominance by *Picea glauca* and *Picea mariana*, and lacking available forage biomass. Consistencies with previously documented small-scale successional shifts, and population estimates and trends that approximate those from this and other boreal forests that support moose provide some confidence that these dynamics represent a trophic cascade and therefore provide an important baseline against which to evaluate long-term and large-scale effects of alternative predator management strategies on ungulate populations and forest succession.

Key words: disturbance; forest simulation model; herbivory; Isle Royale National Park; LANDIS-II; predator management; trophic cascade.

INTRODUCTION

Browsing by ungulates can alter forest productivity, successional trajectories, nutrient cycling, and fire regimes (Hobbs 1996, Danell et al. 2006) and these changes can feed back to alter the sustainability of landscapes for a wide range of species, including ungulate populations. Loss of top predators from forest ecosystems is a major factor contributing to high ungulate population densities and chronic over-browsing across North America (Terborgh et al. 1999, Rooney and Waller 2003, Elmhagen and Rushton 2007). As a consequence, conserving or reintroducing predator populations may be a way to manage the effects of herbivory on ecosystems via induced trophic cascades (Terborgh et al. 1999, Demarais et al. 2012, Ripple and Beschta 2012).

The traditional definition of a trophic cascade includes a change in the biomass of primary producers, which occurs in direct response to a change in the biomass of herbivores, which occurs in direct response to a change in the biomass of top predators (Hairston et al. 1960, Oksanan et al. 1981, Fretwell 1987, and see Peterson et al. [2014] for further discussion). Empirical studies of forested ecosystems subjected to heavy browsing by ungulates suggest that top-predators can mitigate the impacts of browsing to influence species composition and abundance (Potvin et al. 2003, Demarais et al. 2012, Peterson et al. 2014). However, such trophic cascades are difficult to diagnose within predator–ungulate–forest systems because ungulates can only access young and

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short-statured trees while the majority of the live forest biomass is stored in the tissue of large over story trees. For an ungulate population to influence total forest biomass it needs to prevent short-statured trees from entering the tree canopy, a successional process that may take decades in closed-canopy forests. Within such time spans, predator populations can exhibit a high degree of variability, with effects on ungulate populations that may range from strong top-down effects to virtually no effect at all (Peterson et al. 2014). Because these fluctuations occur on a temporal scale that is much shorter than forest succession, it can be difficult to determine how a trophic cascade should manifest itself in terms of long-term and large-scale effects on forest biomass.

Isle Royale National Park is a model ecosystem for empirically examining trophic interactions in forest ecosystems (Peterson et al. 2014). An archipelago in Lake Superior, USA (Fig. 1), Isle Royale is home to populations of wolves and moose that have been intensively studied for over 50 yr (Nelson et al. 2011). Moose are the primary prey of wolves and there are no other ungulates (e.g., white-tailed deer) on the island to buffer the wolf population against declines in the moose population. The moose population has generally fluctuated around 1–2 per km^2 with a wolf population typically between 25 and 50 per 1000 km^2 (15–30 individuals, although it has reached as high as 50; Fig. 1). Inbreeding depression and canine parvovirus have presumably reduced the degree to which wolves regulate the moose population (Peterson et al. 1998) and effects of moose browsing on the vegetation of Isle Royale are well documented (Pastor et al. 1998). However, a recent decline in the wolf population has raised concerns about the eventual extinction of the population and potential increases in the effects of moose browsing (Vucetich et al. 2012). The most recent estimate found just two wolves on the island (Vucetich and Peterson 2016) and the National Park Service is actively deciding whether to intervene by introducing new animals

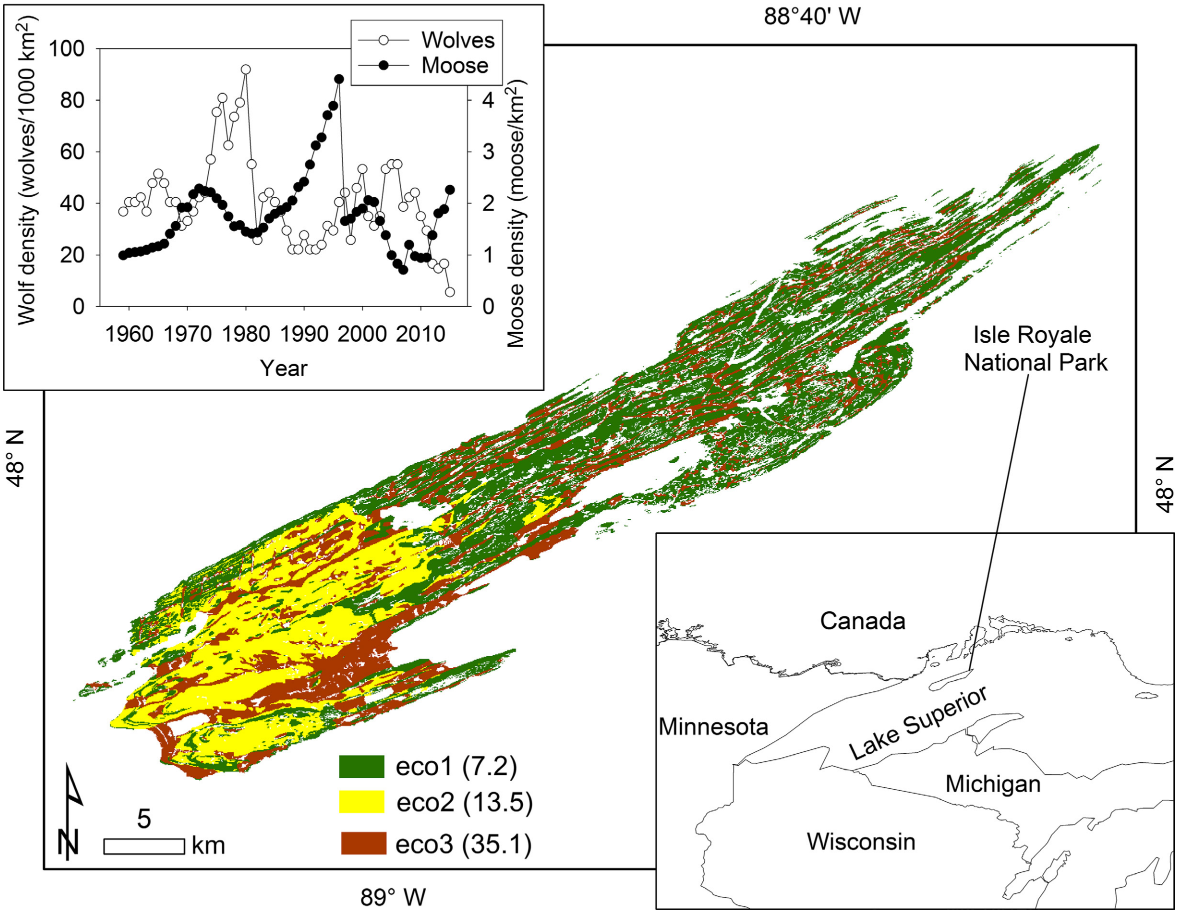

FIG. 1. Isle Royale National Park, USA is an archipelago in Lake Superior, along the north shore of Minnesota and Canada (inset lower right) and home to populations of wolves and moose (inset upper left, data from Vucetich and Peterson [2015]). Model simulations for this study were carried out for the main island and for small islands known to be accessible to moose. Species-specific plant establishment probabilities and growth rates differed by ecoregions, which were based on soil depth and available water holding capacity (awhc, cm). Shallow soils over bedrock (eco1) had a mean awhc of 7.2 cm, deeper glacial soils (eco2) had a mean awhc of 13.3 cm, and alluvial soils (eco3) had a mean awhc of 35.1 (see *Methods* for additional details). [Colour figure can be viewed at wileyonlinelibrary.com]

to the population (Green 2016). This study addresses the potential impacts different wolf management scenarios could have on feedbacks between the moose population and landscape patterns of forage availability, forest biomass, and succession across the entire island and over the next century.

Much of what is known about the effects of moose browsing in boreal forests has come from studies conducted at Isle Royale. A history of heavy moose browsing severely stunts the growth of highly preferred plant species (Risenhoover and Maass 1987, Brandner et al. 1990). This can delay or even prevent recruitment to the tree canopy and generally accelerate the rate of succession to unbrowsed species, such as white spruce (*Picea glauca*; Snyder and Janke 1976, McInnes et al. 1992, Rotter and Rebertus 2015). Deciduous plants are the primary food source for moose on the island during both summer and winter (Risenhoover 1987, Sell 2007, Hodgson 2010). Some of these species (e.g., aspen [*Populus tremuloides*] and paper birch [*Betula papyrifera*]) are relatively tolerant of moderate moose browsing, although their height growth is reduced following tissue removal (De Jager and Pastor 2008, De Jager et al. 2009). Balsam fir (*Abies balsamea*) is heavily browsed during winter in areas where it is rare and where moose densities are relatively high, and is less tolerant of moderate to high browsing rates as compared to deciduous species (De Jager et al. 2009). As a result, browsing prevents *A. balsamea* from entering the canopy in some areas of Isle Royale and causes the species to exist as >40-yr-old shrub-like trees (Vucetich and Peterson 2014). As mature forest stands at Isle Royale age, heavy browsing may limit recruitment, resulting in *Picea glauca*-dominated savanna-like areas (Rotter and Rebertus 2015), which offer little forage biomass for moose. Although the particular plant species and magnitude of effects have been shown to vary, the effects of moose browsing are generalizable across boreal forests: persistently high rates of browsing reduce plant productivity and eventually cause a loss of preferred species from entering the forest canopy, causing associated shifts in forest structure and species composition (Pastor and Danell 2003).

These previous studies suggest that moose browsing plays a key role in structuring forest succession at Isle Royale, despite the presence of wolves. However, no study has examined moose–forest interactions at scales larger than a single valley at Isle Royale or beyond a couple of decades (Pastor et al. 1998, De Jager and Pastor 2009). It is unclear how forest succession could play out over an entire landscape and over a long period of time under alternative predation scenarios. How would moose–forest interactions be different in the presence of a healthy wolf population, exhibiting stronger top-down effects on the moose population, or on the other hand, without any regulatory effects of wolves at all? To address these uncertainties, we used the LANDIS-II modeling platform (Scheller et al. 2007), including a recently developed ungulate browsing extension (De Jager et al. 2017), to conduct a simulation modeling experiment. We simulated reciprocal interactions between the moose population and forest landscape of Isle Royale under three different scenarios of wolf predation. We asked, (1) What if the wolf population goes extinct, new wolves do not recolonize, and Park managers do not reintroduce new wolves to the island (no predation scenario)? (2) Second, what if the wolf population persists as a small population exhibiting weak effects on moose (weak predation scenario)? (3) Finally, what if new wolves migrate to the island or are added to the population and they exhibit strong effects on the moose population (strong predation scenario)? By experimentally maintaining these different predation scenarios for the duration of simulations, we provide an example of what a trophic cascade could look like in predator–ungulate–forest ecosystems, thereby providing management agencies with some criteria against which to evaluate long-term and large-scale effects of alternative predator management strategies.

METHODS

Study area

Isle Royale is in the northwestern part of Lake Superior, approximately 24 km from Minnesota and Ontario, Canada (Fig. 1). The island is a wilderness area, approximately 534 km^2 (72 km in length and 14 km wide at is widest point). The island was formed during the Precambrian Period by uptilted layers of basalt that run in a southwest to northeast direction. North-facing slopes are generally steep and south-facing slopes are more gentle (Huber 1973). Elevation ranges from 426 m above sea level along high ridges to a low of 182 m above sea level in the valleys and along the shore of Lake Superior. The current physiography of the island reflects the most recent major glacial stage (approximately 11000 yr ago), which scoured the bedrock. Glacial deposits are relatively thin in the northeastern part of the island, where the last ice advance was parallel to the ridge-and-valley topography. Glacial till deposits become deeper towards the southwestern part of the island where the direction of ice movement was westward and cut across the ridge-and-valley topography at an angle (Thornberry-Ehrlich 2008, United States Department of Agriculture, Natural Resources Conservation Service 2012).

The vegetation types present on Isle Royale reflect its position within the temperate-boreal forest transition zone (Goldblum and Rigg 2010), with species characteristic of the southern boreal forest. Similar to forests in northern Minnesota, the distribution of forest types reflects subtle differences in water table and soil depth (Frelich 2002). Upland ridges with shallow soils over bedrock consist of boreal hardwood and spruce–fir forests with quaking aspen (*Populus tremuloides*) and paper birch (*B. papyrifera*) succeeding to balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*).

Lowland forests in alluvial valleys tend to be dominated by northern white cedar (*Thuja occidentalis*) and black ash (*Fraxinus nigra*). In the southwestern portion of the island, where glacial soils are deeper, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are present in northern hardwood forests (TNC 1999).

Moose browsing, fire, and wind disturbances have the potential to influence vegetation succession across the island. Isle Royale is within a Wildland Fire Use Zone where lightning-caused fires are allowed to burn. In the 1930s, a large fire burned the central portion of the island, but there have been no large-scale fires since then. Flakne and Cole (1995) characterized the fire regime of Isle Royale as minor and episodic over a 4500-yr period prior to settlement. Less is known about wind disturbance, but historical assessments in nearby Minnesota indicate that less than 0.5% of forest area was annually disturbed by wind prior to settlement (White and Host 2008).

LANDIS-II forest landscape model

We simulated forest change using the LANDIS-II (version 6.0) forest landscape model (Scheller et al. 2007). LANDIS-II simulates the establishment, growth, and mortality of species–age cohorts within sites (i.e., pixels or cells) using species life history attributes (e.g., longevity, shade and fire tolerance, seed dispersal distances, and ability to reproduce vegetatively). These life history attributes are well documented for species of the southern boreal forest and we therefore used previously published parameter estimates (Table 1; Sturtevant et al. 2012, Duveneck et al. 2014). To model succession, we used the Biomass Succession extension (version 3.2; Scheller and Mladenoff 2004). In Biomass Succession, species establishment probabilities (P_{est}) represent the likelihood of establishment of a new cohort given a seed source and adequate light, based on a climate envelope approach (Xu et al. 2009). Maximum growth rate ($ANPP_{max}$) determines the potential aboveground growth of a cohort. Actual growth ($ANPP_{act}$) incorporates a species-specific growth parameter that determines how fast $ANPP_{act}$ reaches $ANPP_{max}$. Growth is further modified by competition and age. Competition is represented by potential growing space, minus space occupied by other cohorts. Effects of cohort age are represented by an increasing decline in growth as species cohorts near longevity. The biomass lost due to age-related mortality is transferred to the detrital pool, where species-specific decay rates regulate decomposition.

Disturbances and other degenerative processes are implemented in LANDIS-II via additional extensions. We parameterized the Base Wind extension (version 2.0; Scheller and Mladenoff 2005) using historical assessments of disturbance in Minnesota (White and Host 2008) and assumed a constant wind regime for all simulations. As mentioned above, Isle Royale is within a Wildland Fire Use Zone. However, there have been no large-scale fires on the island since the 1930s, hence we did not simulate effects of fire.

TABLE 1. Tree species life history parameters used in LANDIS-II simulations.

Species	Longevity (yr)	Maturity (yr)	Tolerance		Seed dispersal (m)		Vegetative reproduction†	Sprout age		Postfire regeneration
			Shade	Fire	Effective	Maximum		Minimum	Maximum	
Abies balsamea	205	20	5	1	30	160	0	0	0	none
Acer saccharum	300	40	5	1	100	200	0.1	0	60	none
Betula alleghaniensis	300	40	4	2	100	400	0.1	0	180	none
Betula papyrifera	165	25	2	2	200	5,000	0.5	0	70	resprout
Fraxinus nigra	150	35	2	1	100	200	0.1	0	75	resprout
Other deciduous	60	20	2	1	20	100	0.7	0	60	none
Pinus banksiana	205	17	1	4	20	275	0	0	0	none
Picea glauca	225	40	3	2	30	200	0	0	0	none
Pinus mariana	200	22	3	3	80	200	0.1	0	100	resprout
Populus tremuloides	140	25	1	1	1,000	5,000	0.9	0	100	resprout
Thuga occidentalis	300	35	5	1	45	60	0.5	50	300	none

† Probability.

Ungulate browsing extension

We simulated reciprocal interactions between forest growth and the moose population using the Ungulate Browsing extension (Version 0.8). For a full description of the extension, see the online user guide (Miranda et al. 2016) and for additional model description as well as validation and sensitivity analysis, see De Jager et al. (2017). At the start of each time step, a fraction of the biomass of each species cohort within each cell is estimated as available forage biomass. These estimates are derived from the portion of annual net primary productivity (ANPP) estimated to be within the height reach of the herbivore (see De Jager et al. 2017).

Available forage biomass, in turn, influences the temporal dynamics of the moose population by defining the carrying capacity (K) of the landscape and according to the discrete-time quadratic model (May 1975)

$$\Delta N_t = RN_t\left(1 - \frac{N_t}{K_t}\right) - MN_t - PN_t \qquad (1)$$

where ΔN_t is the change in the moose population at time t, R is a user-defined population growth rate, M is a user-defined mortality rate due to non-predation factors, and P is a user-defined mortality rate due to predation. K_t is defined as the number of moose that could be supported by the available forage biomass across the entire island at a given time step. The average daily intake rate of an adult moose is approximately 10 kg dry mass in summer and 5 kg dry mass in winter (Miquelle 1983, Renecker and Hudson 1985, Joyal and Ricard 1986, Saether and Anderson 1989). Assuming one-half of the year is winter and one-half is summer, and that 15% of consumed biomass is from herbaceous species (not modeled in this study), this yields an annual forage requirement from woody plants of 2327 kg per moose per year. The total forage biomass available across the island was divided by the annual forage requirements of a single moose to determine the carrying capacity of the landscape at each time step. This approach allows the carrying capacity to emerge from the landscape dynamics that regulate plant growth and forage production and to change over time. R, M, and P were drawn randomly at each time step using minimum and maximum estimates to incorporate stochastic changes in the population. R always ranged between 0.15 and 0.25, reflecting the rate of population growth at Isle Royale during a time of weak predation and an increasing moose population (1989–1995; Peterson et al. 2014). Mortality due to non-predation factors ranged from 0 to 0.10. Predation rates reflected three wolf predation scenarios. First, if the wolf population goes extinct and new wolves do not recolonize the island, then $P = 0$ (no predation). Second, if the wolf population persists as a small population, then $P = 0.03$–0.10 (weak predation), reflecting long-term average predation rates (Peterson et al. 2014). If new wolves migrate to the island or are introduced to the population, then $P = 0.07$–0.15 (strong predation), reflecting higher than average predation rates (Peterson et al. 2014). We maintained the above rates for the duration of model simulations to experimentally examine effects of alternative predation rates.

The moose population is spatially (re)distributed at the start of each time step based on their preference for different plant species and the distribution of available forage across the landscape. Species preference values were assigned based on previous studies that have examined the percentage of available stems that moose tend to remove from different species (Table 2). These preference values are used to weight the availability of forage (by species) to determine site preference at the scale of individual cells. Site preference and forage availability are then used to downscale and spatially distribute the moose population using moving window averages. We used a window size with radius of 1500 m to match the average home range size for moose (Cedarlund and Sand 1994, Hundertmark 2007). For a full description of the methods used to downscale the population, see De Jager et al. (2017). Briefly, the method scales the importance of forage availability by the proximity of the ungulate population to carrying capacity. When the

TABLE 2. Browse extension parameters used in LANDIS-II simulations.

			Growth reduction		Mortality	
Species	Source	Preference	Threshold	Maximum	Threshold	Maximum
A. balsamea	1, 2, 4, 6	0.15	0.2	0.6	0.8	0.1
A. saccharum	2, 3, 6	0.15	0.2	0.6	0.8	0.1
B. alleghaniensis	2, 3, 6	0.15	0.2	0.6	0.8	0.1
B. papyrifera	2, 5, 6	0.25	0.5	0.4	0.9	0.1
F. nigra	1, 2, 6	0	0	1	0.8	0.1
Other deciduous	1, 2, 6	0.25	0.5	0.4	0.9	0.1
P. banksiana	1, 2, 6	0	0	1	0.8	0.1
P. glauca	1, 2, 6	0	0	1	0.8	0.1
P. mariana	1, 2, 6	0	0	1	0.8	0.1
P. tremuloides	1, 2, 3, 6	0.30	0.5	0.4	0.9	0.1
T. occidentalis	1, 2, 6, 7	0.05	0.2	0.6	0.8	0.1

Sources: 1, Hodgson (2010); 2, Risenhoover (1987); 3, Sell (2007); 4, De Jager et al. (2009); 5, De Jager and Pastor (2008); 6, Murie (1934); 7, Parikh (2015).

population is far from carrying capacity, it is allowed to be more selective and target areas of high preference. However, as the population approaches carrying capacity, site preference becomes less important than site forage availability and the population distribution begins to approximate the distribution of available forage. This is done to ensure that 100% of available forage biomass is removed if the population reaches carrying capacity. However, it may also reflect the notion that ungulates can adjust their foraging behavior in proportion to variation in dietary reward and "match" the distribution of food resources (Senft et al. 1987).

The spatial distribution of moose population density determines the total amount of forage removed from each site. Within a site, species are rank-ordered according to their preference values (provided in Table 2). These preference values also identify a target browse removal rate. Forage biomass is first removed from the species with the highest preference, up to the target removal rate and if more biomass needs to be removed to satisfy the local population requirement, then the next most preferred species is selected. This procedure is repeated until the amount of forage required by the local population is reached, or until all cohorts have been browsed at their target rate (preference value). If all cohorts have been browsed at their target rate and the local forage biomass requirements have not been met, then the remaining forage is removed from the most preferred species with any remaining biomass coming form the next most preferred species, and so on until the biomass demand has been met.

Finally, browsing causes an immediate reduction in cohort biomass. However, we modeled additional impacts to cohort growth during the next time step using previously published effects of moose browsing (Table 2). Growth reduction is implemented by a threshold removal rate that initiates growth reduction and by a maximum growth reduction when 100% of available forage biomass is removed. Increases in the likelihood of mortality are implemented similarly, by a threshold removal rate that initiates an increase in cohort mortality and by a maximum increase in the probability of mortality at 100% removal of forage biomass. These parameter estimates are provided in Table 2, for the species modeled at Isle Royale.

Data sets

LANDIS-II requires an input data layer that contains the ages of each species cohort present within each cell of the landscape. To develop this layer, we matched the composition of forest inventory plots (FIA; Woudenberg et al. 2010) to a map of forest types (The Nature Conservancy 1999), and randomly imputed FIA plots within each matching forest type (See Appendix A in De Jager et al. 2017). To estimate the ages of each tree in the FIA plots, we used site index curves for areas closest to Isle Royale (Carmean et al. 1989, Dixon and Keyser 2008). We then grouped all seedlings into a single cohort (age 5) and the remaining trees were grouped into 30-yr age cohorts to start the simulation. Biomass Succession then uses a "spin-up" process in which it estimates the initial biomass of each cohort on the initial landscape by starting in the year equivalent to the oldest cohort and growing each cohort on each cell, up to time = 0. Within LANDIS-II, species establishment probabilities and potential growth rates can vary by ecoregion. Previous studies have demonstrated that variation in soil depth has a strong influence on tree community composition in northeastern Minnesota (Frelich 2002, Sturtevant et al. 2012) and visual inspection of vegetation maps and soil type maps suggest that this is also true at Isle Royale. We therefore based our ecoregion classification on soil type data (SSURGO Soil Survey Staff 2011), which reflected variation in soil water holding capacity (SWHC) in the root zone (1 m depth). This resulted in three ecoregions (Fig. 1; see Appendix A in De Jager et al. [2017] for additional details). In addition, we made all areas of open water, rock, development, and islands not accessible to moose "inactive" in our model simulations. Total active area was 464.6 km^2, approximately 90% of the total undeveloped, non-aquatic area of Isle Royale National Park. We then assigned previously published parameter estimates for P_{est}, ANPP$_{\text{max}}$, and maximum biomass (Table 3) for the active ecoregions that had similar climate and SWHC as those reported for northeastern Minnesota (Duveneck et al. 2014).

Data analysis

We conducted three replicate, 110-yr simulations for each predation scenario (N = 9 total simulations) and determined that model results were relatively similar among the replicates and different among the scenarios. For all outputs, we compared means (± 2 SD) to test for time-specific differences among predation scenarios. We specifically examined temporal differences in (1) moose population density, (2) biomass removal (total and species specific, estimates include total cohort biomass removed due to browsing-induced mortality), (3) total forage availability and the equivalent landscape carrying capacity, (4) total aboveground live biomass (AGB, total and species-specific), and (5) the proportion of the landscape in different forest types. Forest type classification was done with the LANDIS-II Biomass Output (v. 2; Scheller and Domingo 2015) and the Biomass Reclassification (v. 2; Scheller 2014) extensions and was based on the biomass of indicator species. We based our classification scheme on the current distribution of forest types at Isle Royale: (1) boreal hardwood forests (*Populus tremuloides* and *B. papyrifera*), (2) boreal conifers (*Picea glauca, Picea mariana*, and *Abies balsamea*), (3) northern hardwoods (*B. alleghaniensis* and *Acer saccharum*), (4) northern conifers (*T. occidentalis*), and (5) northern dry conifers (*Picea mariana*, *Pinus banksiana*).

Finally, it is not possible to fully validate future model outputs. However, we did validate several near-term model outputs, given available data. We started our model in the year 2006, around the time when forest

Table 3. Ecoregion-specific establishment probabilities (Pest), maximum (Max) annual primary productivity (ANPP), and maximum annual biomass used in LANDIS-II simulations (adapted from Duveneck et al. 2014).

Species	Eco 1			Eco 2			Eco 3		
	Pest	Max ANPP	Max biomass	Pest	Max ANPP	Max biomass	Pest	Max ANPP	Max biomass
A. balsamea	0.0755	700	8885	0.0765	717	9106	0.0496	676	9855
A. saccharum	0.0157	295	12541	0.0785	614	17327	0.0157	295	12541
B. alleghaniensis	0.0377	494	11324	0.0703	637	16294	0.039	530	12127
B. papyrifera	0.0798	500	12255	0.0659	542	13268	0.0124	540	13226
F. nigra	0.057	468	14936	0.0776	496	15833	0.0582	490	15637
P. banksiana	0.0497	391	15042	0.0731	529	17377	0	0	0
Other Deciduous	0.08	400	6000	0.08	400	6000	0.06	400	6000
P. glauca	0.0628	617	15443	0.0496	570	16440	0	0	0
P. mariana	0.0625	571	14570	0.049	610	15303	0.0764	612	15235
P. tremuloides	0.0576	610	11954	0.0719	688	13483	0.0138	795	15582
T. occidentalis	0.0595	459	17309	0.0777	473	17115	0.0599	573	17125

Note: See Fig. 1 for the distribution and description of ecoregions.

inventory and browse surveys were completed at Isle Royale and compared initial model outputs and trends during the first decade with empirical data sets. We compared FIA forest biomass estimates developed by Blackard et al. (2008) with aboveground live biomass derived from Biomass Succession during the spin-up period for time = 0. We compared estimates of moose population density with those estimated by Vucetich and Peterson (2015) at Isle Royale. Finally, we compared model estimates of available forage biomass with previously published and unpublished field measurements made as part of a long-term study at Isle Royale (Pastor et al. 1998, De Jager and Pastor 2009). All unpublished forage availability measurements were made using identical procedures as those reported in De Jager and Pastor (2009).

Results

Population density and forest biomass

Increasing the predation rate resulted in lower moose population densities during the first four decades of model simulations (Fig. 2). In the no predation scenario, the moose population peaked in simulation year 2028 at approximately 4 moose/km^2, a similar density to that found at Isle Royale during the mid-1990s (Fig. 1). Increasing the predation rate to 0.03–0.10 (weak predation) resulted in a lower peak population density (~2 moose/km^2), while further increasing it to 0.07–0.15 (strong predation) resulted in a peak density of approximately 1.3 moose/km^2. During the first 10 years of model simulations, the upward trajectory of the moose population, as well as the population densities of both the no predation and weak predation scenarios, overlapped estimates made at Isle Royale (Fig. 2). Longer-term population densities were similar for all predation scenarios (between 1.00 and 1.75 moose/km^2), although the weak predation scenario had higher population densities than the other two scenarios during many of the later years.

Increasing the predation rate resulted in less biomass (sum of available forage biomass and total cohort biomass lost due to browsing-induced mortality) removed from the landscape during the first few decades (Fig. 2). In the strong predation scenario, annual biomass removal was consistently lower than the other scenarios (2–10 g/m^2). In the no predation scenario, annual biomass removal peaked at 55 g/m^2 in simulation year 2032, a few years after the peak population density. Peak biomass removal occurred later in the weak predation scenario (2039), at approximately 30 g/m^2. Beyond the year 2065, there was no difference in biomass removal rates between the weak and strong predation scenarios (Fig. 2).

At the start of the simulations, available forage biomass was approximately 16 g/m^2 for the entire landscape, which, according to our model, could support a population near 7 moose/km^2 (Fig. 2). Local cell values varied spatially (Fig. 3), but 95% of all values were less than 30 g/m^2 and within the range of forage availability estimates made

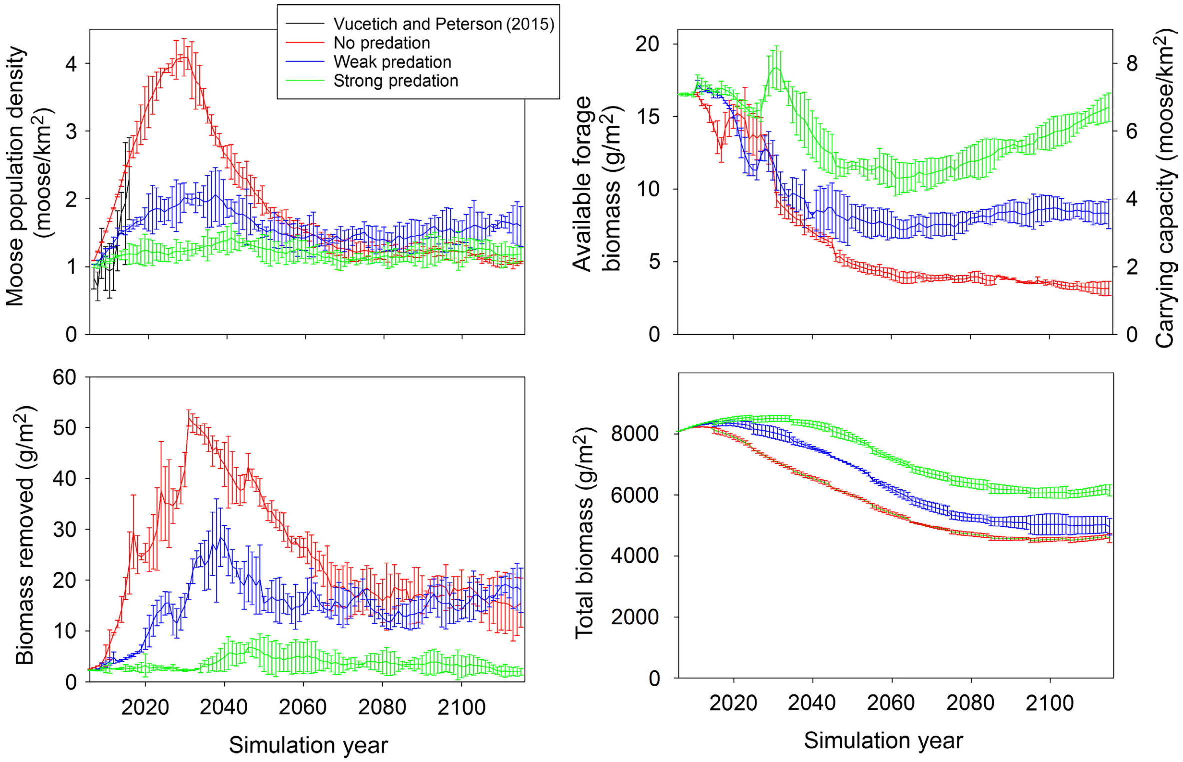

FIG. 2. Trends in population density, available forage biomass, total aboveground live biomass removed from the landscape, and total aboveground live biomass for three predation scenarios (see *Methods, Ungulate browsing extension*). Biomass removed includes both direct removal by the herbivore population (consumption) and indirect loss of biomass due to browsing-induced cohort mortality. Data are means and 2 SD for three replicate simulations. Population estimates for Isle Royale from 2006 to 2015 are provided for reference (± 90% confidence intervals, from Vucetich and Peterson [2015]). [Colour figure can be viewed at wileyonlinelibrary.com]

around the same period of time at Isle Royale (Table 4). The high population densities and biomass removal rates during the first two decades in the no predation scenario caused a strong reduction in forage availability. By the end of the simulations, available forage biomass was reduced to 3.5 g/m^2 and a carrying capacity of 1.4 moose/km^2, which prevented the moose population from recovering over the long-term, despite the lack of predation. Although the population densities and biomass removal rates were not as large in the weak predation scenario as compared to the no predation scenario, they were sufficient to cause a similar reduction in forage availability during the first several decades. However, longer-term forage availability was near 8 g/m^2 and a carrying capacity of 3.5 moose/km^2 for the weak predation scenario. Finally, forage availability fluctuated between 10 and 20 g/m^2 in the strong predation scenario, with a carrying capacity at the end of the model simulations near 7 moose/km^2, similar to the carrying capacity at the start of the simulations. Hence predation maintained long-term moose population densities well below the carrying capacity of the landscape.

Estimates of total aboveground live biomass (AGB) produced by the LANDIS-II Biomass Succession extension for year 0 approximated those from FIA nationwide forest biomass estimates (Appendix S1). The minimum AGB from LANDIS-II was 803 g/m^2 while the minimum for FIA was 2131 g/m^2. These low estimates tended to be associated with lowland forests in alluvial valleys for both data sets (Fig. 1; Appendix S1). The maximum AGB for LANDIS-II was 13680 g/m^2 and for FIA the maximum was 16636 g/m^2. These maximum estimates were mostly associated with northern hardwood forests in the western part of the island for both data sets (Fig. 6; Appendix S1). Finally, the mean for LANDIS-II was 8033 g/m^2 and for FIA the mean was 8837 g/m^2. However, the LANDIS-II model tended to have more pixels with less than 7000 g/m^2 than the FIA data (Appendix S1). AGB initially increased for all three scenarios (Fig. 2). However, the increase in AGB was strongest and lasted the longest in the strong predation scenario, followed by the weak predation scenario and the no predation scenario. Over the course of the simulations, AGB was consistently greatest in the strong predation scenario, intermediate in the weak predation scenario, and smallest in the no predation scenario.

Forest composition

Temporal trends in the species composition of biomass removed from the landscape differed by predation

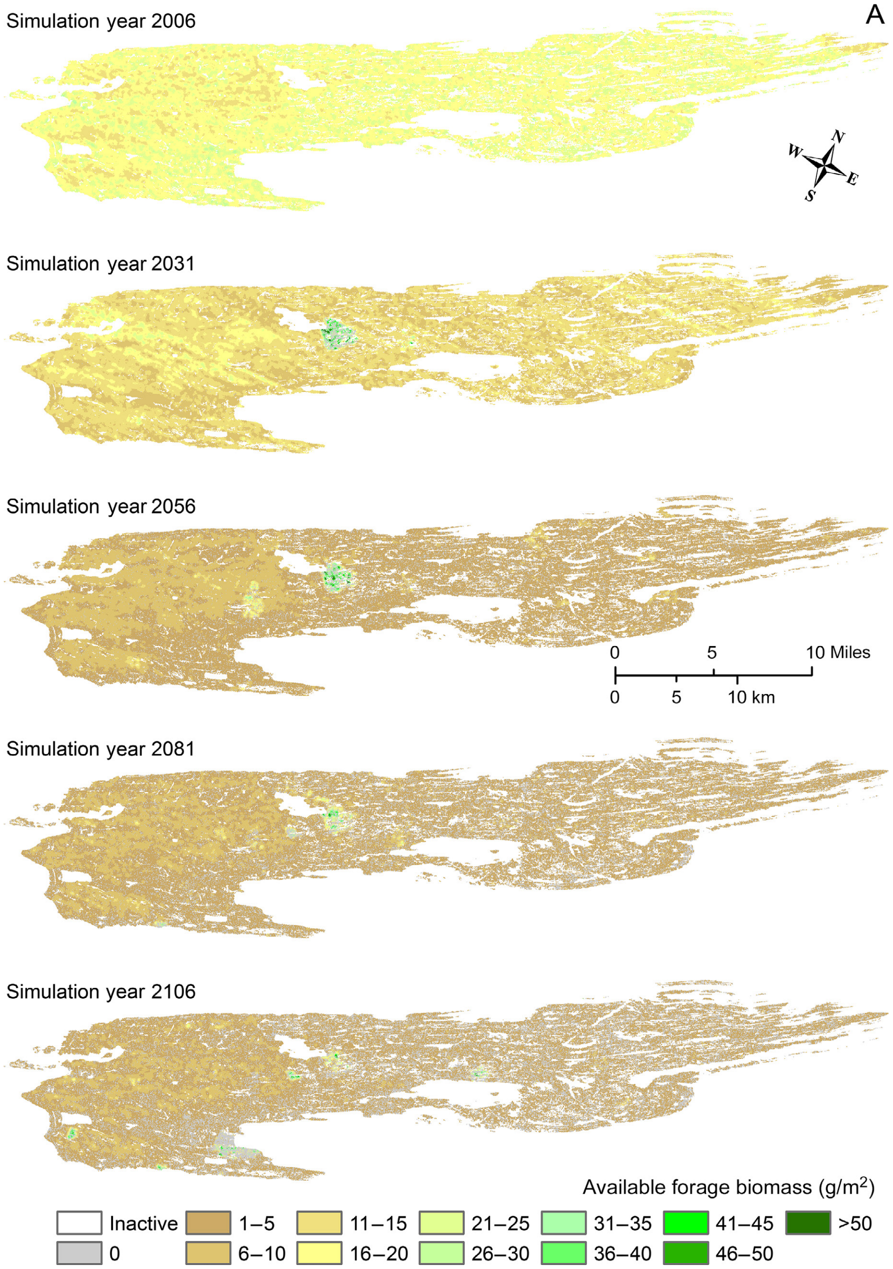

FIG. 3. (A) Maps of available forage biomass for the initial model condition (2006) and each 25 yr after for the no predation scenario. (B) Maps of available forage biomass for the initial model condition (2006) and each 25 yr after for the weak predation scenario. (C) Maps of available forage biomass for the initial model condition (2006) and each 25 yr after for the strong predation scenario.

scenario (Fig. 4) and reflected species-specific preference and tolerance parameters (Table 2). In the strong predation scenario, a greater proportion of the biomass removed came from the highly preferred "other deciduous" species and a smaller proportion came from the less preferred *T. occidentalis* by the end of the simulation, indicating that the population was being sustained by highly preferred species. In contrast, the no predation scenario showed a strong increase in the biomass removed from *T. occidentalis* following the population decline in the simulation years 2030–2050, suggesting that the population was increasingly sustained by less preferred species as the abundance of more highly preferred species was declining.

The composition of total AGB shifted over time, so that the relative abundance of highly preferred species (*Abies balsamea*, *B. papyrifera*, and *Populus tremuloides*) declined over time in all scenarios (Fig. 4). However,

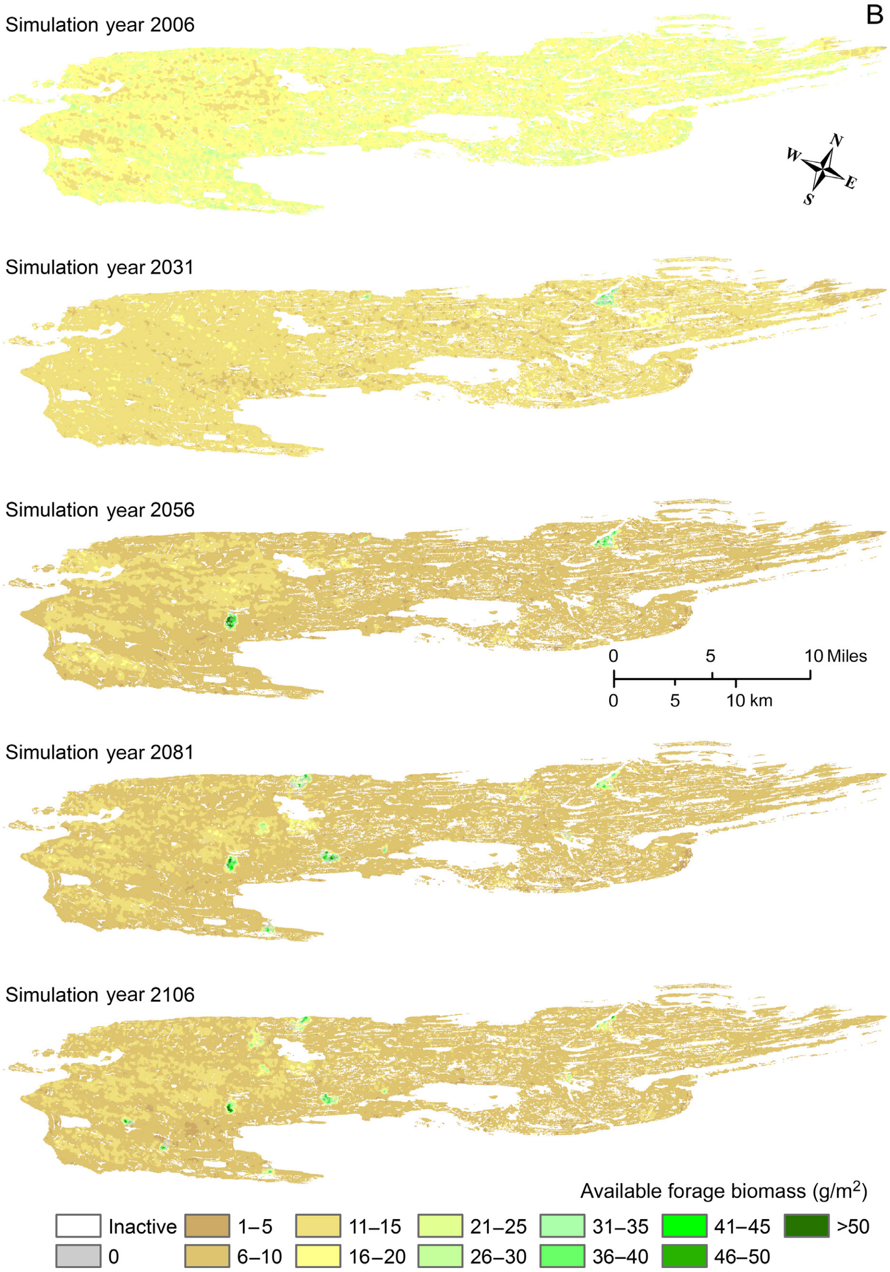

FIG. 3. Continued.

these declines occurred soonest and were strongest in the no predation scenario, followed by the weak predation scenario, and finally the strong predation scenario. On the other hand, the relative abundance of moderately preferred *Acer saccharum* and *B. alleghaniensis* increased in all scenarios, with the strongest increase occurring in the strong predation scenario, followed by the weak and no predation scenarios. The relative abundance of unbrowsed species (*Picea mariana*, *Picea glauca*, and *F. nigra*) increased most in the no predation scenario, followed by the weak and strong predation scenarios. Finally, the relative abundance of *T. occidentalis* and the other deciduous species declined in the no predation scenarios but increased in both predation scenarios.

Trends in the proportion of the landscape classified as northern and boreal hardwood and conifer forests differed among the predation scenarios (Fig. 5). Northern hardwood forests increased over time under the strong predation scenario, increased slightly in the weak predation scenario, and did not increase in the no predation

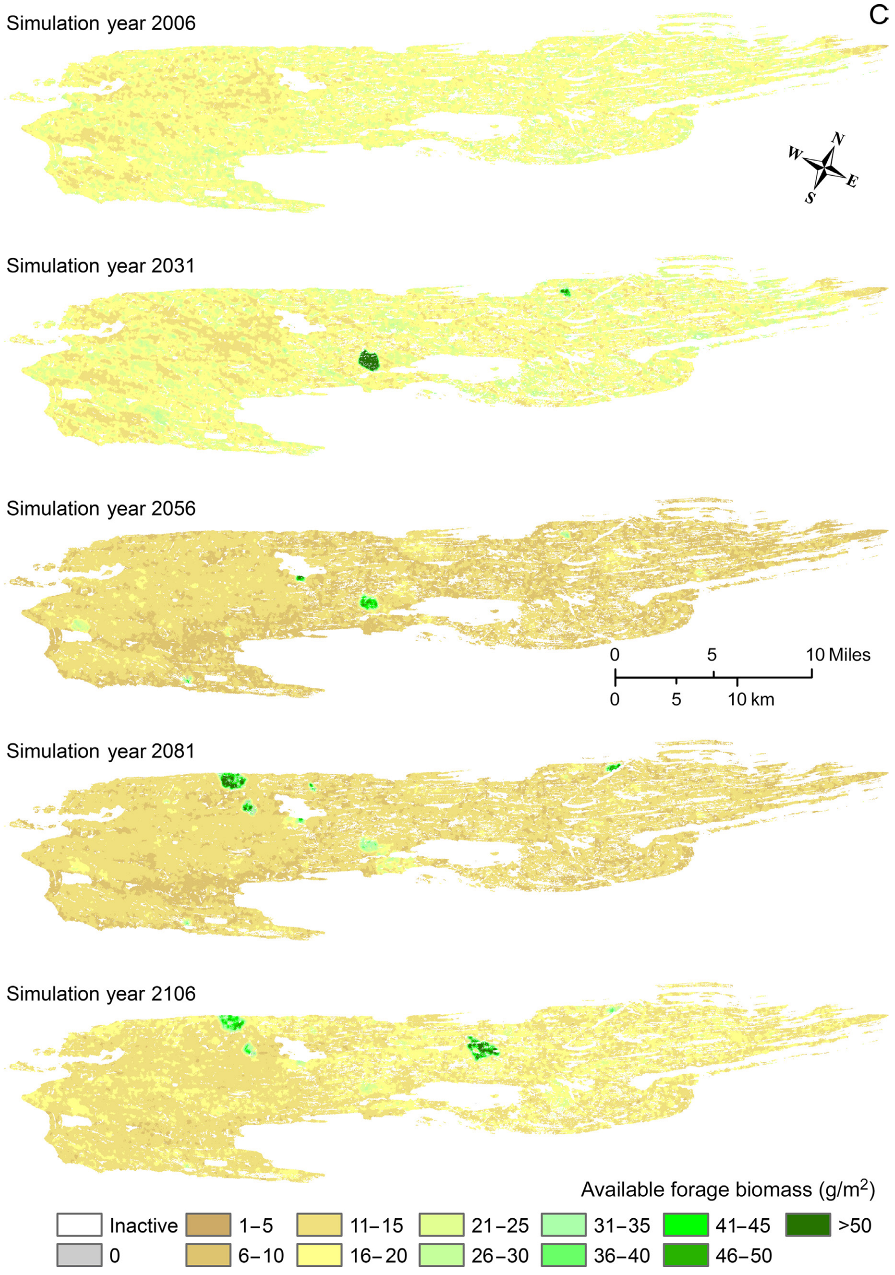

FIG. 3. Continued.

TABLE 4. Estimates of total annual (summer + winter) available forage biomass made at Isle Royale National Park.

Location	Year	Minimum	Maximum	Mean	SD	Area surveyed	Source
Lane Cove (sp)	2004–2005	0	46.2	11.1	9.1	300 $2 m^2$ plots	A. L. Hodgson and J. Pastor (*unpublished data*)
Lane Cove	2005–2007	0	40.5	11.2	8.2	200 $2 m^2$ plots	De Jager and Pastor (2009)
Lane Cove	2015	0	65.1	14.7	11.2	100 $2 m^2$ plots	N. R. De Jager (*unpublished data*)
Moskey Basin (sp)	2004–2005	0	125.2	21.6	18.7	300 $2 m^2$ plots	A. L. Hodgson and J. Pastor (*unpublished data*)
Moskey Basin	2005–2007	0	92.8	13.7	10.9	200 $2 m^2$ plots	De Jager and Pastor (2009)

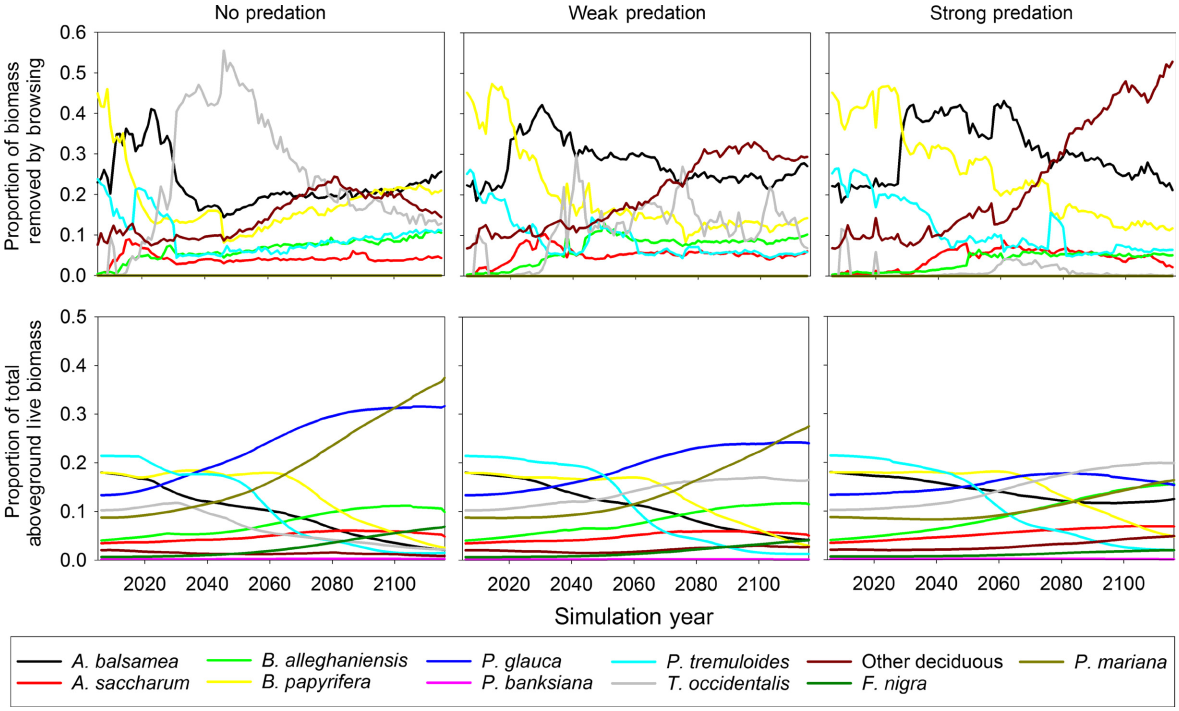

FIG. 4. The composition of biomass removed from the landscape, both directly (via consumption) and indirectly (via browsing-induced cohort mortality) (top panels) and the composition of total above ground live biomass (lower panels) for three predation scenarios. Proportions are means of three replicate simulations within each predation scenario. Standard error bars are not shown but were used to assess differences among the scenarios. Genera are spelled out in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

scenario, reflecting moderate browsing effects on (*A. saccharum* and *B. alleghaniensis*). Northern conifers increased more strongly in the strong and weak predation scenarios than in the no predation scenario, reflecting moderate browsing effects on *T. occidentalis*. Over the long-term all scenarios showed a strong decline in boreal hardwood forests, reflecting shifts toward later successional boreal conifer species. However, boreal hardwoods increased initially in the strong and weak predation scenarios but not in the no predation scenario, and declines in boreal hardwood species occurred sooner in the no predation scenario, reflecting heavy browsing of *B. papyrifera* and *Populus tremuloides*. Boreal conifers increased earlier in the simulations for the no predation scenario and more of the landscape was in boreal conifer cover at the end of the simulations as compared to the scenarios with predation, reflecting the lack of browsing on *Picea mariana* and *Picea glauca*. Visual inspection of species-specific biomass maps indicated that the expansion of boreal conifer cover was due to increases in *Picea glauca* and *Picea mariana* and not by *Abies balsamea*, which declined strongly without predation (Appendix S2: Fig. S1). Expansion of northern conifer and hardwood forests was mostly concentrated in the western portion of the island, where those forest types were initially more abundant, whereas transition to boreal conifers took place over the central and eastern portions of the island (Fig. 6).

DISCUSSION

A trophic cascade is thought to occur when the biomass of primary producers changes in response to changes in herbivore biomass brought about by predation (Hairston et al. 1960, Oksanan et al. 1981, Fretwell 1987). Unlike the trophic interactions leading to insect pest outbreaks (e.g., Royama 1992), trophic cascades associated with predator–ungulate–forest systems can be both subtle and complicated to quantify. For example, predator populations and predation rates are highly variable in space and time (Peterson et al. 2014), which makes it difficult to define the long-term and large-scale characteristics of trophic cascades. Second, because ungulates can only impact small-statured tree cohorts, often in the forest understory, the long-term consequences of herbivory on forest succession may not be realized until the overstory reaches longevity, which may take several decades. These aspects of forest ecosystems make it difficult to characterize trophic cascades involving forest ungulates, set management objectives related to predator populations, or evaluate the effects of those actions on forest biomass and succession. In this study, we coupled a forest growth and biomass model (Biomass Succession, Scheller and Mladenoff 2004), with a model of ungulate foraging and population dynamics (Ungulate Browsing, De Jager et al. 2017) to experimentally simulate long-term and large-scale reciprocal interactions between the moose population and

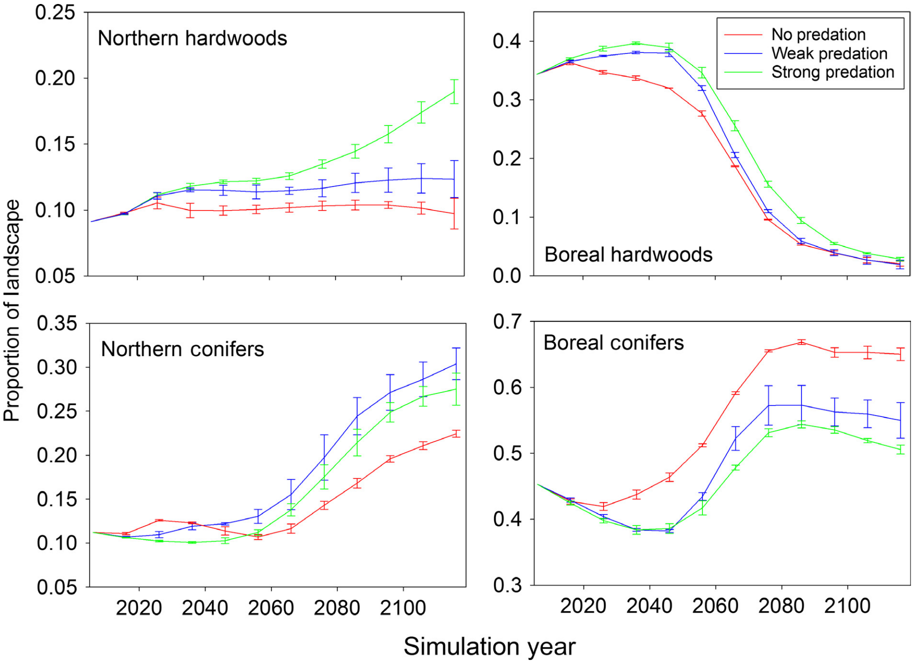

FIG. 5. Trends in the proportion of the landscape in four different forest types for three predation scenarios. Data are means of three replicate simulations (± 2 SD) within each predation scenario. [Colour figure can be viewed at wileyonlinelibrary.com]

forest landscape of Isle Royale in the context of different sustained predation rates. By sustaining defined predation rates over the long term, we were able to isolate the potential effects of different predator management strategies in this system and develop a better understanding of the characteristics of a trophic cascade.

Differences in moose population density, biomass removal rates, and aboveground biomass among the different scenarios began to emerge within the first couple of decades, suggesting that effects of browsing (or lack of browsing) on the forest understory could initiate a trophic cascade very soon after a change in predator management strategy. On the other hand, changes in the composition of aboveground biomass and the distribution of primary forest types across the island did not occur until later in the simulations, following senescence of the existing forest overstory. Interestingly, long-term moose population densities were approximately similar among the predation scenarios, but the causes and consequences of these similarities were very different. Predation served to maintain more modest initial population densities, leading to weaker effects on forage biomass and a larger carrying capacity. The predation scenarios resulted in a regulation of the moose population, despite high estimates of carrying capacity. Such results are consistent with the traditional view of a trophic cascade where the biomass of herbivores decreases and the biomass of primary producers increases in response to predation (Hairston et al. 1960, Oksanan et al. 1981, Fretwell 1987). On the other hand, in the no predation scenario, an initial large increase in the moose population resulted in a long-term reduction in available forage biomass and landscape carrying capacity, preventing the moose population from ever recovering to high densities despite the lack of predation. Hence, the long-term lack of top-down control could not be identified based on estimates of population density (i.e., herbivore biomass) alone. This result differs somewhat from the traditional view of a trophic cascade in that a reduction in predator biomass did not ultimately lead to an increase in herbivore biomass, but rather a reduction in the biomass of all lower trophic levels because the landscape simply could not sustain high herbivore population densities over the long term.

Effects of browsing on forest succession

Increasing the predation rate in our model simulations led to progressively higher moose population densities and biomass removal rates during the first few decades of simulations, which subsequently caused increasingly larger effects on available forage biomass, total aboveground live biomass, and forest composition. In a previous study (De Jager et al. 2017), we simulated a no browsing scenario, with results that were comparable to the strong predation scenario simulated in this study. In our strong predation scenario, the moose population was never within more than 30% of carrying capacity and was most often less than 20% of carrying capacity. Such browsing rates were less than the threshold removal rates for negative impacts on cohort growth for most species in the diet of moose (Table 2). As a consequence, although the moose population was removing cohort biomass, it

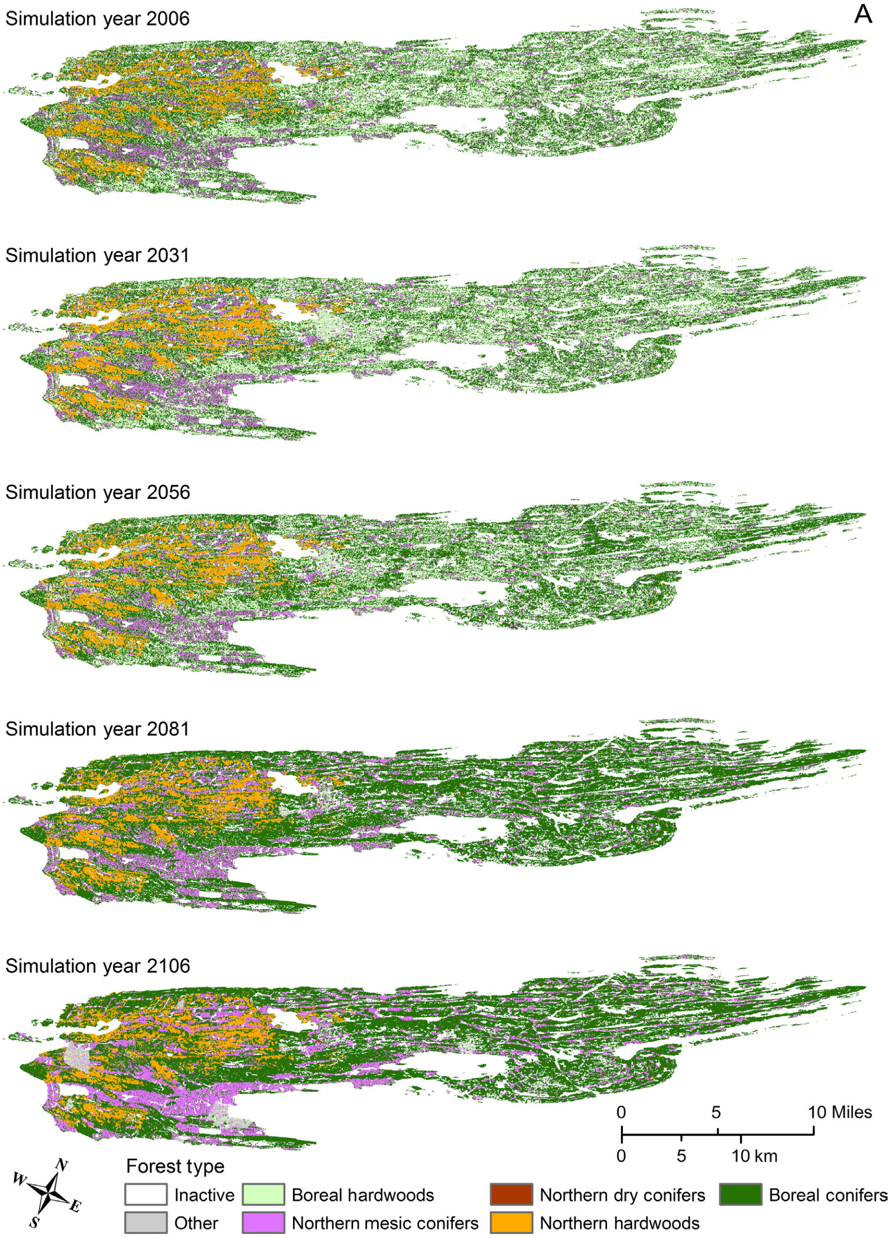

FIG. 6. (A) Distribution of different forest types at Isle Royale for the initial model condition (2006) and each 25 yr after for the no predation scenario. (B) Distribution of different forest types at Isle Royale for the initial model condition (2006) and each 25 yr after for the weak Predation scenario. (C) Distribution of different forest types at Isle Royale for the initial model condition (2006) and each 25 yr after for the strong predation scenario.

was not typically causing reductions in growth or increases in cohort mortality during subsequent time steps. Our strong predation scenario was therefore functionally equivalent to having no moose on the island at all. In contrast, the moose population was typically within 40–50% of carrying capacity in the weak predation scenario and within 60–70% of carrying capacity in the no predation scenario, corresponding to forage biomass removal rates that were much more likely to impact cohort growth and survival.

Differences in aboveground biomass among predation scenarios occurred quickly, within the first two decades, while changes in forest composition occurred later in the simulations, following senescence of the existing mature forest stands at Isle Royale. The species most negatively impacted by higher browsing rates in the weak and no predation scenarios were the highly preferred deciduous species (*Populus tremuloides* and *B. papyrifera*) and the moderately preferred conifer, *Abies balsamea*. In addition, browsing prevented increases in the biomass of

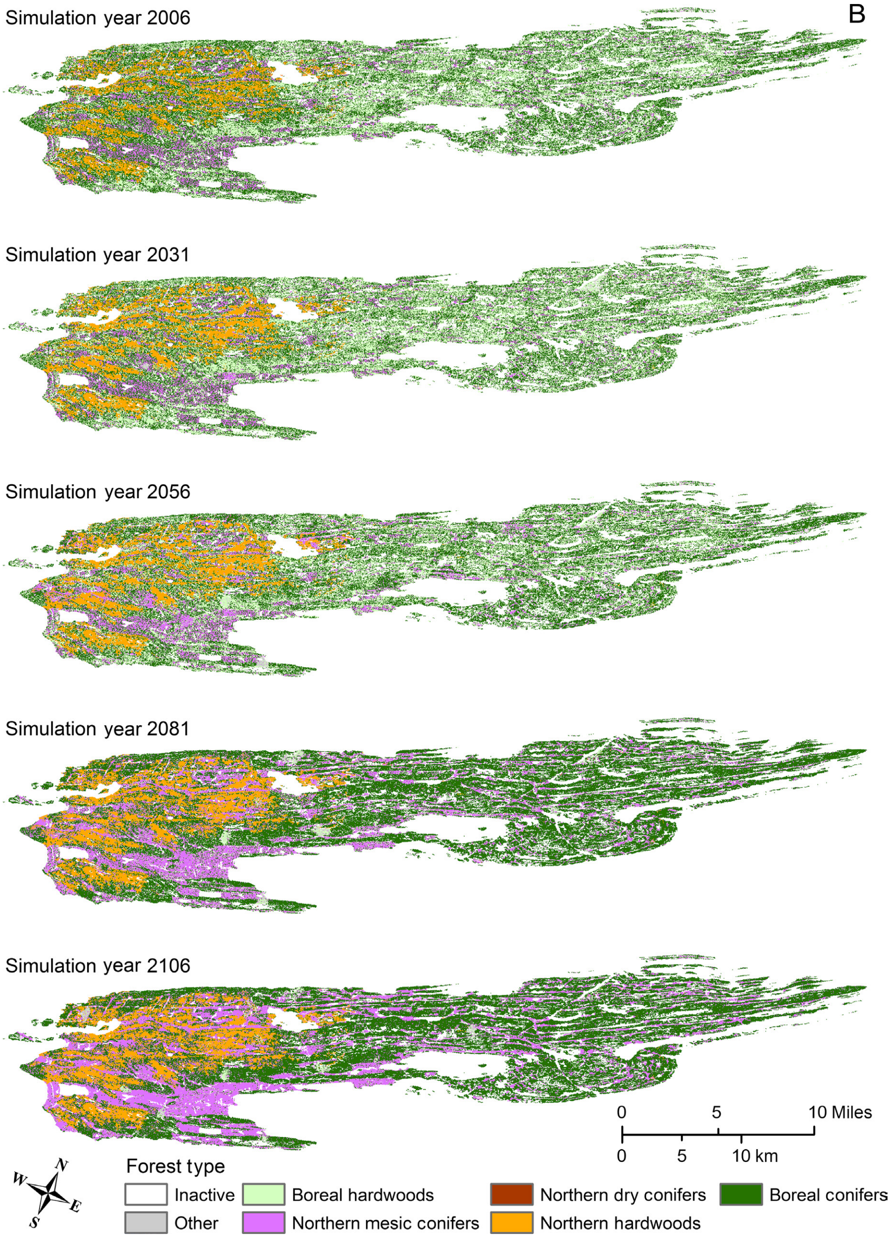

FIG. 6. Continued.

moderately preferred *Acer saccharum* on the western portion of Isle Royale. The species most positively impacted by higher browsing rates were unbrowsed conifers (*Picea glauca* and *Picea mariana*). Moose browsing at Isle Royale limits recruitment of highly preferred plant species (Risenhoover and Maass 1987, Brandner et al. 1990). On the western end of the island, Sell (2007) suggested that moose browsing may limit the expansion of northern hardwood forests as a result of browsing on *Acer saccharum*. Our results are consistent with this prediction, as northern hardwood forests on the western end of the island only expanded in the strong predation scenario. Over the central and eastern portion of the island, several studies have indicated that browsing accelerates the rate of succession to unbrowsed species (Snyder and Janke 1976, McInnes et al. 1992, Rotter and Rebertus 2015). In particular, deciduous species, such as *Populus tremuloides* and *B. papyrifera* are browsed year-round, while *Abies balsamea* is heavily browsed in winter, especially in areas where it is rare and where moose densities are relatively high. Browsing of these species has been shown to reduce their growth (De Jager and Pastor 2008, De Jager et al. 2009) and result in localized shifts toward unbrowsed *Picea glauca* (Snyder and Janke 1976, McInnes et al. 1992, Rotter and Rebertus 2015).

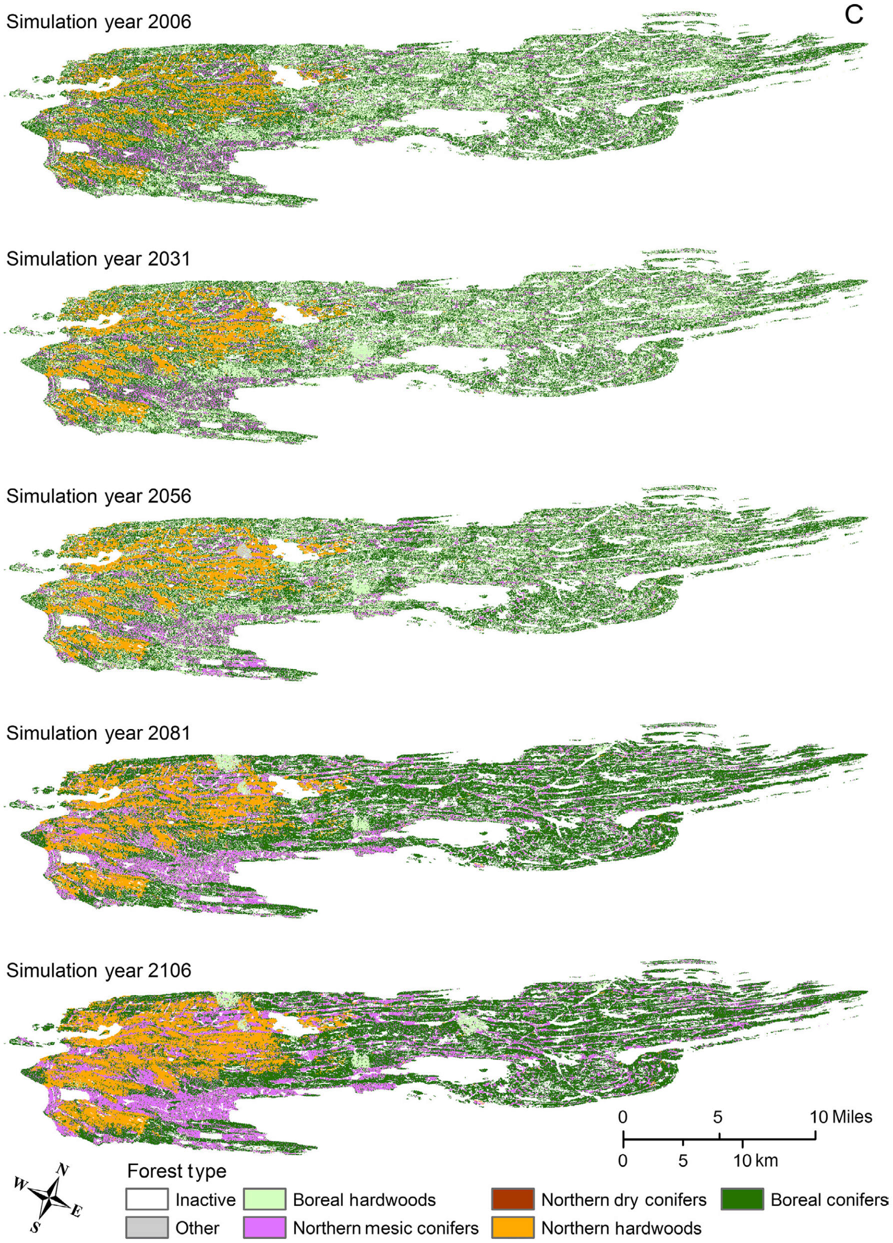

FIG. 6. Continued.

The results of our forest type analysis suggest that browsing of early successional species may increase the rate of forest succession toward unbrowsed late successional species, but does not cause different successional trajectories. Over the long-term, the forests of Isle Royale are projected to shift toward dominance by boreal conifers, regardless of predation scenario. These results are similar to modeling results from Seagle and Liang (2001) who showed that browsing in Eastern U.S. riparian forests increased the rate of succession toward unbrowsed *Fagus grandifolia*, but did not alter the trajectory of succession. Some of the life history attributes that make a species successful during early succession also make it highly palatable to ungulates (e.g., rapid growth rates and high tissue N concentrations; Herms and Mattson 1992). Apart from browsing, we also simulated wind disturbance, which also tends to favor shade-tolerant (i.e., late-successional) species by affecting the older cohorts (He and Mladenoff 1999, Frelich 2002). Both processes (windthrow and ungulate browsing) appear to accelerate succession. However, balsam fir was less prevalent within the boreal conifer forests of the no predation scenario relative to the strong predation scenario, indicating that, although similar forest types may emerge, the abundance of individual species could vary. It should also be pointed out that LANDIS-II does not simulate competition with non-woody species. Encroachment of heavily browsed areas by non-woody species could fundamentally alter successional trajectories. For example, in very heavily browsed areas of Isle Royale, avoidance of *P. glauca* can lead to the development of "moose–spruce savannas" as overstory trees reach longevity and are not replaced, leaving behind low density, low productivity spruce-dominated parkland-like areas (Rotter and Rebertus 2015). Such dynamics have also been reported in some areas of the Cape Breton Highlands in Nova Scotia, Canada in response to heavy moose browsing (Smith et al. 2010) and at Anticosti Island, Québec in response to white-tailed deer herbivory (Potvin et al. 2003). Hence, heavy browsing may, in fact, cause large differences in successional trajectories where browsing of woody species interacts with unbrowsed herbaceous species.

Effects of predation on the moose population

There is a long history of discussion about whether predator populations regulate prey populations (Cole 1971, Despain et al. 1986, McLaren and Peterson 1994). Our study does not address this question. In natural systems, predator and prey populations can fluctuate dramatically in response to a potentially wide range of factors (Erlinge et al. 1984). Even in a single-predator–single-prey system such as Isle Royale, the moose and wolf populations have varied considerably over time periods that are much shorter than forest successional processes (Peterson et al. 2014). The purpose of our study was to attempt to isolate the potential long-term and large-scale effects of predation by holding rates relatively constant in an effort to better characterize what trophic cascades could look like in boreal forest systems. Our results should, therefore, be interpreted accordingly.

There is no historical analogue for the strong predation scenario that we simulated. Inbreeding depression and other density-dependent phenomena have generally limited the ability of the Isle Royale wolf population to sustain such high predation rates (Peterson et al. 2014). This "what-if" scenario probably represents a future with repeated additions of wolves to the island, either through migration or direct management intervention. Unlike the weak and no predation scenarios, the strong predation scenario did not result in an initial increase in the moose population and the population had negligible effects on the availability of forage and the carrying capacity of the landscape. On the other hand, although our weak predation scenario did not capture the extreme high and low predation rates observed at Isle Royale, it did reflect the long-term average predation rates (Peterson et al. 2014). In this scenario, the population peaked around 2 moose/km^2 before settling on a long-term average near 1.5 moose/km^2, similar to the long-term average population density at Isle Royale (Peterson et al. 2014). Nevertheless, future applications of this modelling approach could implement predation rates that vary spatially and temporally as functions of other model components or extrinsic factors. For example, temporal changes in the predation rate could be modeled as a function of ungulate population density or predator–ungulate ratios (Vucetich et al. 2002). Spatial variability could be implemented to reflect spatial effects of territoriality in wolf populations.

With only two wolves remaining on the island, the no predation scenario may be the most likely future for Isle Royale, at least in the near term. We initiated our simulation model using data from ~2006, a period when above average predation rates played a role in reducing Isle Royale's moose population to its lowest level (Peterson et al. 2014) and facilitated a strong increase in forage production (De Jager and Pastor 2009). However, since 2011 predation rates at Isle Royale have been near zero and the moose population has increased strongly and consistently since then (Fig. 1; Peterson et al. 2014). In the absence of wolf predation, and aided by initially high estimates of forage availability, our simulations yielded an upward trend in the moose population that closely matches the recent population trends at Isle Royale. This upward trend in the modeled population continued until a peak of approximately 4 moose/km^2 in 2028, at which time the population reached the island carrying capacity. Thereafter, both the population and the carrying capacity of the island declined in concert with each other for the next couple of decades. It should be pointed out that these dynamics reflect observed population growth rates (random between 0.15 and 0.25). The timing and perhaps the magnitude of the population peak may differ if the population were to experience higher or lower growth rates than previously measured at Isle Royale. Nevertheless, these dynamics differed from those in either of the predation scenarios and resulted in strong effects on forage production.

The moose population dynamics in the no predation scenario may be similar to those reported at Isle Royale prior to wolf colonization, when the moose population reached similarly high densities during the late 1920s before declining due to forage limitations (Hickie 1936). Subsequent increases in forage production and the moose population were primarily supported first by a large fire in 1936 that regenerated browse across much of the middle portion of the island and second by the establishment of a wolf population. Were it not for these two factors, it is possible that the long-term carrying capacity of the island would have remained low and more tightly coupled to the moose population over the past 80 yr, similar to our model projections for the next 100 yr. Isle Royale's moose population also peaked near 4 moose/km^2 during the mid-1990s following effects of canine parvovirus that likely lead to several years of a below average wolf population. However, a severe winter caused a dramatic decline in the moose population before it could completely reduce available forage and the population subsequently rebounded. This later population cycle differs from our model results in that we did not include a mechanism that could result in such a large short-term catastrophic reduction in the moose population and hence it remained tightly coupled to forage production throughout the population decline, ultimately limiting the potential for recovery of forage biomass or the moose population over the long-term. Future efforts could evaluate the importance of other external drivers of moose population dynamics (e.g., harsh winters, disease, etc. …), that could decouple the population from available forage biomass and evaluate the potential for short-term recovery (with or without predation).

Modeling considerations

The LANDIS-II model was designed to study the emergence of large-scale (10000–20000000 ha) and long-term (>100 yr) patterns of forest succession in the context of management actions and disturbances. The design and logic of the LANDIS-II model are consistent with our current understanding of how forest ecosystems function and change over time (see Scheller et al. [2007] for a more complete description). In keeping with the general LANDIS-II modeling approach, the browsing extension that we employed here was designed to address questions about browsing effects on forest succession and how changes in forest biomass might feedback to influence the sustainability of landscapes for ungulate populations over the long term (see De Jager et al. [2017] for full description). Unlike other spatially explicit ways to model herbivory (see models in Weisberg et al. 2006), the model we used was developed to operate with a temporal resolution equal to or greater than a single year. Hence it does not represent mechanistic foraging process (Spalinger and Hobbs 1992) or animal energetics (Moen et al. 1997) at finer time scales. However, these simplifications allow the model to operate over large-scales and long time periods, making it possible to examine effects on landscape patterns of forest succession.

Although it is not possible to fully validate our model outcomes for future years, we identified several consistencies with previously published measurements and trends, which provides some confidence that this approach could be broadly applicable to other forest–ungulate systems. For example, our model was able to produce estimates of aboveground live biomass within the height reach of moose (i.e., forage biomass) that were well within the range of previously published values for Isle Royale. These values are also similar to estimates made in other boreal forests that support moose populations (Persson et al. 2005, De Jager and Pastor 2008, Lord and Kielland 2015). Further, using simple calculations of the annual forage biomass required by individual moose, the model was able to generate reasonable estimates of landscape carrying capacity. As a consequence, estimates of population density also fell within previously published values for Isle Royale and other boreal landscapes (Ball et al. 2000, Paragi et al. 2015). Forage biomass, carrying capacity, and population density estimates were generally more similar to previously published values in our weak predation scenario, which is the scenario that most closely matches the historical predation rates at Isle Royale. Furthermore, in previous applications of the model, we showed that forest successional patterns resulting from browsing were more consistent with those reported in the literature than simulations that did not include browsing (De Jager et al. 2017). In the present study, we further show that predation can influence forest productivity, aboveground biomass, and successional trends when predation rates are experimentally held relatively constant over the long term, with patterns that were largely consistent with our current understanding of moose–forest interactions.

The interaction between predation and other disturbances, such as wind, fire, and harvesting, may influence forage production and moose population dynamics and is an important consideration for future modelling efforts. We used a wind regime that reflected historical assessments made in Upper Midwestern U.S. forests, with patch sizes and recurrence intervals derived from White and Host (2008). Our results indicated that between 0.1% and 0.5% of the simulated landscape was annually impacted by wind events in our simulations and these estimates are similar to those reported in White and Host (2008). Wind disturbance was especially important in the no predation scenario. By the simulation year 2056, the only locations producing significant amounts of forage were those impacted by wind disturbances, which released previously suppressed cohorts and improved local light conditions for new cohort establishment. In fact, it appeared that wind disturbance was the primary mechanism supporting long-term forage production and the moose population in the no predation scenario. Wind, fire, and harvesting all regenerate available browse and create areas that are often heavily utilized by moose (Timmerman and McNicol 1988). However, moose appear to select habitats with a mix of conifer cover to avoid predation and early successional forests with abundant forage (Courtois et al. 2002). Hence the size and frequency of disturbances that create canopy openings are often key considerations where management agencies seek to balance forest resources with ungulate populations.

Since this experiment was applied in a National Park, we did not consider effects of hunting on the moose population or harvesting on the forest. Similarly, we did not investigate the influence of external drivers, such as climate change, on system dynamics. Clearly a warming climate trend has the potential to influence vegetation trends (Duveneck et al. 2014), as well as other disturbance regimes (e.g., wind, Frelich 2002). Given that human actions can directly modify all major components of predator–ungulate–forest systems, further model development for unprotected areas should benefit from the ability to evaluate a number of alternative management and environmental scenarios. Fortunately, the LANDIS-II framework coupled with the new Ungulate Browsing extension enables the investigation of more complex scenarios as these factors interact with ungulate populations.

Conclusions

Isle Royale National Park is known as a model ecosystem for understanding trophic cascades in predator–ungulate–forest ecosystems. In this study, we synthesized our current understanding of this system in a way that allowed us to project the consequences of alternative predation scenarios. More broadly, there are numerous studies of, e.g., ungulate food preferences, exclosure experiments documenting the effects of ungulates, and studies of ungulate population dynamics in a wide range of systems. However, understanding how such information translates into long-term and large-scale effects on forest succession, as well as the feedbacks to ungulate populations is challenging. Our modelling approach may, therefore, be useful in other ecosystems where insight and quantification of long-term and large-scale trophic cascades are needed. Consistencies between model estimates and dynamics with previous studies suggest that similar approaches could be taken in a range of forest ecosystems to evaluate the extent to which predation or other types of population regulation influences ungulate populations and forest succession.

Acknowledgments

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.1526/full

DATA AVAILABILITY

Input files for Isle Royale National Park/Landis-II modelling are available at U.S. Geological Survey ScienceBase-Catalog repository https://doi.org/10.5066/F7RJ4GKW