**TITLE:** Simulation modelling to quantify status and trends in the vegetation of Isle Royale National Park, as it relates to forest succession, wolf predation, herbivory by moose and beaver, and climate change

**PROBLEM STATEMENT AND IMPLICATIONS:**

In response to a decade-long decline in the wolf population of Isle Royale National Park, ultimately resulting in just two wolves remaining, the National Park Service (NPS) began reintroducing wolves to the island over the past winter. Although NPS considered a number of factors when determining whether to reintroduce wolves, the long-term and large-scale effects of rising moose and beaver populations on the island’s vegetation were the most important factors (NPS 2017).

Isle Royale is internationally recognized for its populations of wolves and moose (Peterson et al. 2014). Despite effects of predation on the moose population, both the short and longer-term impacts of moose browsing can be seen across the island (Fig. 1). However, a number of factors may interact with moose browsing to shape the vegetation of Isle Royale National Park (e.g., forest successional processes, herbivory by beaver, and effects of a changing climate). Yet no studies have quantified the extent to which the island’s vegetation has been shaped by these factors. The lack of empirical support for how the vegetation of Isle Royale relates to the effects of wolf predation in combination with such other factors is problematic given the logistical challenges associated with wolf relocation, the high degree of uncertainty about the effects of climate change (Duveneck et al. 2014) and the potential for wildlife biologists to overestimate the effects of predation on ecosystems (Mech 2012). There is a clear need for studies that shape a comprehensive understanding of the controls over Isle Royale’s vegetation and a further need to effectively communicate such an understanding to Park managers, wolf biologists, and visitors.



Figure 1. A moose exclosure at Isle Royale National Park showing the long-term effects of moose browsing (inside versus outside of the fenced area in 2006 and 2017) and the shorter-term effects of the lack of moose browsing due to a decade of low moose population density (outside of fenced area in 2006 vs. outside of fenced area in 2017).

It is not possible to disentangle all of the factors that might influence patterns of vegetation change over large landscapes with traditional experimental approaches or by conducting observational studies on their own. However, when combined with landscape-scale simulation models, experiments and observational studies can help to foster a more integrated understanding. By using simulation models to evaluate hypothetical scenarios, researchers can isolate the possible effects of one or more factors while holding others constant. When model results are compared with results from manipulative experiments or observational studies, it becomes more likely to sort out when and where certain factors are most likely to be responsible for vegetation change.

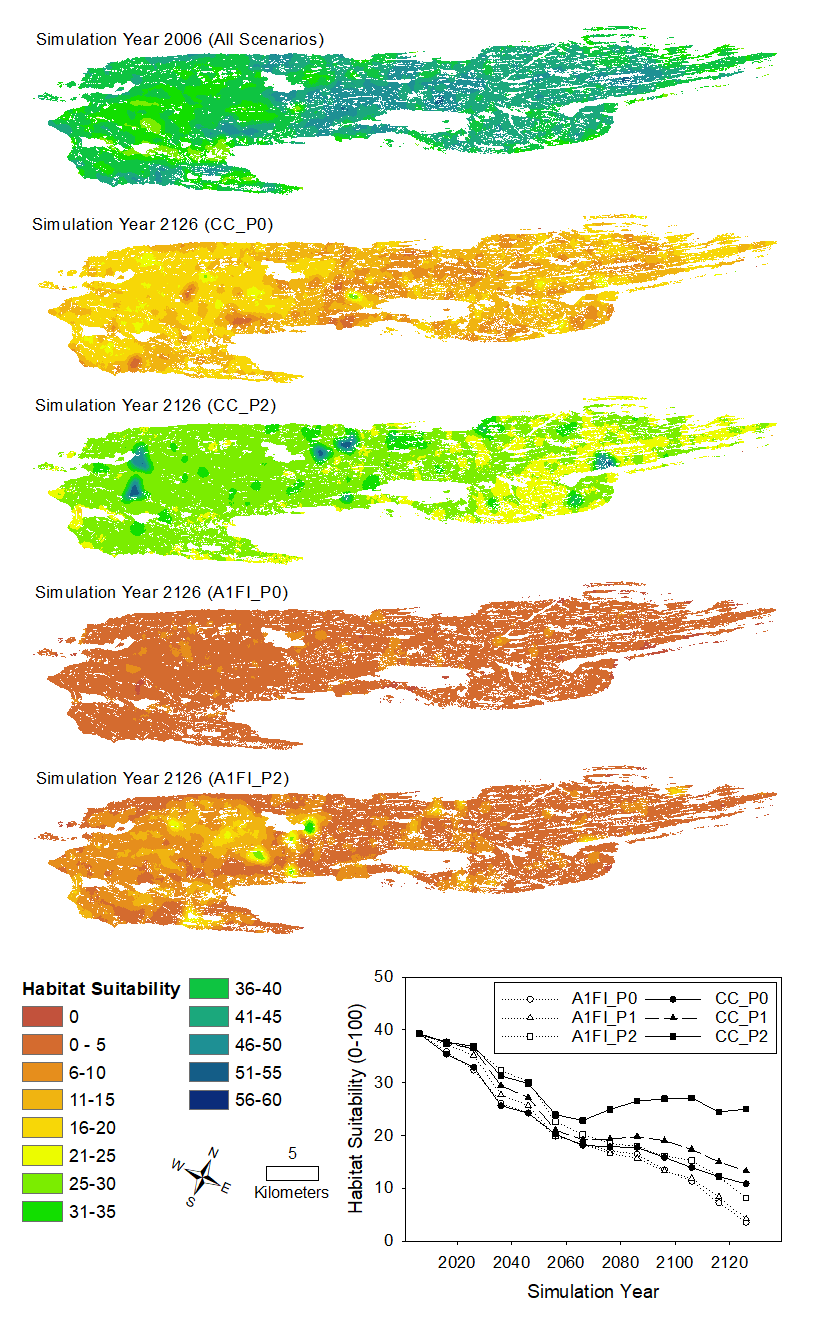
For example, over the past few years we have developed a state of the art spatial simulation model that links forest successional processes, moose population dynamics, and effects of moose browsing on the vegetation of Isle Royale National Park. Our work has helped to better understand the potential for wolf reintroduction to modify rates and patterns of moose browsing and associated changes in vegetation and the island’s ability to support a moose population over the long-term (~100 years) (De Jager et al. 2017a and b). Simulations conducted without moose browsing provided a prediction of what the future forests of Isle Royale might look like given natural forest successional processes (De Jager et al. 2017a). These simulations point to changes from early successional communities (e.g., birch and aspen forests) to late successional communities (e.g., spruce and fir forests). Additional simulations conducted with increasing wolf predation rates provided predictions of what the forests might look like given both natural forest successional processes and changing rates in moose browsing pressure (De Jager et al. 2017b). Our main findings were that browsing can accelerate the rate of forest succession, especially when wolf predation rates are low, because moose preferentially feed on early successional species such as birch and aspen and avoid late successional species. However, because moose also feed heavily on balsam fir, the shift from early successional species to late ones was dominated by shifts to white and black spruce, species that moose do not eat. The net result of accelerated forest successional changes is a drastic reduction in the potential for Isle Royale to support a moose population over the long-term (~100 years) in the absence of wolf predation. Perhaps most importantly, scenarios that included high rates of wolf predation resulted in similar forest successional patterns as observed when simulating no moose population at all, suggesting that wolf reintroduction could create forest conditions that balance management objectives related to wolf and moose populations with objectives related to healthy and sustainable forests. These findings were included in the Park’s Environmental Impact Statement as a primary motivation to reintroduce wolves to Isle Royale (NPS 2017).

Figure 2. Map outputs from model simulations including effects of predation by wolves on patterns of moose browsing and the effects of climate change on habitat suitability for moose at Isle Royale National Park. All scenarios utilized the same initial landscape (c. 2006, top panel). Outputs following simulated 120 year periods are shown for CC\_P0 (current climate, no predation by wolves), CC\_P2 (current climate, strong predation by wolves), A1FI\_P0 (high emissions climate change scenario, no predation by wolves), and A1FI\_P2 (high emissions climate change scenario, strong predation by wolves). Over the long-term, predation by wolves is projected to have little impact on habitat suitability for moose given the effects of climate change on the boreal plant communities that moose depend on (De Jager et al. In Prep).

More recently, we expanded our modelling work to explore how climate change might interact with wolf predation and moose browsing to alter the future forests of Isle Royale (De Jager et al., In Prep). Our results are revealing that the interactive effects of wolf predation and climate change are temporally variable and dependent on forest successional processes. During the first 50 years of model simulations, when the effects of climate change were minor, increased rates of predation by wolves reduced peak moose population densities and maintained higher carrying capacities for moose. During this same period, early successional and highly palatable aspen and birch forests transitioned to late successional spruce forests, regardless of climate change. Beyond 50 years, the effects of climate change and predation were driven by effects on balsam fir, a late successional species that is both highly palatable to moose and very sensitive to changes in temperature and precipitation. High rates of predation by wolves on moose allowed balsam fir to persist over the long-term, but only under the current climate scenario. Climate change caused a reduction in balsam fir and the island’s ability to support moose, regardless of predation. Our results suggest that with the simulated forest successional trajectory of Isle Royale and in the face of climate change, predation by wolves will play a diminishing role in terms of moose population and forest ecosystem dynamics over the next 100 years. It is possible that the effects of climate change will create an unsuitable habitat for moose and wolves over the long-term (Figure 2).

Despite all we have learned about the vegetation of Isle Royale and the potential for different factors to alter long-term successional patterns via modelling studies, we have yet to compare model outputs with empirical data to identify how and where the forests are changing and what the main drivers of such changes might be. Further, herbivory by beaver has not been accounted for in our modelling efforts, despite local observations suggesting that their impacts on riparian vegetation may be substantial. Finally, as we continue to incorporate additional factors (e.g., moose browsing, climate change, beaver herbivory) into our model, it will become increasingly important to find ways to effectively communicate the ever-increasing suite of model outcomes to Park managers in ways that help them make more informed decisions.

**OBJECTIVES:**

The studies outlined below will help us further develop a modelling framework that integrates ecological concepts, experimental results, and observational data sets to forecast future environmental conditions under a changing climate and alternative management scenarios at Isle Royale National Park. Our long-term approach to improving problem solving at Isle Royale is consistent with ‘futures studies’, which aim to aid decision making by adaptively improving experimental designs and long-term monitoring studies to generate data that addresses key uncertainties in model parameters and methods (Coreau et al. 2009).

We seek to accomplish the following task: **Simulate the** **effects of a) forest succession, b) climate change, c) moose browsing, and d) beaver herbivory.**

**STUDY AREA AND METHODS:**

The study area for our data analysis and modelling efforts will remain the main island of Isle Royale National Park and moose-accessible smaller islands.

We will compare empirical maps of vegetation change with maps resulting from forest simulation modelling. This will help us to validate model outcomes and to better understand where and how different factors might be influencing the vegetation of the island. One factor that we suspect is important in riparian areas is herbivory by beaver. Whereas moose forage on small understory trees, causing long-term changes in vegetation, beaver selectively harvest large over-story trees and therefore have the potential to cause immediate changes in vegetation. We intend to use existing data to quantify the degree of selectivity by beaver on various tree species and ages, as well as determine maximum foraging distances from active beaver lodges. This information can then be incorporated into our simulation model to evaluate how forest successional changes relate to beaver activity.

Upon revising and updating the spatial simulation model, we will conduct a simulation modelling experiment to attempt to isolate the effects of a) moose browsing, b) climate change, c) beaver herbivory, and d) natural forest successional changes, as well as how these factors interact with each other to influence vegetation changes and habitat suitability for moose over 100-year periods. These model results can be compared with results from our empirical investigations to better shape a comprehensive understanding of when and where various factors influence the vegetation of Isle Royale National Park.

**PROJECT DURATION/SCHEDULE:**

We anticipate completing one peer-reviewed manuscripts for publication in scientific journals with drafts available at or before the end of 2021.Any data created will be made available via the USGS Science Data Catalogue or GitHub.

**DELIVERABLE PRODUCTS:**

December 30, 2021 Draft manuscript of spatial simulation model results. Final story map published and publicly accessible.

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